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On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study

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To Karin

for her support during all these years

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Abstract

Mountainous forests fulfil a multitude of functions, and climatic change may have a strong impact on many of them. Modelling approaches have often been used to evaluate the possible impact of climatic change on forest structure and functioning, but little is known about the applicability of the models in a changing climate. In the present study, the structure and behaviour of forest gap models, a prominent model type, were analysed to obtain a model that simulates realistic tree species composition along climate gradients but incorporates only a minimum number of assumptions. The European Alps were selected as a case study, and the analysis started from the gap model FORECE (Kienast & Kuhn 1989: Vegetatio **79**, 7-20).

Analysis of existing forest gap models: The statistical analysis of the simulation results from multiple simulation runs of FORECE showed that 200 patches (runs) are required to calculate reliable statistics. This sample size is markedly larger than that used in previous studies.

The sensitivity of FORECE to structural simplifications was evaluated. It was found that six ecological factors present in FORECE may be omitted without reducing the plausibility of the simulated forest dynamics. Light availability, drought stress, summer warmth, and nutrient availability are important for determining tree growth; low winter temperature, browsing, and again light availability are required to model sapling establishment. Tree mortality can be portrayed by combining an age-related and a stress-induced mortality rate.

Finally, the formulation of climatic influences in a model simplified according to the above results was analysed. It was found that many forest gap models implicitly assume a constant climate and are likely to produce inconsistent results when applied to study climatic change. Moreover, model behaviour is quite sensitive to the exact formulation of climatic influences, which advocates their careful scrutinization and improvement.

Development of the FORCLIM model: Based on the above findings, a new forest gap model was developed. It consists of three submodels: (1) FORCLIM-E, a model of the abiotic environment including more reliable calculations of the annual sum of degree-days, drought stress and winter temperature than its predecessors. (2) FORCLIM-P, a tree population dynamics model incorporating a new equation for maximum tree growth and a new formulation for reducing the maximum growth rate by environmental constraints. (3) FORCLIM-S, a model of the turnover of soil organic matter adapted for European conditions from the LINKAGES model (Pastor & Post 1986: Biogeochemistry **2**, 3-27). FORCLIM contains 540 model parameters, whereas the FORECE model included more than 1300 parameters.

Behaviour of FORCLIM along a transect in the European Alps: The behaviour of the three submodels in isolation and of various submodel combinations was studied along an altitudinal transect in the European Alps. The model combinations FORCLIM-E/P & -E/P/S yielded species compositions conforming to descriptions of near-natural forests of the area. In the model FORCLIM-E/P/S, a temporally changing nitrogen availability is simulated, leading to increased competitivity of species that tolerate low nitrogen concentrations, e.g. oaks *(Quercus spp.)*. The model combination FORCLIM-E/P requires less than 20% of the simulation time of its predecessor.

A new, efficient method was developed for estimating the steady-state species composition of forest gap models. The model output from one single patch is averaged over time instead of simulating the transient dynamics on 200 patches. The method is almost 8 times faster than the transient experiment.

Analysis of parameter sensitivity: The sensitivity of FORCLIM to the uncertainty inherent in the estimation of all the 420 species-specific parameters was evaluated individually. It was found that the simulated species composition is quite robust to changes of the species parameters. However, the abundance of the single species may vary considerably depending on the parameter values used, and the simulated quantity of a given species should be interpreted cautiously. The model was found to be most sensitive to the parameter describing the tolerance of low nitrogen availability, followed by those of the maximum growth equation, drought tolerance, winter temperature, and light availability.

Model validation: Model behaviour was tested systematically in a climatological parameter space spanned by the annual mean temperature (T) and the annual precipitation sum (P) in central Europe as well as along a latitudinal gradient in eastern North America.

The study in the (T,P) space revealed that FORCLIM produces more plausible species compositions and more realistic gradients in a larger fraction of this space than the FORECE model. In two areas where the simulation of realistic drought stress is important, both models encountered major difficulties and need to be improved.

FORCLIM is also capable of simulating the characteristic features of eastern North American forests, ranging from the tundra-woodland transition in Canada to forests in southwestern Georgia. In most instances, it is more successful than the FORENA model developed for these conditions (Solomon 1986: Oecologia **68**, 567-579). Again, problems were encountered along drought gradients, where both FORENA and FORCLIM produce less realistic results.

Based on these studies, it is concluded that FORCLIM may be applied to study the impact of a changing climate on the species composition of near-natural forests in a large part of central Europe as well as in eastern North America.

Possible impact of climatic change on forests in the Alps: Three climate scenarios for the year 2100 and five forest models were used to evaluate the possible effects of climatic change on the simulated species composition at six sites along an altitudinal gradient in the European Alps. The results represent the current “best estimate” of the response of the species composition to the anticipated climatic changes, but they should not be interpreted literally as predictions due to the large uncertainty inherent both in the climate scenarios and in the forest models themselves. However, it can be stated that near-natural forests at mid altitudes are buffered well against the changes anticipated for the year 2100, whereas sites close to the alpine and the dry timberline are likely to undergo drastic changes of species composition, including forest dieback phenomena.

These results strongly support the implementation of abatement policies to fight the increase of greenhouse gas concentrations in the atmosphere on the global as well as the national scale.

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Kurzfassung

Gebirgswälder erfüllen viele Funktionen, und eine Klimaveränderung könnte die meisten von ihnen stark beeinflussen. Um abzuschätzen, welche Auswirkungen Klimaänderungen auf die Struktur und Funktion von Wäldern haben könnten, werden oft ökologische Modelle verwendet. Allerdings ist wenig über die Anwendbarkeit der Modelle für diese Fragestellung bekannt. Die vorliegende Studie analysiert die Struktur und das Verhalten einer wichtigen Modellklasse, der sogenannten “Gap-Modelle”. Ziel der Arbeit war es, ein Modell herzuleiten, das die Artenzusammensetzung von Wäldern entlang Klimagradienten realistisch wiedergibt, gleichzeitig aber nur eine minimale Anzahl von Annahmen enthält. Die europäischen Alpen wurden als Fallstudie ausgewählt, und die Analyse ging vom Modell FORECE aus (Kienast & Kuhn 1989: Vegetatio **79**, 7-20).

Analyse existierender Gap-Modelle: Eine statistische Analyse der Resultate von n stochastischen Simulationsläufen von FORECE zeigte, dass $n = 200$ Läufe benötigt werden, um die statistischen Eigenschaften der Modellresultate verlässlich berechnen zu können. Dieser Stichprobenumfang ist bedeutend grösser als der bisher verwendete.

Die Sensitivität von FORECE gegenüber strukturellen Vereinfachungen wurde untersucht: Sechs ökologische Faktoren von FORECE werden nicht benötigt, um eine realistische Dynamik der Artenzusammensetzung zu simulieren. Die Verfügbarkeit von Licht und Nährstoffen, die Bodentrockenheit und die Wärmesumme sind wesentlich, um das Wachstum der Bäume wiederzugeben. Die Wintertemperatur, der Wildverbiss und wiederum die Verfügbarkeit von Licht werden benötigt, um die Etablierung von jungen Bäumen zu modellieren. Die Kombination einer alters- und einer stressbedingten Sterberate erlaubt es, die Mortalität von Bäumen realistisch zu formulieren.

Anhand eines Modells, das gemäss diesen Erkenntnissen vereinfacht worden war, wurde schliesslich die Formulierung der klimatischen Einflussgrössen analysiert. Die Analyse zeigte, dass viele Gap-Modelle implizit davon ausgehen, das Klima sei konstant. Deshalb liefern diese Modelle oft inkonsistente Resultate, wenn sie eingesetzt werden, um Klimaänderungen zu studieren. Ausserdem ist das Verhalten der Modelle sehr sensitiv bezüglich der Formulierung von klimatischen Einflussgrössen. Deshalb sollten diese Modelle sorgfältig überprüft und verbessert werden.

Entwicklung des Modells FORCLIM: Gestützt auf diese Erkenntnisse wurde ein neues Gap-Modell entwickelt, das aus drei Untermodellen besteht: (1) FORCLIM-E, ein Modell der abiotischen Umwelt, das besser abgestützte Formeln zur Berechnung der jährlichen Summe der Tagesgrade, des Trockenheitsstresses und der Wintertemperatur beinhaltet. (2) FORCLIM-P, ein Modell der Populationsdynamik von Bäumen, das eine neue Gleichung für die maximale Wachstumsrate und eine neue Formulierung der Umwelteinflüsse auf diese Rate enthält. (3) FORCLIM-S, ein Modell für die Dynamik des organischen Kohlenstoffs im Boden. Ausgehend vom Modell LINKAGES (Pastor & Post 1986: Biogeochemistry **2**, 3-27) wurde FORCLIM-S für europäische Verhältnisse angepasst. FORCLIM umfasst lediglich 540 Modellparameter, während sein Vorgänger FORECE mehr als 1300 Parameter aufwies.

Verhalten von FORCLIM entlang einem Transekt in den europäischen Alpen: Das Verhalten der drei Untermodelle wurde einzeln und in verschiedenen Kombinationen entlang einem Höhengradienten in den Alpen untersucht. Die Modellkombinationen FORCLIM-E/P und -E/P/S ergaben Artenzusammensetzungen, die den Beschreibungen von

naturnahen Wäldern der jeweiligen Standorte entsprechen. Das Modell FORCLIM-E/P/S simuliert eine zeitlich stark variierende Verfügbarkeit von Stickstoff, was die Konkurrenzkraft von Arten erhöht, die gut an diese Verhältnisse angepasst sind (z.B. Eichen, *Quercus spp.*). FORCLIM-E/P benötigt lediglich 20% der Simulationszeit, die für FORECE aufgewendet werden musste.

Eine neues Verfahren wurde entwickelt, um die Artenzusammensetzung im Gleichgewicht schätzen zu können. Die Resultate einer einzelnen Simulation werden über die Zeit gemittelt statt über *n* transiente Simulationsläufe. Die Methode liefert eine Gleichgewichtsschätzung in $^1/_8$ der Zeit, die für das transiente Experiment benötigt wird.

Analyse der Parametersensitivität: Die Sensitivität von FORCLIM auf die Unsicherheit in der Schätzung aller 420 artspezifischen Parameter wurde für jeden Parameter einzeln untersucht. Die simulierte Artenzusammensetzung ist robust gegenüber Veränderungen der Spezies-Parameter; die Abundanz der einzelnen Arten hingegen variiert beträchtlich je nach den verwendeten Parameterwerten und sollte deshalb nur mit Vorsicht quantitativ interpretiert werden. Das Modell erwies sich am sensitivsten bezüglich des Parameters für Stickstoffbedarf, gefolgt von jenen der Wachstumsgleichung, der Trockenheitstoleranz, der Wintertemperatur und des Lichtbedarfs.

Validierung des Modells: Das Verhalten des Modells wurde systematisch in einem Parameterraum, der von der Jahresmitteltemperatur (T) und der Jahresniederschlagssumme (P) aufgespannt wird, sowie entlang einem Gradienten im östlichen Nordamerika untersucht.

Die Studie im (T,P)-Raum zeigte, dass FORCLIM plausiblere Artenzusammensetzungen und realistischere Gradienten in einem grösseren Teil dieses Raums liefert als FORECE. In zwei Bereichen, wo es wichtig ist, den Trockenheitsstress realistisch zu simulieren, wurden bei beiden Modellen Mängel sichtbar, die verbessert werden sollten.

FORCLIM erwies sich auch als geeignet, die charakteristischen Eigenschaften von Wäldern im östlichen Nordamerika von der kanadischen Tundra bis nach Georgia realistisch wiederzugeben. In den meisten Fällen ergab FORCLIM plausiblere Resultate als das Modell FORENA, das für diese Bedingungen entwickelt worden war (Solomon 1986: Oecologia **68**, 567-579). Wiederum lieferte aber FORCLIM – wie auch FORENA – weniger realistische Resultate entlang Trockenheitsgradienten.

Diese Untersuchungen erlauben die Schlussfolgerung, dass FORCLIM auch angewendet werden kann, um zu untersuchen, wie sich Klimaveränderungen auf die Artenzusammensetzung naturnaher Wälder in einem Grossteil von Mitteleuropa sowie im östlichen Nordamerika auswirken.

Mögliche Auswirkungen einer zukünftigen Klimaänderung auf Wälder im Alpenraum: Drei Klimaszenarien für das Jahr 2100 und fünf Waldmodelle wurden verwendet, um die möglichen Auswirkungen einer Klimaänderung auf die simulierte Artenzusammensetzung an sechs Standorten entlang einem Höhengradienten in den Alpen zu untersuchen. Die Resultate stellen die “beste Schätzung” (“best estimate”) der Reaktion der Artenzusammensetzung auf die erwartete Klimaänderung dar, sollten aber nicht im wörtlichen Sinn als Prognosen aufgefasst werden, da grosse Unsicherheiten sowohl bezüglich der Entwicklung des zukünftigen Klimas als auch bezüglich der Formulierung der Waldmodelle selber bestehen. Trotzdem kann man die Schlussfolgerung ziehen, dass die naturnahen Wälder in mittleren Lagen gegenüber Klimaänderungen gut gepuffert sind, während Standorte in der Nähe der alpinen und ariden Waldgrenze vermutlich drastische Änderungen der Artenzusammensetzung bis hin zu Zusammenbrüchen erleben könnten.

Diese Ergebnisse bestätigen, dass es sinnvoll wäre, auf globaler wie auch auf nationaler Ebene Massnahmen zu treffen, die verhindern, dass die Konzentration von Treibhausgasen in der Atmosphäre weiter zunimmt.

1. Introduction

1.1 Climatic change and mountainous forests

Carbon dioxide and other trace gases in the earth's atmosphere are relatively transparent to the incoming solar radiation, but they absorb a large portion of the infrared energy radiated back into space (Schneider 1989). This phenomenon is known as the “greenhouse effect”. It causes the average surface temperature of the earth to be 35 °C higher than its radiation temperature as seen from interplanetary space (Siegenthaler & Oeschger 1978). Without the greenhouse effect, our planet simply would be too cold to support life.

With the onset of fossil fuel burning, large amounts of carbon dioxide were emitted into the atmosphere, causing a steady increase of its concentration from the preindustrial level of 285 ppm to 355 ppm at present (Siegenthaler & Oeschger 1987, Houghton et al. 1992). The palaeoclimatic record shows that the concentrations of carbon dioxide and methane were closely correlated with temperature and have been changing continuously during the last 200'000 years (Barnola et al. 1987, Kuo et al. 1990, Jouzel et al. 1993). So why should we bother if climate changes today due to human activities?

During the last 1'500 years the 20-year means of summer temperatures in Scandinavia oscillated less than ±1 °C around modern values (Briffa et al. 1990, 1992), with some longer warm (e.g. Medieval Warm Epoch) as well as cool periods (e.g. Little Ice Age). Brimblecombe & Pfister (1990) showed that such relatively small climatic changes had major impacts on agricultural yield and, consequently, on the welfare of the human population. Houghton et al. (1990, 1992) produced various scenarios of future greenhouse gas emissions, and Wigley & Raper (1992) examined the implications for climate and sea level of the latest, moderate scenarios (Houghton et al. 1992). They found that both the magnitude and the rate of the expected global temperature change are far beyond the limits of natural variability. Thus, future climatic change may have severe consequences for the biosphere and its components (Bolin et al. 1986, Davis 1990).

Many studies dealt with the possible impact of climatic change on soils (Bouwman 1990, Anderson 1992), agricultural land (Parry et al. 1988a,b), forests (Shugart et al. 1986, Shands & Hoffman 1987, Fabian 1991, Thomasius 1991, Shugart et al. 1992), and on the whole biosphere (e.g. Emanuel et al. 1985, Smith et al. 1992, Prentice et al. 1992, Solomon & Shugart 1993, Cramer & Solomon 1993). The fate of forests is of particular interest not only from a regional or national, but also from a global perspective (Wisniewski et al. 1993): The equivalent of the entire atmospheric carbon dioxide passes through the terrestrial biota every 7 years, with about 70% of the exchange occurring through forests (Waring & Schlesinger 1985). Thus, climate-induced changes of primary productivity, soil respiration or the areal extent of forests may lead to a significant biospheric feedback to the climate system. For example, Tans et al. (1990) hypothesized that the carbon content of temperate forests in the northern hemisphere is currently increasing, thus removing part of the emitted CO_2 from the atmosphere (“missing sink”, Post et al. 1990).

Forests in mountainous areas have a multitude of functions: They may protect settlements and roads from avalanches, they regulate runoff and prevent erosion, and they form a part of the largest terrestrial biotic carbon pool. Forests and meadows make a varied landscape and provide the environment necessary for many touristic activities, and – last but not least – forests are exploited for fuel, pulpwood, and timber. Climatic change may have a strong impact on all these functions (Bolin et al. 1986). Hence studies of the impact of climatic change on mountainous forests could be of practical relevance to politicians, foresters, and the broad public (Hostettler 1991, Tranchet et al. 1993).

One of the characteristic features of mountainous areas is their complex spatial pattern with steep gradients over short distances. For example, in the central part of the European Alps the distance between the lower (dry) timberline in the bottom of the Rhone valley and the alpine (cold) timberline is in the order of 10 km only. Thus, mountainous forests may show a broad spectrum of responses to climatic change. On the other hand, predicting these responses is more difficult than in flat terrain and requires to study many factors explicitly and in detail.

The major emphasis of the present study is to contribute to impact assessments of climatic change on mountainous forests, selecting the European Alps as a case study. To achieve this goal, the climatic and ecological factors governing the long-term dynamics of near-natural forest ecosystems in this area shall be elaborated first. Then the sensitivity to climatic change of these forests shall be studied extensively by means of scenarios describing the anticipated climatic changes.

1.2 Methods for the analysis of forest ecosystems

The term “forest dynamics” spans huge ranges both in time and space: The enzymatic reactions of photosynthesis operate within fractions of a second; foliage development takes a few weeks, while tree growth lasts decades to centuries, and the dynamics of soil organic matter span millennia. On the other hand, the germination of a seed takes place on a few square centimetres, a sunfleck moving over the forest floor covers a few square meters; a dominant tree in the canopy occupies 0.01-0.1 ha, and the quasi-equilibrium of a forest landscape may be reached on the scale of several hectares only (Shugart & Urban 1989). Levin (1992) hypothesized that the central problem in ecology is that of pattern and scale, and that the various temporal, spatial, and organizational scales should be interfaced in order to understand the dynamics of ecosystems.

Due to the size of trees, even the measurement of simple indices of forest ecosystems, such as allometric relationships or total biomass, requires much personnel, time, and money (Burger 1945-1953, King 1991, Woods et al. 1991, Smith et al. 1991, Wang et al. 1991). On the other hand, the longevity of the dominant organisms makes measurements on a temporal scale appropriate for the whole ecosystem practically impossible (Botkin 1981, Shugart 1990). Not surprisingly, empirical studies of forests typically cover a few years and a few ares at most. For example, many investigations on the direct effects of carbon dioxide on vegetation (Eamus & Jarvis 1989) dealt with the short-term increase of photosynthesis (Oechel & Strain 1985), growth rates of tree seedlings (Bazzaz & Williams 1991), or competition in model ecosystems (Miao et al. 1992, Körner & Arnone 1992). The effects on natural forest ecosystems can not be estimated simply by extrapolating these findings across scales (O'Neill et al. 1986), and their incompatibility makes it difficult to deal with several scales simultaneously on an empirical basis (Shugart & Urban 1989). Thus, other methods are required to investigate the couplings and feedbacks between scales in ecosystems. The present study is based on the assumption that ecological models provide an opportunity to do so.

Unfortunately, ecologists continue to be substantially separated into those who build and use quantitative models, and those who don't (Botkin 1981). In fact, ecological models can be neither built nor tested without a sound empirical basis. The “empirical” (field-oriented) and the “theoretical” (model-oriented) approaches have complementary functions and depend on each other (Fischlin 1982): Field data serve as a basis for developing and testing an ecological model; on the other hand, sensitivity analyses conducted with the model can be used to test our understanding of the system and to identify research needs, which may serve as guidelines for future field work in the daunting complexity of ecosystems.

The palaeoecological record (Delcourt & Delcourt 1987, 1991) shows that biotic responses to past climatic changes were very complex (Davis 1990). Past changes affected each species differently; some communities present on today's landscape have formed only recently, such as the beech-hemlock zone in eastern North America about 6000 years ago (Graham & Grimm 1990). Moreover, many of the communities that were present during the Quaternary have no modern analog (Davis 1990), and the same will probably occur in the future. Thus, the present communities will not simply shift geographically, and they can not be expected to exhibit predictable responses and feedbacks to climate. Consequently, assessments of the impact of climatic change on mountainous forests should be based on models that are detailed enough to predict the species composition and the functioning of these future no-analog ecosystems (Shugart 1990).

1.3 Spatial scales in forests and corresponding models

Many authors have classified forest models according to a wide variety of criteria (Reed 1980, Shugart & West 1980, Shugart 1984, Dale et al. 1985, Reynolds & Acock 1985, Joyce & Kickert 1987). All these classifications concentrate on a few types of models only; none of them covers models across many scales. Thus, the following review of forest models will be organized according to a scheme similar to the one used by Ågren et al. (1991): The classification criterion used here is the spatial scale of the models, ranging from landscape models to physiological ones. Global models (e.g. Goudriaan & Ketner 1984, Emanuel et al. 1985) are excluded from the review because their large spatial scale renders them inappropriate for a detailed study of the behaviour of mountainous forest ecosystems. Moreover, even the most detailed global models (e.g. Prentice et al. 1992) are not capable of predicting species composition.

Landscape models: Most landscape models view a landscape as composed of patches of ecosystems or vegetation types, or they assume the vegetation cover to be homogenous. Waggoner & Stephens (1970) used a Markov model (Caswell 1989) to predict the distribution of five vegetation types on the landscape scale. Similar models were presented by Shugart et al. (1973) and Loucks et al. (1981). A disadvantage of this approach is that the transition probabilities are aggregate indices which implicitly parametrize many phenomena, including competition and climatic effects. The application of these models in a changing climate thus would require to formulate time-variant transition probabilities. However, such a formulation would not be causal and does not appear trustworthy enough for a study of climatic change. Other landscape models concentrate on primary productivity (e.g. Kauppi & Posch 1985, 1988). A prominent model that includes primary productivity and the hydrological cycle is FOREST-BGC (Running et al. 1987, Running & Coughlan 1988, Running & Gower 1991). Running & Nemani (1991) used this model for assessing the possible impact of climatic change on forest productivity and hydrology.

A major drawback of models on the landscape scale is that none of them was designed to predict the structure of the landscape (e.g. species composition or vegetation types) and its productivity simultaneously. However, both features are of interest in the present study, and landscape models therefore are of limited value.

Ecosystem models: A large effort for building ecosystem models was initiated by the International Biological Programme (Reichle 1981). Models on this scale typically assume either that a forest consists of a single species (Swartzman 1979, McMurtrie & Wolf 1983) or that its composition does not change with time (Shugart et al. 1974, Sollins et al. 1976, Dixon et al. 1978a,b, Aber et al. 1991). The temporal resolution of these models is on the scale of hours to weeks, and the compartments ignore any differences between individuals, species, and often even trophic levels. They take the forest as a functional entity with superorganism-like behaviour (cf. Huston et al. 1988). This makes it difficult to apply such models to study the transient behaviour in function of climatic variables (Davis 1990). However, they can be quite useful to assess productivity, assimilate allocation, transport mechanisms, and energy flow through ecosystems.

Sollins et al. (1981) noted that a major problem with models formulated on the ecosystem scale is the lack of sufficient validation data, such as gross ecosystem respiration or the effects of defoliating insects on net primary productivity. Moreover, the scope of these models was to increase the understanding of forests as they are today. This justifies their basic assumptions but renders them inappropriate for studies of climatic change.

Models using populations and functional groups: Models at this scale were used to simulate the management of single-species stands (e.g. Kimmins et al. 1981). Other applications included studies of the interactions between a few populations or functional groups of organisms, most often plants (Malanson 1984, Moore & Noble 1990, Osho 1991). These models typically were built for management purposes, thus ignoring many ecological factors and emphasizing those aspects of forest ecosystems that are relevant for managers, such as stand structure and wood volume. Most of the models neglect climatic effects completely or treat them only marginally. Hence their application to study climatic change appears to be questionable.

Individual-based models: Yield tables commonly used in forest management are a prominent type of static single tree models for monospecific stands (e.g. Schober 1987). Bossel et al. (1985) and Bossel (1987) developed the dynamic model SPRUCE to simulate the effects of air pollution on tree growth; a disadvantage is that SPRUCE was restricted to single species stands. Bossel et al. (1991) developed a similar model for tropical forests that explicitly simulates every tree in five distinct canopy layers; yet it still does not allow for changes of species composition. Single tree models that were built to simulate mixed species stands include the classic matrix model by Horn (1975a,b), which was used to project the species composition of the Hubbard Brook Experimental forest in New Hampshire from simple field measurements. The development of mixed-species, mixed-age stands as a function of their environment was simulated with a very detailed spatial model called FOREST (Ek & Monserud 1974). The size and location of each tree were kept track of; thus shading and competition could be modelled realistically. This detail made simulation studies extremely tedious, but it did not offer clear advantages over non-spatial models (cf. Shugart 1984). Simpler approaches that also consider tree position explicitly include the geometric models of Galitsky (1990) and Faber (1991). Their main emphasis was to investigate the mechanisms underlying competition for space and not to simulate realistic forest dynamics.

Another type of individual-based forest models was introduced by Siccama et al. (1969). Based on the theory of gap phase replacement described by Watt (1925, 1947), they developed a stochastic succession model of the Hubbard Brook forest. The model simulates the establishment, growth, and mortality of trees on small patches, a patch being the area that can be dominated by a large canopy tree. Within a patch, the location of a tree thus could be neglected, which avoided the need to use a distance-dependent approach. Botkin et al. (1970, 1972a,b) presented JABOWA, the prototype of these “forest gap models”. The models include many biotic and abiotic influences on establishment, growth, and mortality of trees. These three processes operate on different spatial and temporal scales; forest gap models couple them explicitly and allow to study their effects on long-term forest dynamics (Shugart & Urban 1989). Moreover, the models integrate processes on different organizational levels, such as the growth of individual trees, competition of tree populations at the patch level, and ecosystem characteristics at the scale of many patches.

Their integrative capability may be an important reason why forest gap models produce plausible successional patterns for a wide range of forest ecosystems (e.g. Shugart 1984).

Forest gap models are fairly general tools and can be used to study a variety of phenomena, ranging from age structure and species composition to primary productivity and nutrient cycling of forest ecosystems (Shugart 1984). This is a distinct difference to all the other models reviewed above, which were built to answer specific questions; for example, productivity models are not usually capable of treating succession because the choice of state variables implicitly assumes that forest composition is constant. Moreover, forest gap models are an explicit quantification of a sound ecological theory (Watt 1947, Shugart 1984) which is consistent with many field observations (Moore 1990).

Physiological models: Models of physiological processes like photosynthesis and respiration typically work on time scales of minutes or hours; they simulate tissue development and plant growth (e.g. Sinclair et al. 1976, Tenhunen et al. 1980, Reynolds et al. 1980, Running 1984, Eckersten 1985, Webb 1991). An application on larger time scales and for whole ecosystems is impractical, if not impossible due to the different scales involved. However, these models can give important guidelines about processes to be incorporated into more aggregated models and about the choice of adequate equations for process formulations.

Conclusion: From the above review I conclude that forest gap models offer the highest potential for modelling forest dynamics in mountainous terrain: These models bridge several spatial, temporal, and organizational scales, they consider many abiotic and biotic factors explicitly, and they represent quantifications of distinct hypotheses of the factors determining forest dynamics. Moreover, forest gap models have already been used successfully to simulate forest dynamics in the European Alps (Kienast & Kuhn 1989a,b).

1.4 Forest gap models

Forest succession may be defined as the directional change with time of the attributes of a single site, such as species composition and vegetation physiognomy (Finegan 1984). It is obvious that succession can be observed on a wide variety of scales, depending on the exact definition of the term “site”. An early approach, which has pervaded much of the ecological literature, views succession from a holistic ecosystem perspective (Clements

1916, 1928, 1936, Margalef 1968, Odum 1969). According to this concept, ecosystems possess “emergent” properties that can not be predicted from the structure and behaviour of lower organizational levels such as populations. The notion of a stable, homeostatic climax community is central to the Clementsian view of vegetation dynamics (Shugart 1984).

A fundamentally different view of forest succession was proposed by Gleason (1917, 1927, 1939), Jones (1945), and in the classic paper by Watt (1947). Their individualistic (reductionist) theory stresses the importance of population dynamics and competition between organisms, and it acknowledges the nonequilibrium nature of vegetation at small scales (Drury & Nisbet 1973, Connell & Slatyer 1977, Bormann & Likens 1979, Pickett & White 1985, Remmert 1991). The essential concept is that a forest can be abstracted as a mosaic of patches, a patch being the area dominated by a canopy tree. With its death, the environment is radically altered, leading to a wave of seedling establishment and the release of suppressed trees. In the simplest case, one of the competing trees comes to dominate the canopy, and the cycle repeats (Shugart 1984). The notion of cyclical change in plant communities, the explicit consideration of spatial patterns and the importance of the life history characteristics of the species involved can be considered as the cornerstones of the “Gleasonian” view of forest dynamics.

Forest gap models like JABOWA (Botkin et al. 1972a,b) adopt an individualistic view of the forest ecosystem and simulate the establishment, growth, and death of individual trees on small forest patches (typically 0.01-0.1 ha) as a mixture of deterministic and stochastic processes. However, these models also take into account processes that operate at the scale of the “Clementsian” ecosystem, such as the effects of canopy closure and soil resources on tree growth. To obtain forest development on the ecosystem level, the successional patterns of many independent patches are averaged. In these models, tree establishment is a stochastic function of climatic (abiotic) as well as biotic factors, such as temperature, shading, and the amount of leaf litter present. The growth of each tree is simulated in a deterministic manner by decreasing the maximum potential growth rate at its respective age by factors that are less than optimum. Examples of growth factors considered are the growing-season temperature, soil moisture, and light availability. The equation for maximum growth has a sigmoid shape and is based on the assumption that annual gross productivity is proportional to the amount of sunlight the leaves receive. Tree death is determined stochastically with a function based on the assumption of a constant mortality rate throughout tree life. Moreover, most gap models include a stress-induced mortality function that kills trees if they attain less than a certain minimum growth rate. Shugart

(1984) provides a more detailed description of the common characteristics of forest gap models.

During the last 20 years, many forest gap models have been developed based on the parent model JABOWA, which was built to simulate succession in a northern hardwood forest of the eastern United States (Botkin et al. 1970, 1972a,b; the name of the model stands for the three authors, F. JAnak, D. BOtkin & J. WAllis). The aim of their study was *"to introduce a minimal number of assumptions and to find the simplest mathematical expression for each factor that was consistent with observations."* (Botkin et al. 1972a, p. 850). They were remarkably successful in that respect, but the model was fairly expensive to run given the computer resources of that time.

The adaptation of JABOWA for southern Appalachian forests led to the model FORET (Shugart & West 1977), which was equally successful in predicting the effect of a fungal disease (the chestnut blight) on forest composition. Subsequently an amazing proliferation of forest gap models took place: Models were developed for tropical forests (Doyle 1981), forests in Australia (Shugart & Noble 1981), in the western United States (Kercher & Axelrod 1984), in Central Europe (Kienast 1987), and in the boreal zone (Leemans & Prentice 1989, Bonan & van Cleve 1992, Shugart et al. 1992). Moreover, the approach seems not to be restricted to forests: Smith et al. (1989) and Coffin & Lauenroth (1990) successfully developed gap models for grasslands. Thus, the gap dynamics hypothesis proved to be a viable concept in a wide variety of ecosystems. It is also remarkable that these models are closely related to each other: Many of the equations formulated for JABOWA more than 20 years ago are still being used today without modification (Botkin 1993).

Parallel to the adaptation of forest gap models for various ecosystems, ever more details were added to these models, such as nitrogen availability and nutrient cycling (Aber et al. 1979, 1982, Aber & Melillo 1982, Weinstein et al. 1982, Pastor & Post 1985), the influence of fire (Kercher & Axelrod 1984), ecological indicator concepts (Kienast 1987), seed dispersal by birds (Keane et al. 1990), herbaceous vegetation (Kellomäki & Väisänen 1991), and detailed biophysical-ecophysiological submodels (Martin 1990, 1992, Bonan & van Cleve 1992, Friend et al. 1993). However, the increasing complexity of forest gap models made simulation studies ever more tedious and precluded detailed model analyses. For example, current models typically include 1000 to 1500 parameters (Shugart 1984, Kienast 1987); hence, an all inclusive sensitivity analysis is almost prohibitive. Not surprisingly, only few sensitivity studies have been conducted, covering only a subset of the parameters (Kercher & Axelrod 1984, Dale et al. 1988, Botkin & Nisbet 1992) or species-poor forests (Leemans 1991). Thus, there arises the question whether the essence of the original hypothesis of forest dynamics behind these models has been cluttered by ornaments, whether all the details present in current forest gap models are necessary for producing realistic successional characteristics, and whether simpler models could provide equally valid descriptions of forest ecosystems. Moreover, such models would be easier to interpret ecologically and would allow for a more detailed analysis of their behaviour.

Although forest gap models originally were not built to study the effects of a changing climate on forest ecosystems (Botkin et al. 1972a,b) and in spite of their ill-known behaviour, they have been applied extensively to study the possible impacts of future climatic change on forests. The direct fertilizing effects of CO_2 were investigated by Botkin et al. (1973) and Shugart & Emanuel (1985); authors concentrating on the effects of changing temperatures and/or precipitation were Solomon et al. (1981, 1984), Solomon (1986), Solomon & West (1987), Pastor & Post (1988), Dale & Franklin (1989), Kellomäki & Kolström (1992), Solomon & Bartlein (1993), Kräuchi & Kienast (1993), and Urban et al. (1993). A few studies dealt with the simultaneous effects of CO_2 fertilization and climatic change (Luxmoore et al. 1990, Kienast 1991, Post et al. 1992, Prentice et al. 1991, 1993, Bowes & Sedjo 1993), while others investigated the effects of a changed disturbance regime (Overpeck et al. 1990, O'Brien et al. 1992). While these applications are heuristically useful, extensive tests should be conducted to determine whether forest gap models implicitly assume a constant climate. If they do so, these assumptions should be replaced by explicitly considering the influence of climate on ecological processes. Moreover, it would also be important to know how sensitive the models are to different formulations of climatic influences (Bonan 1993). Like this, forest gap models could become more reliable tools for projecting the impact of climatic change on forest dynamics.

Since forest gap models also have been adapted for Europe, it seemed more promising to take an existing forest gap model as a starting point for the present work than to build a new one from scratch. In early 1990, when this study was incepted, there were two forest gap models for European conditions: FORECE, which had been used extensively for simulating forest succession in the European Alps (Kienast 1987, Kienast & Kuhn 1989a,b), and FORSKA, at that time a model restricted to Scandinavian boreal forests (Leemans & Prentice 1989). Thus, FORECE was chosen as a basis for this study.

The main advantage of FORECE was its capability to produce species compositions according to phytosociological descriptions of the forests under study (Ellenberg & Klötzli 1972). Important disadvantages were that it was one of the more complex models at that time, and that it did not include soil carbon dynamics, which would be important for calculating the carbon balance of forest ecosystems (Pastor & Post 1985). In the meantime, two more models have been developed for European conditions: SIMA (Kellomäki et al. 1992), a slightly modified version of the LINKAGES model (Pastor & Post 1985), and FORSUM (Kräuchi & Kienast 1993, Kräuchi 1994), a successor to FORECE including detailed submodels of soil water dynamics, deer browsing, and management.

1.5 Objectives of this study

Based on the research conducted with forest gap models by many authors during the last 25 years and the apparent success of these models for simulating realistic species composition, this thesis shall address the following questions:

First, do complex forest gap models like FORECE produce plausible simulation results for the right reasons? Do the factors that are most important for simulating forest dynamics correspond to our ecological knowledge on those dynamics, or do these complex models simply represent empirical parametrizations assembled during decades of model development without evident relationships to ecological theory?

Second, what is the minimum number of assumptions, i.e. ecological factors, that must be incorporated in such a model to simulate realistic dynamics of mountainous forests? Is it possible to simplify some of the remaining equations, and can the parameter space of the models be reduced further by skilful grouping?

Third, do forest models like FORECE contain implicit assumptions about climate, so that their validity is restricted to simulating forest dynamics at specific sites and under current climate only? If this is true, can these assumptions be replaced by explicit formulations of climatic influences, so that the models are applicable along climate gradients and under a changing climate as well?

Finally, how sensitive is the simulated species composition of near-natural forests in the European Alps to the climatic change anticipated for the next 100 years as compared to the climatic changes that have occurred in the last 500 years?

To answer these questions, the following steps shall be followed:

1) The systems theoretical and ecological properties of FORECE shall be scrutinized, the significance of the ecological factors present in FORECE shall be evaluated, and the model shall be simplified in order to determine the smallest set of factors capable of simulating plausible patterns of forest succession in the European Alps (chapter 2).

2) Based on these analyses, a new forest gap model (FORCLIM) shall be developed, which encapsulates this set of ecological factors and does not include implicit assumptions about climate. Great care shall be taken to develop reliable formulations for the influence of climatic parameters on ecological processes (chapter 3).

3) The behaviour of the various submodels and of the complete model shall be evaluated along an ecological gradient in the European Alps (chapter 4). Then the sensitivity of FORCLIM to the species parameters shall be studied so that its limitations are better known, and its behaviour shall be tested extensively in function of climatic parameters (chapter 5).

4) The sensitivity of forest ecosystems to past climatic variations and anticipated future climatic changes shall be investigated at sites typical of today's vegetation zones in the European Alps (chapter 6).

This thesis serves also as a case study in the project “Workstation-assisted Ecological Modelling & Simulation and the Impact of Climate Change on Ecosystems in an Alpine Region (FORAGROCLIM)” carried out by Systems Ecology at ETHZ, where tools for interactive modelling and simulation on personal computers and workstations are being developed (Fischlin 1991). These tools will be used and evaluated both for the analysis of FORECE and for the development of the FORCLIM model.

Moreover, the thesis is a contribution to the established core project *“Global Change and Terrestrial Ecosystems”* (GCTE; Steffen et al. 1992) of the International Geosphere-Biosphere Programme (IGBP 1990). Specifically, it shall contribute to the modelling and understanding of the structure and functioning of terrestrial ecosystems, i.e. to Focus 2 (*“Change in Ecosystem Structure”*) and Activity 2.1 (*“Patch Scale Dynamics”*) of the GCTE project.

2. Analysis of existing forest gap models

This chapter starts with an analysis of the model formalism of forest gap models (section 2.1). Section 2.2 presents simulation studies with the FORECE model, which are used to exemplify the type of basic simulation results produced by forest gap models and to analyse some of their statistical properties. These considerations provide the basis for an ecological analysis in section 2.3: First, the sensitivity of the FORECE model to structural simplifications is investigated in order to derive a minimum set of ecological factors that are necessary to model forest dynamics in the European Alps (section 2.3.1). Second, the set of climate-dependent factors remaining after the simplification procedure is analysed for its sensitivity to alternate formulations (section 2.3.2).

Throughout the thesis, the nomenclature of the European tree species follows Hess et al. (1980). Their scientific and common names are listed in Appendix I.

2.1 Model formalism

Zeigler (1976) distinguished the following categories of model formalisms: Differential Equation System Specifications (DESS), Discrete EVent System Specifications (DEVS), and Sequential Machines (SM, i.e. discrete time models). It is often difficult to specify to which of these three formalisms complex models belong, because the mathematical equations are not published in detail, the various submodels may be based on different formalisms, or the formalism used for the mathematical model does not correspond to the one used in the simulation model, i.e. in the computer code. For example, the tree growth equation of forest gap models most often is described as a differential equation (DESS, Botkin et al. 1972a,b, Shugart 1984), while the descriptions of tree establishment and tree death suggest that these processes are simulated using a discrete event model (DEVS). However, forest gap models typically are implemented as discrete-time models (SM) with an annual time step. Hence, there arises the question to which formalism these models conform.

Individual-based models (DeAngelis & Gross 1992) such as forest gap models have obvious relationships to DEVS: For example, in forest gap models an individual tree shows up (much like a customer in the classical DEVS example of a grocery), it grows and enters complex relationships with its environment (does his/her shopping), and it dies (leaves the shop). Thus, a conventional forest gap model (Botkin et al. 1972a,b, Kienast 1987) formally may be considered as a set of coupled models with two components:

1) a discrete event model (DEVS) for tree population dynamics (sapling establishment, tree growth, and tree mortality) as a function of the biotic and abiotic environment

2) a discrete time model (SM) for the calculation of the abiotic environment based on a monthly time step, aggregating most of the output to the annual time scale.

One of the advantages of DEVS compared with the sequential machine approach is that the model can be ignored at those time steps when *"nothing significant happens"* (Zeigler 1976). However, no tree population dynamics submodel in a forest gap model was implemented according to the DEVS formalism. The reason is that, unfortunately, in forest gap models something *"significant"* happens to every object in every year, i.e. either tree growth or mortality. This has led modellers to implement the population dynamics part of forest gap models as discrete time models, too.

The other criteria proposed by Zeigler (1976) allow the following categorization of forest gap models: they are stochastic (they contain random variables), and time invariant (time does not enter explicitly as an argument of the rules of interaction in the models). Part of their state variables are continuous (e.g. the diameter of a tree), and others are discrete (e.g. the memory for "slow growth"). The population dynamics model is nonautonomous (it requires abiotic input data), and the same goes for the discrete time model (it requires monthly weather data). The latter property is concealed in most models because they incorporate a stochastic weather generator (Botkin et al. 1972a,b).

For the following analysis, I adopt the view that the submodel of tree population dynamics in forest gap models is a discrete-time model ($t = 0, 1, 2, ...$), usually with a time step (Δt) of one year. This means that establishment, growth and death of trees must depend only on the current state vector $\underline{x}(t)$ and input vector $\underline{u}(t)$ since they are time invariant (Zeigler 1976, Eq. 2.1).

$$\underline{x}(t+\Delta t) = f(\underline{x}(t), \underline{u}(t)) \tag{2.1}$$

Eq. 2.1 implies that in the simulation model the following must be avoided: Imagine that a variable x_1 currently has the value $x_1(t)$ and is updated to $x_1(t+\Delta t)$. Later during the same time step, the variable x_2 is updated from $x_2(t)$ to $x_2(t+\Delta t)$. Now, if x_2 is a function of x_1, Eq. 2.1 is violated because

$$x_2(t+\Delta t) = f(\underline{x}(t), x_1(t+\Delta t), \underline{u}(t)) \tag{2.1'}$$

Many gap models work on variables which are constantly being updated (e.g. Botkin et al. 1972, Shugart & West 1977, Pastor & Post 1985, Kienast 1987, Leemans & Prentice 1989). For instance, the FORECE model (Kienast 1987) features the procedure sequence BIRTH, GROW, and KILL, which removes some of the saplings added during the same time step, although they would formally enter the system only in the next time step (Fig. 2.1 left). Moreover, some gap models repeatedly calculate auxiliary variables within one time step, such as the leaf area index, although they would formally depend only on $\underline{x}(t)$ and $\underline{u}(t)$ (Kienast 1987).

Given states and inputs at time *t*, the following computational sequence results in a correct updating of the new states at time $t+\Delta t$: (1) determining which trees will die, (2) calculating the growth increment of the trees which will survive, and (3) establishment of saplings within Δt (Fig. 2.1 right). However, most forest gap models do not conform to this scheme (Tab. 2.1). Since a correct update mechanism avoids repeated calculation of some variables within the same Δt, e.g. leaf area index, simulations become more efficient: In the case of the FORECE model, the version with a correct updating is approximately 25% faster.

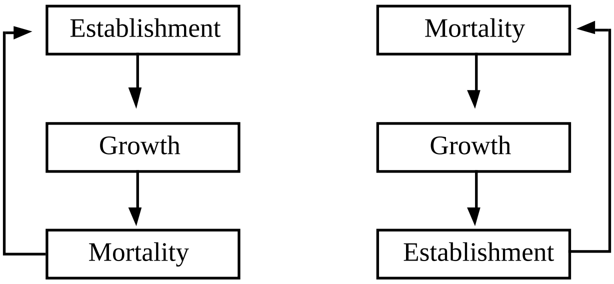

Fig. 2.1: Sequence of procedure calculations as incorporated in the simulation model FORECE (left) leading to inconsistencies, and a corrected sequence (right). Arrows to the left and the right symbolize the transition from one time step to the next; the other arrows indicate the sequence of calculation within a time step.

Tab. 2.1: Comparison of various forest gap models with respect to the state vector update, the typical number of simulations performed, the patch size used, and the corresponding size of the equilibrium landscape (equals the number of simulations times patch size). E stands for Establishment, G for Growth and M for Mortality. A consistent sequence of calculation would be M – G – E.

Model name	Number of simulations	Patch size [m2]	Equilibrium landscape size [ha]	State vector update	Reference
JABOWA	100	100	1	E – M – G	Botkin et al. (1972a,b)
FORET	100	833	8.3	M – E – G	Shugart & West (1977)
LINKAGES	20	833	1.7	E – G – M	Pastor & Post (1985)
FORENA	10	833	0.8	M – E – G	Solomon (1986)
FORECE	50	833	4.2	E – G – M	Kienast (1987)
FORSKA	5	1000	0.5	E – G – M	Leemans & Prentice (1989)
EXE	10	833	0.8	E – G – M	Martin (1992)

A different solution to the updating problem can be achieved when each state variable x_i of the mathematical model is represented by two variables in the simulation model, e.g. “x_i” and “x_iNew”. Like this, the update equations of the variables may be calculated in any sequence if they all use the “x_i” variables only and assign their updated values to the “x_iNew” variables. At the end of the time step, the update of the state vector is performed by assigning all the “x_iNew” variables to the respective “x_i” variables (cf. Fischlin et al. 1990).

To test the sensitivity of the FORECE model to a change in the update mechanism, the original model written in FORTRAN (Kienast 1987) was translated to the programming language Modula-2 (Wirth 1985, Wirth et al. 1992). The programming library Dialog-Machine (Fischlin 1986) and the simulation software ModelWorks (Fischlin et al. 1990) within the RAMSES environment on Apple Macintosh computers (Fischlin 1991) were used to implement this model version, which is called FORECE V1.0. Then a correct updating mechanism (Fig. 2.1 right) was implemented in Modula-2 as well, leading to version 1.1 of the FORECE model.

The differences between FORECE version 1.0 and 1.1 were examined in detail by means of extensive simulation studies along an altitudinal gradient in the European Alps (results not shown). The implementation of a consistent update mechanism of the state variables in FORECE did not lead to significant changes of the simulated species composition, although the correct updating is fundamentally different from a systems theoretical viewpoint. This seems to confirm Shugart's (1984) finding that no single part of a forest gap model is very sensitive to its exact formulation. However, the influence of the changed update mechanism on the frequency distribution of tree numbers is not negligible, and this may be important in studies that compare and validate gap models (e.g. Leemans 1992).

In conclusion, forest gap models can be viewed as a mixture of discrete time and discrete event models, which for practical reasons are implemented as discrete time models (Sequential Machines, Zeigler 1976). However, many gap models do not conform to the formalism of a sequential machine in the way they handle the update of state variables and should be revised in this respect.

2.2 Statistical analysis

2.2.1 Characteristics of model behaviour on a single forest patch

The basic unit of the gap dynamics hypothesis in forests is a small area of land in the order of 100 to 1'000 m^2 (0.01-0.1 ha; cf. Tab. 2.1). Various terms have been proposed to denote such a unit (Botkin et al. 1972a,b, Pickett & White 1985, Kienast 1987): The term “plot” is ambiguous since it may also denote a graphical representation of data. A “gap” would be close to the term “gap dynamics”, yet this is confusing since such a “gap” could also carry a mature stand. The term “patch” is unambiguous and clear; therefore I will refer to the basic unit of the gap dynamics hypothesis as a patch, corresponding to the title of the book by Pickett & White (1985).

Before setting out for a detailed analysis of forest gap models, it may be useful to have a look at the simulation results produced on one single patch of $^1/_{12}$ ha in the FORECE model, exemplifying both the nature of gap dynamics and some of their basic statistical properties.

MATERIAL & METHODS

The FORECE model V1.1 was used to simulate forest dynamics at two sites on one patch each: The site Davos is typical of forests in the subalpine zone, which are composed of a few coniferous species. These forests have comparably low biomass, and tree growth generally is slow. The site Bern is representative of the mixed deciduous forests on the

Swiss Plateau, which are much richer both in terms of species composition, total biomass, and soil fertility (cf. Appendix III for the location and climatic data of the sites). The additional site-specific parameters required by FORECE for the two sites are given in Tab. 2.2. The simulations covered 12'000 years at each site.

Emanuel et al. (1978) used spectral analysis to evaluate the behaviour of the FORET model (Shugart & West 1977). They found that up to 0.05 cycles per year account for a considerable portion of the spectral energy, corresponding to cycles with a length of 20 years. To resolve these cycles, the sampling interval must not be larger than half the cycle length. Thus the monitoring interval was set to 5 years in order to allow for an estimation of the spectrum of the model output.

Statistical analyses of the time series data (Shumway 1988) were performed by means of the SYSTAT V5.2.1 software (Wilkinson et al. 1992) on Apple Macintosh computers. The first 1'000 years of each simulation were discarded in order to concentrate on model behaviour after the transient phase.

Tab. 2.2: Additional site-specific parameters required by the FORECE model for the sites Bern and Davos (from Kienast 1987 and Kienast, pers. comm.; cf. Kienast & Kuhn 1989a,b).

Parameter	Davos	Bern
Maximum aboveground biomass [t/ha]	300	540
Field capacity [cm]	27	30
Wilting point [cm]	20	20
Start of vegetation period [day number]	150	120
End of vegetation period [day number]	227	273
Frost threshold (March) [°C]	1.0	3.5
Frost threshold (April) [°C]	4.0	6.5
Frost threshold (May) [°C]	8.0	9.5
Soil moisture indicator value [–]	4	5
Seed for random number generator	-12'672	-12'672

RESULTS & DISCUSSION

Davos

A typical part of the time series of species biomasses and tree numbers at the site Davos is shown in Fig. 2.2. From the point of view of biomass (Fig. 2.2 top), Norway spruce *(Picea excelsa)* is the dominating species. Swiss stone pine *(Pinus cembra)* becomes important only after gap formation (years 7'500-7'600, 8'300-8'550), and the occurrence of alder *(Alnus viridis)* is episodic when large gaps have been formed by the death of canopy dominants (year 8'550). Tree numbers (Fig. 2.2 bottom) exhibit strong fluctuations, with peaks occurring generally after biomass has been low. However, there is no obvious relationship between the height of the peaks of tree numbers and the values of the biomass minima. The reason is that gap formation principally allows for increased sapling establishment because of higher light availability, but actual establishment rates are modified by other factors such as weather as well.

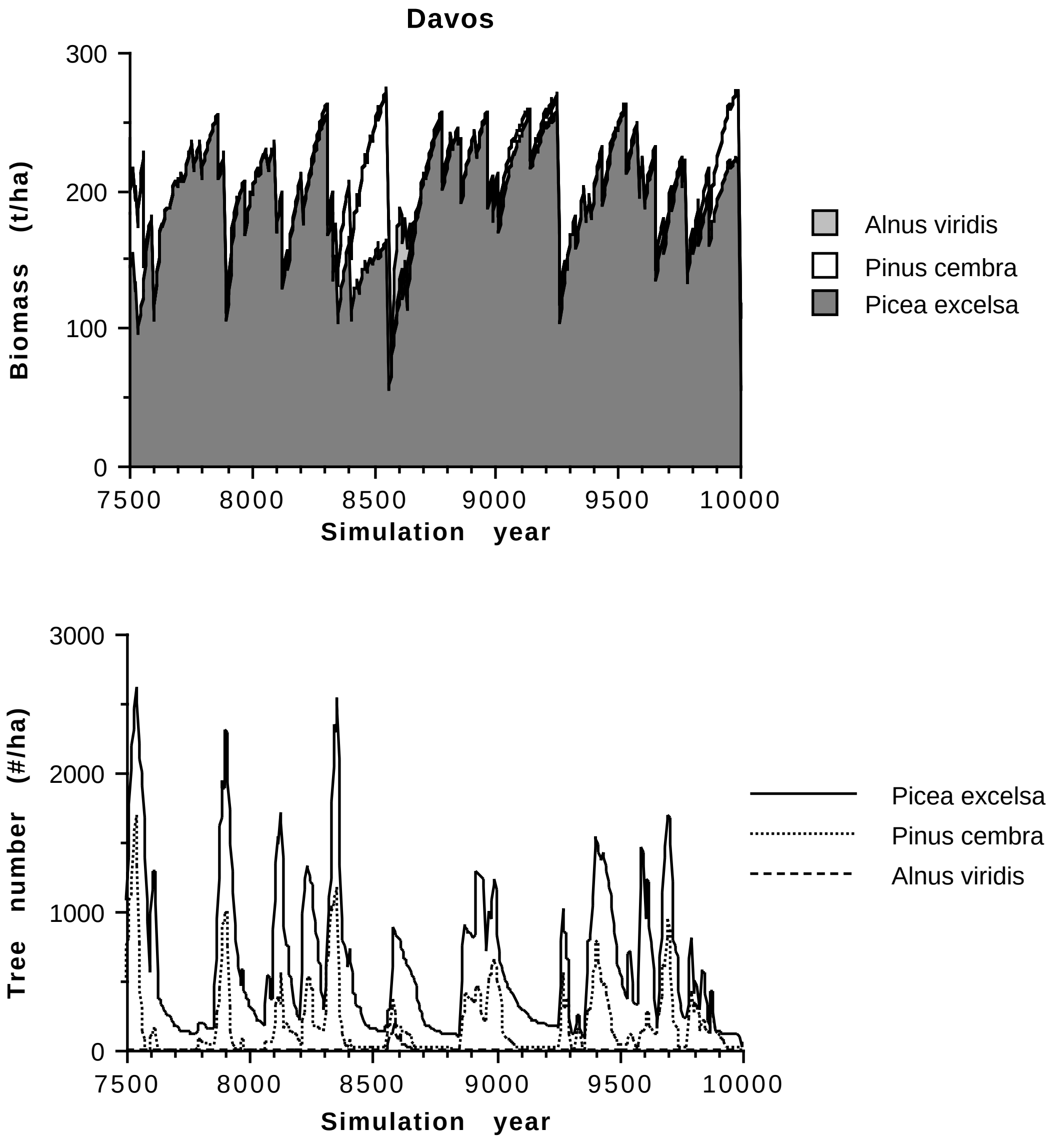

Fig. 2.2: Excerpt from the simulation results of a single forest patch at the site Davos. Top: Cumulative species-specific biomass. Bottom: Tree numbers.

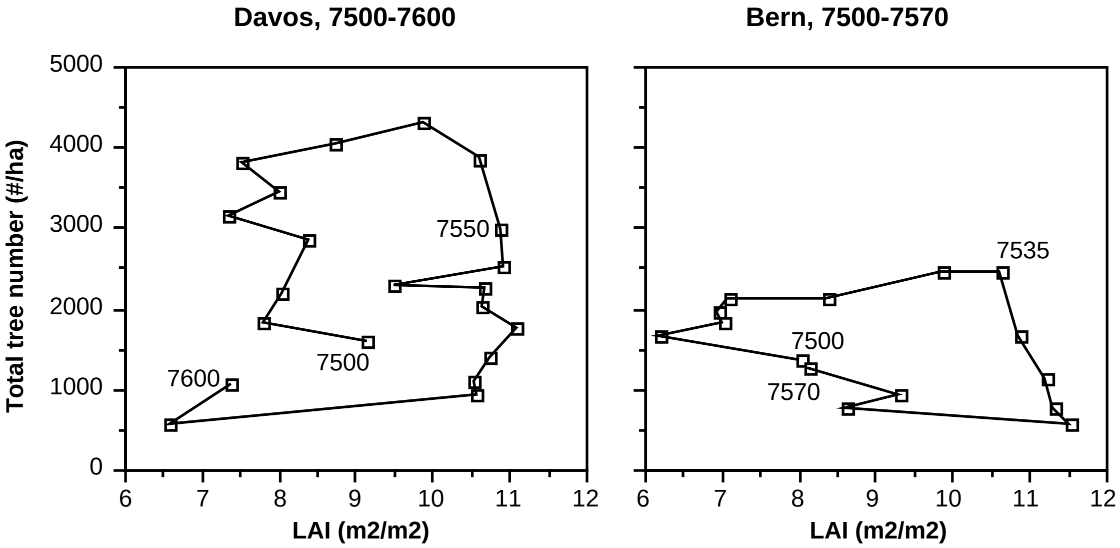

Fig. 2.3: Phase diagram of total tree number vs. double-sided leaf area index (LAI) at Davos (left) and Bern (right). Numbers in the graphs denote simulation years.

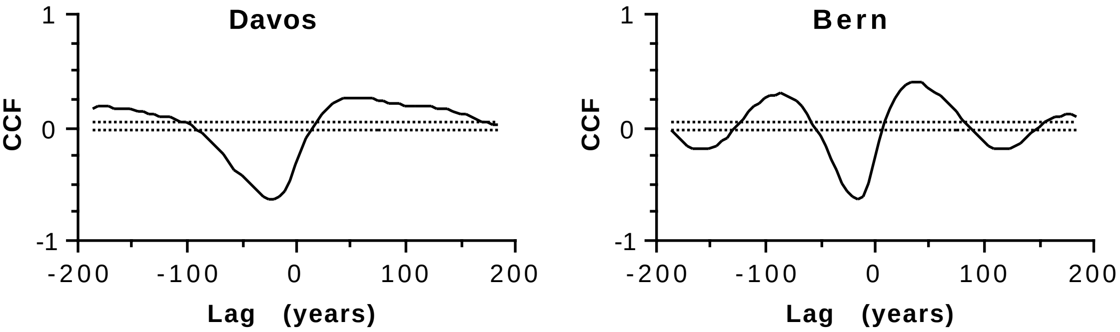

Fig. 2.4: Cross-correlation functions (CCF) of total tree numbers vs. leaf area index at Davos (left) and Bern (right) for the simulation years 1'005-12'000. The dotted lines indicate the 95% confidence limits for CCF = 0.

To elaborate the pattern underlying the simulated time series of biomass and tree numbers, the total number of trees was plotted against leaf area index (LAI), which is closely correlated with total aboveground biomass (Fig. 2.3): There is a cyclical behaviour of these variables because low LAI causes enhanced sapling establishment, which in turn increases LAI until light availability drops to a point where establishment is reduced again. Finally, LAI decreases strongly when a canopy dominant dies, and the cycle repeats. However, the examples in Fig. 2.3 represent ideal rather than typical cases. In the model, the cycles may be interrupted earlier because a large tree dies prematurely, or they often last longer because a suppressed subdominant tree comes to dominate after the death of a large tree; thus LAI increases again without a previous increase of tree numbers. From the cross-correlation function over the whole 11'000 year period (Fig. 2.4) one may conjecture that the typical cycle length of these gap-phase dynamics is about 200 years. However, the peaks are rather broad. Spectral analysis (Fig. 2.5) sheds more light on this behaviour: The spectrum of total tree numbers shows that there is a hump centered around a frequency of 0.005 cycles/year, yet there is no clear peak. Thus, the cycles have a characteristic length, which is closely related to the average lifespan achieved by the canopy dominants at Davos, but the length of any given cycle varies yet considerably.

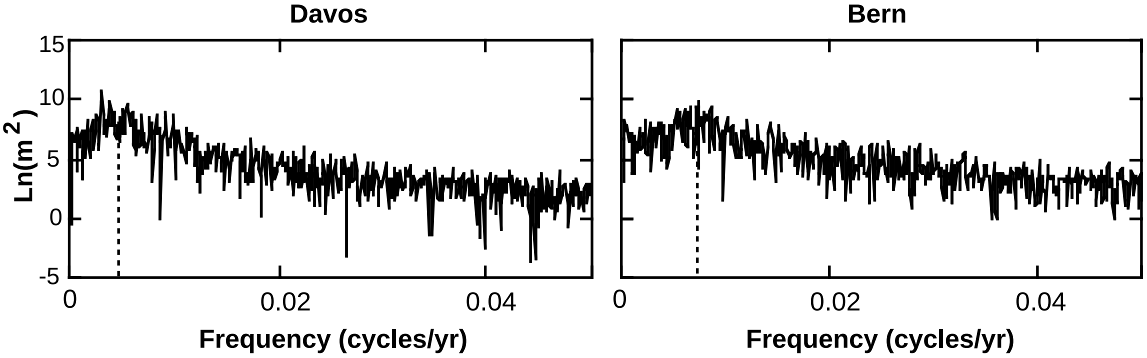

Fig. 2.5: Periodogram of total tree numbers at the site Davos (left) and Bern (right) for the years 1'005-11'240. m is the magnitude of the signal; the dotted lines indicate the approximate location of the maximum magnitude.

Bern

The biomass dynamics at Bern in the years 7'500-10'000 are shown in Fig. 2.6. It should be noted that the main point here is not whether the simulated species composition is realistic (cf. Kienast & Kuhn 1989a,b); among others, the time window in Fig. 2.6 is too small to allow for such assertions. It is more important to evaluate the pattern of species replacement in a mixed deciduous forest as compared to a subalpine site.

Compared to the site Davos (Fig. 2.2), a completely different successional pattern becomes evident (Fig. 2.6). In this mixed deciduous forest, there are hardly any self-replacing species. Two alternating phases can be distinguished: There are comparably short periods when one or a few trees dominate the patch and attain large biomass (e.g. *Fagus silvatica* in the years 8'300-8'500, *Tilia platyphyllos* and *Acer spp.* 8'600-9'000, *T. platyphyllos* and *F. silvatica* 9'600-10'000). The other phases are characterized by heavy competition and comparably small biomass; no canopy dominants emerge.

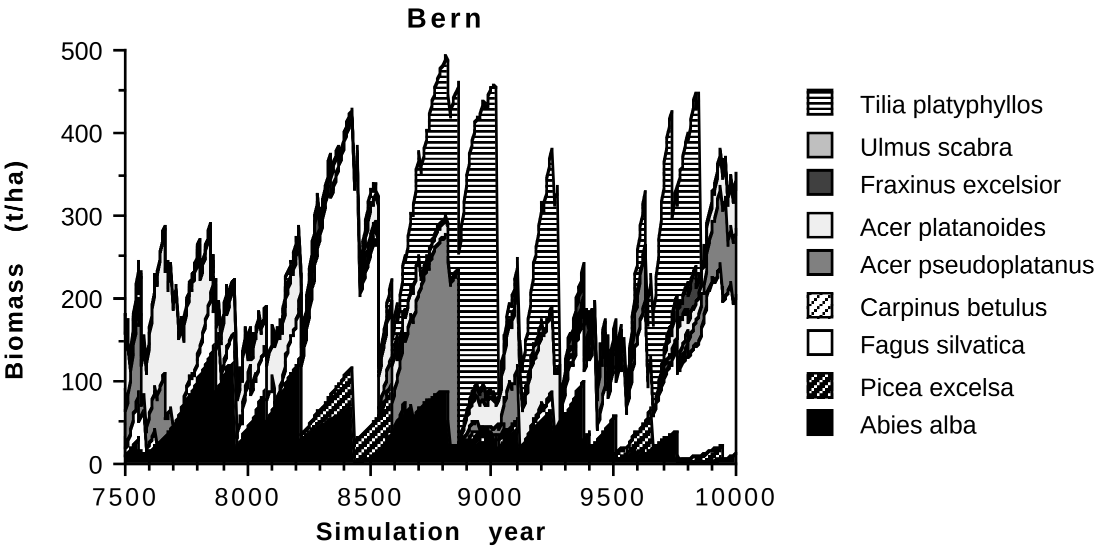

Fig. 2.6: Excerpt from the time series of cumulative species-specific biomass of a single forest patch at the site Bern.

A plot showing the cyclical behaviour of total tree numbers against leaf area index at the site Bern is given in Fig. 2.3. The cross-correlation function (Fig. 2.4) and the spectrum of tree numbers (Fig. 2.5) suggest that the typical cycle length in this forest is around 100-140 years, i.e. less than at Davos. This is due to the shorter average lifespan of the dominating species at the site Bern, such as *Fagus silvatica*.

How long does the memory of species-specific biomass values and tree numbers last? At both sites, the autocorrelation functions of these variables drop below significant thresholds at lags smaller than 300 years (cf. Fig. 2.7 for an example). For the dominating species at the site Bern, the largest significant lag is 230 years, and for most species-spe-

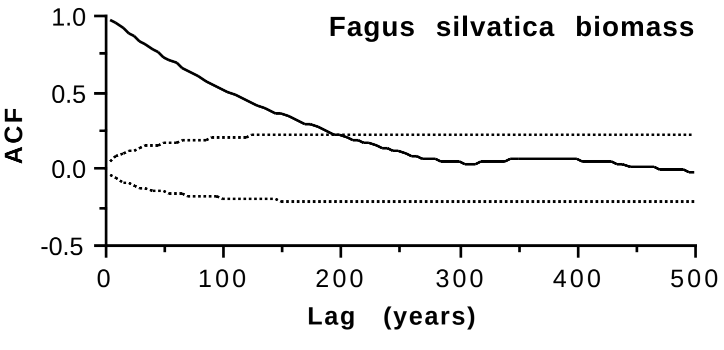

Fig. 2.7: Autocorrelation function (ACF) of the biomass of *Fagus silvatica* at Bern. The dotted lines indicate the 95% confidence limits for ACF = 0.

cific biomass variables it is less than 200 years. It should also be noted that the largest significant lag of tree numbers is always smaller than the largest significant lag of the corresponding biomass.

In conclusion, the Davos and Bern simulations represent two examples of the various patterns possible under the gap-phase dynamics hypothesis: A species-poor, slowly growing forest whose pattern is dominated by one self-replacing species on the one hand, and a species-rich, fast growing forest with a diverse array of species replacement and competition on the other hand. In this sense, the FORECE model can be viewed as a valid computer based description of the gap dynamics hypothesis (Watt 1947, Shugart 1984).

The length of a gap dynamics cycle in the simulated unmanaged forests, i.e. ≈200 and ≈150 years at Davos and Bern, respectively, is higher than the rotation length in managed forests of the area (e.g. Dengler et al. 1990). However, the idea that extremely old trees are abundant in “virgin” forests is supported neither by the present simulation study nor by field data (e.g. Leibundgut 1993). We may conclude that two samples taken from the same forest patch in the model can be considered to be independent from each other if the lag between them is at least 200 years.

2.2.2 Statistical sampling of the stochastic process

For many applications of gap models, the behaviour of a single patch is of little interest because the major emphasis is on the dynamics of a larger area of forested land. Thus, the results from several patches may be averaged to obtain the dynamics on larger scales. Immediately there raises a question: How many patches do we have to simulate if we want their average to be reliable? How fast does this average converge towards the expected value? Are 5 patches sufficient, does it take 50, or even 500 (cf. Tab. 2.1)?

MATERIAL & METHODS

Species biomass and the numbers of trees originating from multiple simulation runs are rarely normally distributed at a given point in time (Fig. 2.8). Therefore, simple measures of convergence like the coefficient of variation (Zar 1984) do not provide robust estimates of model convergence. For highly skewed distributions, a more robust statistical measure is the interval between the 10% and the 90% percentile (p_{10}, p_{90}) for the range of the samples and the median (med), which characterizes their location. The quotient given in Eq. 2.2 was used for this characterization. Theoretically, q should converge toward a non-zero value as the sample size approaches infinity.

$$q = \frac{p_{90} - p_{10}}{\text{med}} \tag{2.2}$$

To perform the analysis, the site Bern on the Swiss plateau (cf. Appendix III) was chosen because it is representative of a large area of the Swiss Plateau. The site-specific parameters were taken from Kienast (1987). The q value was calculated for three species each playing a key role at this site, i.e. *Abies alba* with a low abundance at the beginning and intermediate abundance during later stages; *Fagus silvatica* with high abundance at the beginning and intermediate abundance after about 600 years; and *Ulmus scabra*, a species with low abundance throughout the succession (Kienast 1987). Three points in time were selected for the analysis, i.e. the simulation years 400, 800 and 1200. By doing so, temporal autocorrelation becomes negligible (cf. section 2.2.1).

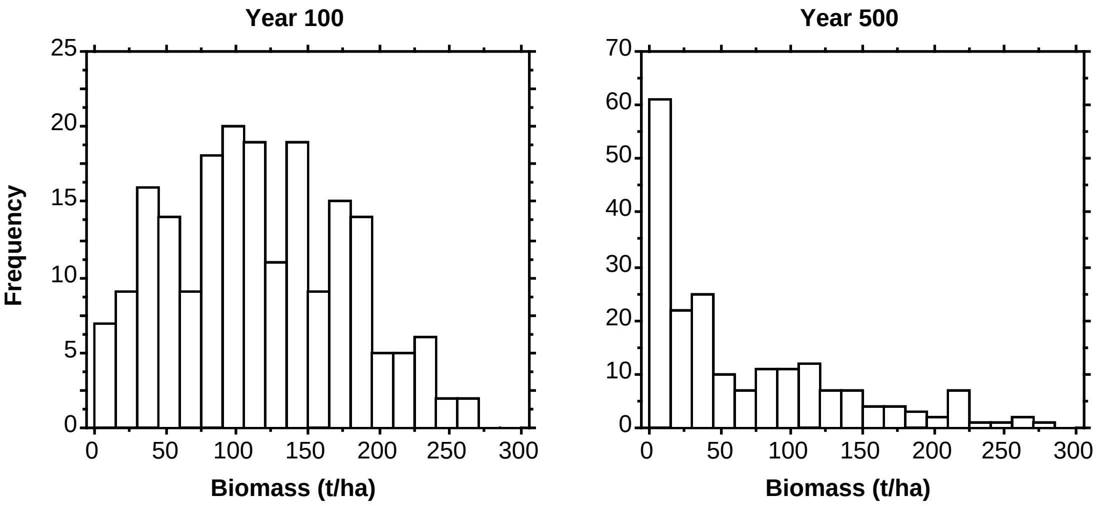

Fig. 2.8: Distribution of the biomass of *Fagus silvatica* from 200 simulation runs of the FORECE model V1.0 at the site Bern in the years 100 (left) and 500 (right).

Since the original FORECE model (Kienast 1987) does not allow for performing more than 50 simulation runs at a time, the FORECE model version 1.0 as translated to the programming language Modula-2 (see section 2.1) was used to perform 4'000 simulation runs on an Apple Macintosh II computer. From this data base *n* random samples were taken to calculate the quotient from Eq. 2.2. The procedure was repeated 10 times for each sample size (*n* = 5, 10, 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 400). Additionally, the statistical properties of the full sample of 4'000 runs were calculated according to Eq. 2.2 (cf. Bugmann & Fischlin 1992).

RESULTS AND DISCUSSION

The results from the analysis of model convergence are shown in Fig. 2.9. All three species reveal similar patterns at all years: For less than 100 simulations, the q value is highly variable. A clear tendency of convergence is visible between 100 and 200 simulation runs per analysis. The further reduction of variability becomes small if the sample size is larger than 200 simulation runs. Generally the scatterplots resemble a funnel-shaped function (Fig. 2.9). Model convergence is slow, reflecting the highly stochastic nature of gap models. For the FORECE model, we estimate that approximately 200 simulations are needed if meaningful statistics are to be calculated from the model output, and we surmise that this result is valid for many other forest gap models, too, because their structure is quite similar to FORECE (Botkin 1993). This is markedly more than a sample size of not more than 50 runs, which appears to be a generally accepted standard (Tab. 2.1). It would even be desirable to perform more than 200 runs, but this will yield little improvement relative to the additional simulation time needed.

The quasi-equilibrium landscape concept holds that the vegetation attributes of a landscape exhibit constancy when the size of the disturbances is small relative to the size of the landscape (Whittaker 1953, Bormann & Likens 1979). Shugart (1984, p. 165) quantified this concept and suggested that the minimum area required for the quasi-equilibrium is about 50 times the size of a typical disturbance. Patch size in forest gap models is chosen so as to represent the typical disturbance size (Shugart & West 1979); hence 50 patches should be sufficient to calculate the properties of the quasi-equilibrium landscape. In a recent paper, Busing & White (1993) showed that the physical structure (e.g. total basal area and total biomass) of an old-growth hemlock-hardwood forest in Tennessee can be approximated well by the 50:1 rule. However, the composition of the landscape, e.g. relative basal area of the species, did not yet equilibrate at an area 50 times the disturbance size (Busing & White 1993). It is interesting to note that their finding corresponds to the results of the present convergence analysis. However, these new results do not interfere with the concept of a quasi-equilibrium landscape (Bormann & Likens 1979); they just modify its quantification (Shugart 1984; cf. Turner et al. 1993).

3. The forest model FORCLIM

3.1 Structure of FORCLIM

Conventional forest gap models (e.g. Botkin et al. 1972a,b, Shugart 1984, Kienast 1987) are formulated as one large model. While this approach is useful for small models, the complexity of forest gap models makes it difficult to keep an overview. An alternative concept is to formulate several independent submodels and to assemble them in a modular fashion to form a complete forest gap model. This approach bears several advantages: The structure of the ecosystem model becomes clearer, the couplings between submodels are explicit, and it is easy to exchange a submodel without affecting the others. Consequently, the FORCLIM[1] model is divided into three submodels (cf. Fig. 3.1):

- Environment: This submodel provides time-dependent abiotic variables. It generates weather data (W) and uses these data to calculate bioclimatic output variables (B). The environment submodel does not depend on any of the other submodels and acts as an input model.

- Plants: The plant submodel calculates establishment (E), growth (G), and mortality (M) of trees on a forest patch. It requires bioclimatic variables and nitrogen availability as input and calculates litter production as an output.

- Soil: The soil submodel tracks the decay of plant litter (L) and humus (H) in the soil as a function of bioclimatic variables. It calculates the amount of nitrogen available for plant growth.

The dynamics of soil organic matter are considered explicitly in the FORCLIM model for two main reasons: First, such a submodel calculates the availability of soil resources as a function of weather variables, thus avoiding earlier approaches that implicitly contained climatic information (Botkin et al. 1972a,b, Kienast 1987; cf. Fischlin et al. 1994). Second, the explicit consideration of soil carbon dynamics makes it possible to assess the

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[1] FORCLIM is an acronym for "FORests in a changing CLIMate"

carbon balance of the whole forest ecosystem, which is important for the biospheric feedback to the climate system (Trabalka & Reichle 1986, Post et al. 1990, Tans et al. 1990).

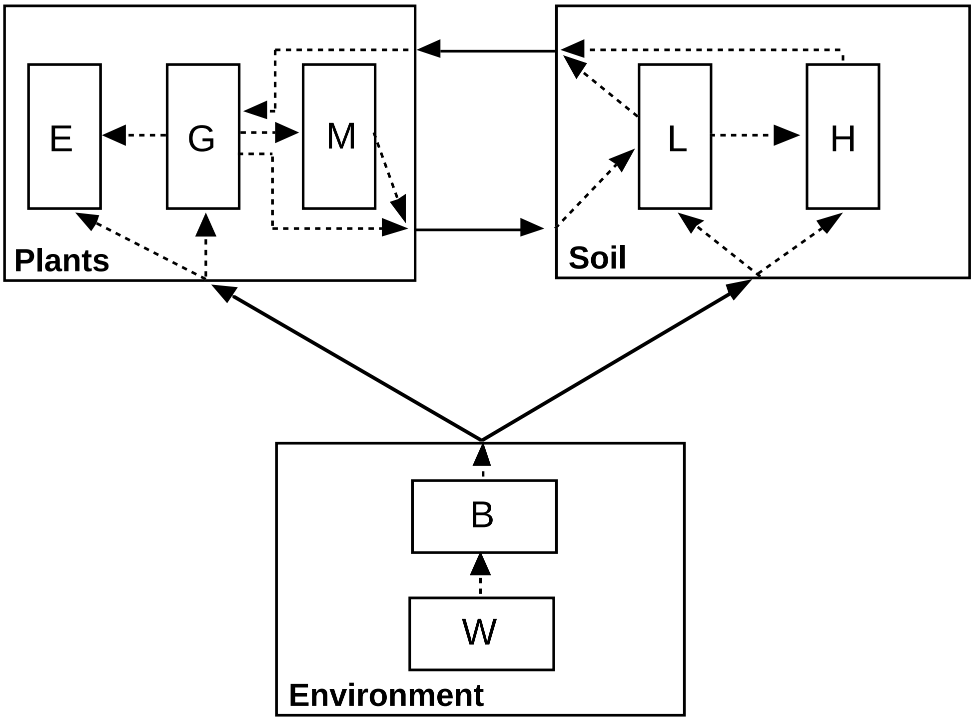


Fig. 3.1: Structure of the FORCLIM model. Dotted lines denote the dependencies within the three submodels. The symbols are explained in the text.

3.2 Model assumptions

3.2.1 Plant submodel: Tree population dynamics

A basic paradigm of population ecology states that there are four key processes determining the abundance of a population (e.g. Fischlin 1982, Begon et al. 1990): natality, mortality, immigration, and emigration. Since trees are sessile and the dispersal of most tree species is comparably slow, migration phenomena are not considered explicitly in FORCLIM. The basic processes therefore are the establishment and the mortality of trees (Fig. 3.2). However, we are interested not only in the abundance, but also in the structure of the population. Moreover, tree mortality rates are influenced to a large extent by competition; thus tree growth has to be modelled as well (Fig. 3.2).

TREE ESTABLISHMENT

The germination of seeds operates at small temporal and spatial scales as compared to many other processes in forest ecosystems such as tree growth (cf. section 1.2). The factors influencing seed bank dynamics, germination, and establishment of small plants are very difficult to develop mechanistically in an ecosystem model (Shugart 1984), and the establishment of trees from seeds is the result of a long chain of random events (Botkin et al. 1972a). Mortality rates of germinating seeds, seedlings, and small saplings are overwhelmingly high (Kimmins 1987), so that only a minute fraction of the seeds will ever become trees. These complicated phenomena can be portrayed in a simple manner with a few environmental filters, such as light availability and growing season temperature (Shugart 1984).

The following environmental filters ("flags") are used for tree establishment in the FORCLIM model (cf. section 2.3.1): (1) Winter minimum temperature (uWiT) is used to exclude the species that do not tolerate extremely cold winters (gWFlag, Fig. 3.2; Ellenberg 1986, Woodward 1988). (2) Light availability at the forest floor as determined by the canopy trees prevents establishment of light-demanding species (gLFlag; Kimmins 1987, Fig. 3.2). (3) Mammals exert a considerable influence on tree recruitment in the European Alps (Näscher 1979, Eiberle & Nigg 1986, Liss 1988, Albrecht 1989, Rechsteiner 1993); thus browsing is incorporated to simulate the influence of species like red and roe deer *(Cervus elaphus* L., *Capreolus capreolus* L.), whose population dynamics are not modelled explicitly in FORCLIM (gBFlag, Fig. 3.2). (4) To avoid establishment of saplings that would be killed anyway because they subsequently would fail to grow, the annual sum of degree-days (uDD) is used as an environmental filter in FORCLIM (gDFlag, Fig. 3.2).

Like most forest gap models, FORCLIM is aimed at modelling forest succession under natural conditions. Therefore forest management practices such as planting and artificial thinning are disregarded in the present model.

Most forest gap models establish tree individuals with very similar sizes (Shugart 1984). Since tree growth in these models is treated deterministically, the size of all the individuals of a given species established in a given year will remain similar throughout their lifespan. Thus in the FORCLIM model these individuals are assumed to have identical size and are established as one tree cohort. Tree growth then may be calculated once for each cohort instead of each tree.

TREE GROWTH

The mechanisms underlying tree growth, such as photosynthesis and the allocation of the various forms of carbon to tree organs, which lead to processes like shoot elongation, leaf development, and root growth, are not modelled explicitly in FORCLIM. It is not that these mechanisms are not important in tree growth. Rather, they operate on small temporal scales and equilibrate fast, so that they are not evident at the scale of the annual growth rate of a whole tree (Shugart 1984). Whittaker & Marks (1975) argued that the enlargement of a system requires a redesign of its proportions. Similarly, the dimensions of a tree as they enlarge change in ways that maintain their functional balance. This allows to calculate the dimensions of many tree organs from the dimension of other organs that are simpler to measure. Such "allometric" relationships are widely used in forest science and forestry (e.g. Burger 1945-1953, Mitscherlich 1970, King 1991, Woods et al. 1991, Smith et al. 1991, Wang et al. 1991).

A tree dimension that is easily measured is the diameter at breast height (D). According to the approach used in most forest gap models, in FORCLIM it is assumed that tree growth can be expressed adequately as an increase in diameter at breast height, which thus is one of the two state variables characterizing each tree cohort (Fig. 3.2). Allometric relationships are used to calculate other tree measures from the diameter, such as height (Huang et al. 1992), leaf weight and leaf area (Burger 1945-53), stemwood biomass (Woods et al. 1991) and the production of twig and root litter (Pastor & Post 1985).

The following internal constraints on diameter growth are considered in FORCLIM: Under optimal conditions, i.e. full sunlight, abundant nutrients, optimum temperature and adequate soil moisture supply, gross photosynthesis is proportional to the photosynthetic surface of the tree, i.e. its leaf area, and respiration is proportional to tree volume (Moore 1989). The latter assumption neglects that the fraction of nonliving tissue of a tree increases with its age, but it is assumed that this still constitutes a reasonable approximation (Shugart 1984).

Given this basic relationship for diameter growth under optimal conditions, the effects of the abiotic and biotic environment are used to modify the optimal growth rate, which results in the actual growth rate of every tree cohort (Fig. 3.2).

One of the most important external constraints on tree growth is shading, which determines the amount of light a tree receives and thus the amount of energy available for photosynthesis (gALGF, Fig. 3.2). Gap models are geometrically explicit in the vertical dimension, but most of them use a very simple approach to model crown geometry: All the leaves are assumed to be concentrated at the top of the stem (Botkin et al. 1972a,b). This assumption is not as unrealistic as it may appear; for example, Schulze et al. (1977) found that in a *Picea excelsa* forest more than 70% of the annual CO_2 uptake was attributable to the needles exposed to direct sunlight at the top of the crown. Leemans and Prentice (1989) argued that sun angles in the boreal zone often are so low that most direct sunlight incides from the side and not from above, making an explicit consideration of true crown geometry necessary. For the present study, which deals with forests at temperate latitudes where sun angles are much higher, the simple crown geometry of conventional forest gap models (Shugart 1984) seems appropriate.

The following climate dependent constraints are used in FORCLIM: The direct effects of temperature are modelled as the annual sum of degree-days (uDD). Woodward (1988) showed that this index correlates well with the distribution of plant species (gDDGF), although it may lack a physiological basis (Bonan & Sirois 1992). The water content of the rooting zone is used to model the effect of drought stress (uDrStr) on growth (gSMGF, Cramer & Prentice 1988), assuming that it is indicative of the water availability for plants.

In their classic fertilizer trials, Mitchell & Chandler (1939) found that tree growth increases in a well predictable manner with increasing soil nitrogen concentrations (uAvN). Aber et al. (1979, 1982) and Pastor & Post (1985) incorporated these findings in forest gap models, and the same approach is used in FORCLIM (gSNGF).

The possible direct effects of atmospheric CO_2 on tree growth (“CO_2 fertilization”) are still hotly debated in the literature (e.g. Eamus & Jarvis 1989, Overdieck & Forstreuter 1991, Körner 1993). While the short-term effects of enhanced CO_2 concentrations on photosynthesis and water-use efficiency of tree seedlings and saplings seem to be well established (e.g. Strain & Cure 1985), the long-term effects on older trees and whole ecosystems remain undetermined and can not be extrapolated simply from the findings at smaller scales (Eamus & Jarvis 1989). These authors also noted that at the ecosystem scale *“recourse must be made … to modelling”* (p. 8). Simulation studies dealing with this problem typically found that the response at the ecosystem scale is much smaller than the increase in the growth rate of the single trees (e.g. Shugart & Emanuel 1985) or even that there is no response at the ecosystem scale at all (e.g. Luxmoore et al. 1990). Based on these studies and in view of the large uncertainties concerning this issue, the hypothesized direct effects of atmospheric CO_2 on tree growth are neglected in FORCLIM.

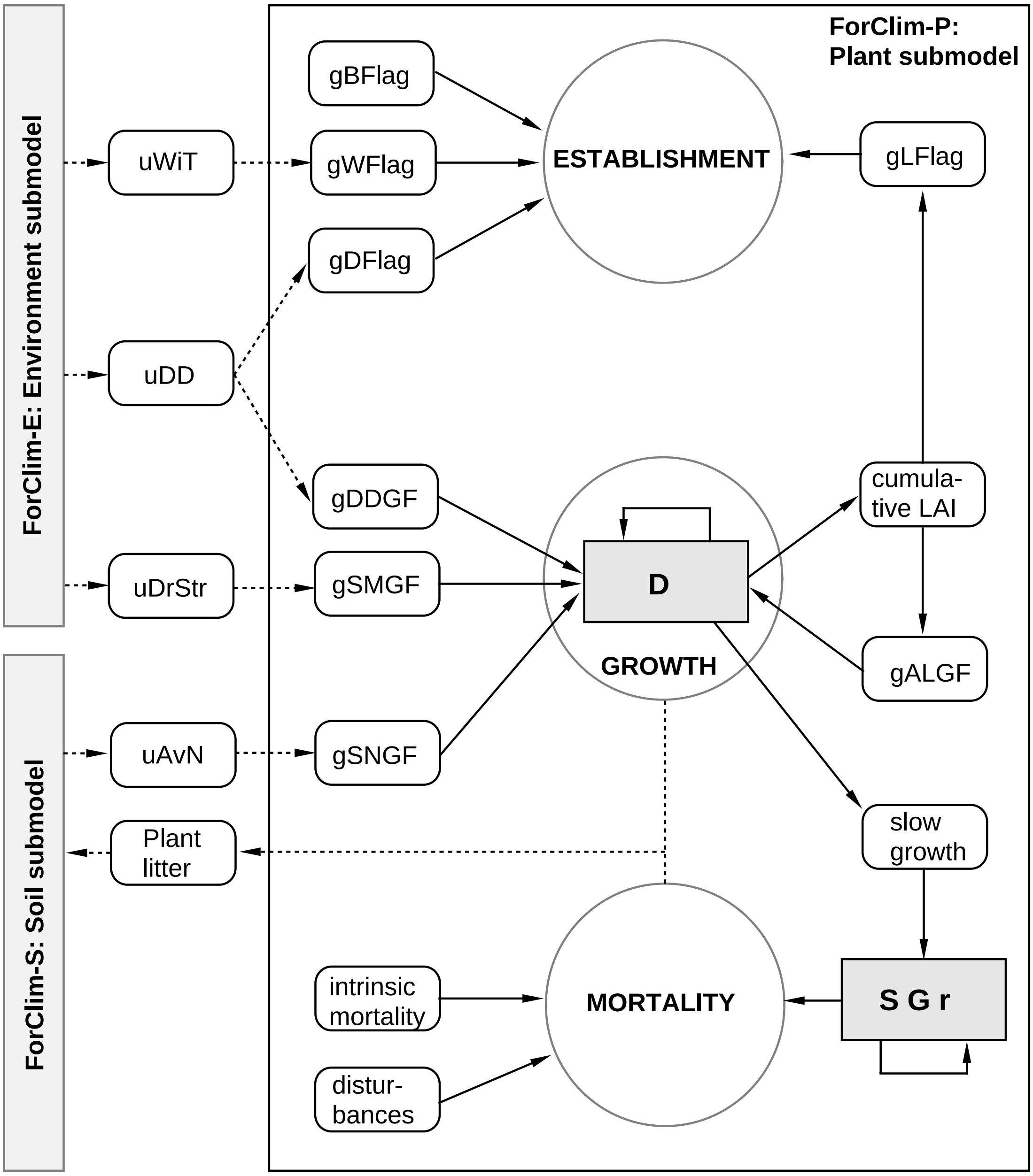


Fig. 3.2: Structure of the plant submodel FORCLIM-P. Square boxes denote state variables; boxes with rounded edges are auxiliary variables. Arrows from x to y indicate that y = $f(x)$, and broken lines denote the calculation of input/output variables. The identifiers are explained in the text.

The final problem for calculating the annual diameter increment of trees is: How shall the several growth factors be combined to arrive at one single, composite index of environmental conditions? In the JABOWA model (Botkin et al. 1972a,b) all the growth factors were combined in a multiplicative manner to reduce the maximum diameter increment. This approach is based on the assumption that all the factors are mutually dependent and that any favourable factor can compensate for any other unfavourable factor, which may be exaggerated. Moreover, generally too small growth increments will be obtained, especially if many factors are considered. For example, if each of four growth factors is 0.5, then $0.5^4 = 0.0625$, i.e. the actual growth rate is only 6% of maximum growth. A different approach was used e.g. in the FORECE model (Kienast 1987); it consists of applying what has been called “Liebig's Law of the Minimum” (cf. Pomeroy & Alberts 1988): Only the smallest of all the growth factors is used to reduce maximum growth. In this approach it is assumed that the growth factors are independent of each other, and that no compensation is possible. The advantage is that unrealistically low growth rates are avoided, but this approach is satisfactory only if few factors are present: The more factors are considered the more probable it is that some of them can compensate for others. Thus a synthesis of the two approaches will be developed in the FORCLIM model, which tries to combine the desirable features of each approach.

TREE MORTALITY

Age-dependent mortality rates of trees can be obtained from tree life tables (e.g. Harcombe 1987) and often have a characteristic U-shape: The mortality rate of young trees is high, indicating strong competition for light and considerable self-thinning, followed by a lower, constant mortality rate of the vigorous adult trees, and a higher mortality rate of old trees (Goff & West 1975, Harcombe 1987). The latter may be a consequence of their lower vigour and their size; these factors make them more susceptible to disease, windthrow, and lightning.

These features of tree mortality rates can be modelled by combining a constant and a stress-induced mortality rate (Fig. 3.2): The former reflects processes that are not modelled explicitly in FORCLIM, such as attacks by fungi or insects and the death of small trees by falling boles. This mortality rate is augmented when a tree grows very slowly: Due to shading, small trees often reach a small fraction of the possible maximum growth rate only. On the other hand, large trees often show negligible absolute growth rates. Thus, the stress-induced mortality is assumed to occur if diameter growth has been less than a certain absolute increment or a certain fraction of the maximum increment for several years (SGr, Fig. 3.2; Kienast 1987, Solomon & Bartlein 1993). The variable SGr contains a memory for past environmental conditions; therefore it is a state variable in the model (Fig. 3.2). It should also be noted that the stress-induced mortality provides a link between tree growth and tree mortality.

Disturbances extrinsic to the forest patch, such as forest fires and windthrow, provide a third source of mortality, which is episodic (Shugart 1984). This mortality is included in the FORCLIM model using a simple approach: All the trees currently present on the patch are killed if such a disturbance occurs. Other sources of tree mortality, such as forest management practices like thinning and logging, are disregarded in FORCLIM.

3.2.2 Soil submodel: Turnover of soil organic matter

Nitrogen is one of the major plant nutrients, and its availability limits plant growth in many terrestrial ecosystems (Kimmins 1987). The nitrogen cycle in forests is intimately coupled with the carbon cycle (Shaver et al. 1992): The amount of organic matter returned to the soil depends on primary productivity, which is limited by nitrogen availability (Waring & Schlesinger 1985, Lyr et al. 1992). In turn, nitrogen availability is largely determined by nitrogen mineralization, the conversion of organic nitrogen to ammonium with concomitant release of CO_2 (Alexander 1977); nitrogen mineralization itself depends on climate and on the type of carbon compounds with which the nitrogen is associated (Mellilo et al. 1982, McClaugherty et al. 1985). Thus in an analysis of the turnover of soil organic matter at the ecosystem scale, the couplings between the carbon and nitrogen cycles should be considered explicitly (Pastor & Post 1985).

The basic paradigm for most decomposition models developed to date was formulated by Jenny et al. (1949); Olson (1963) formalized it in a simple exponential-decay model. However, the parameters of this model are specific for each soil, depending on climate and the type of litter returned to the soil. Thus, it was a logical step to relate decay rates to environmental parameters such as temperature and precipitation (or a combination of these), and to simple chemical indices of substrate quality (e.g. Meentemeyer 1978, Melillo et al. 1982). Several models of the carbon cycle were constructed for forests (Aber & Melillo 1982, Weinstein et al. 1982, Pastor & Post 1985, Aber et al. 1991), and grasslands (Jenkinson & Rayner 1977, Parton et al. 1987, Verberne et al. 1990) (cf. the review in Ågren et al. 1991). However, most of these models do not treat explicitly the effects of climatic parameters and substrate chemistry on decomposition rates. The LINKAGES model by Pastor & Post (1985) fulfils both requirements. Moreover, this model was used successfully in many subsequent studies (Pastor & Post 1986, 1988, Shugart & Urban 1989, Martin 1992, Pastor & Naiman 1992). Therefore, the FORCLIM submodel for soil organic matter turnover was derived from LINKAGES (Fig. 3.3).

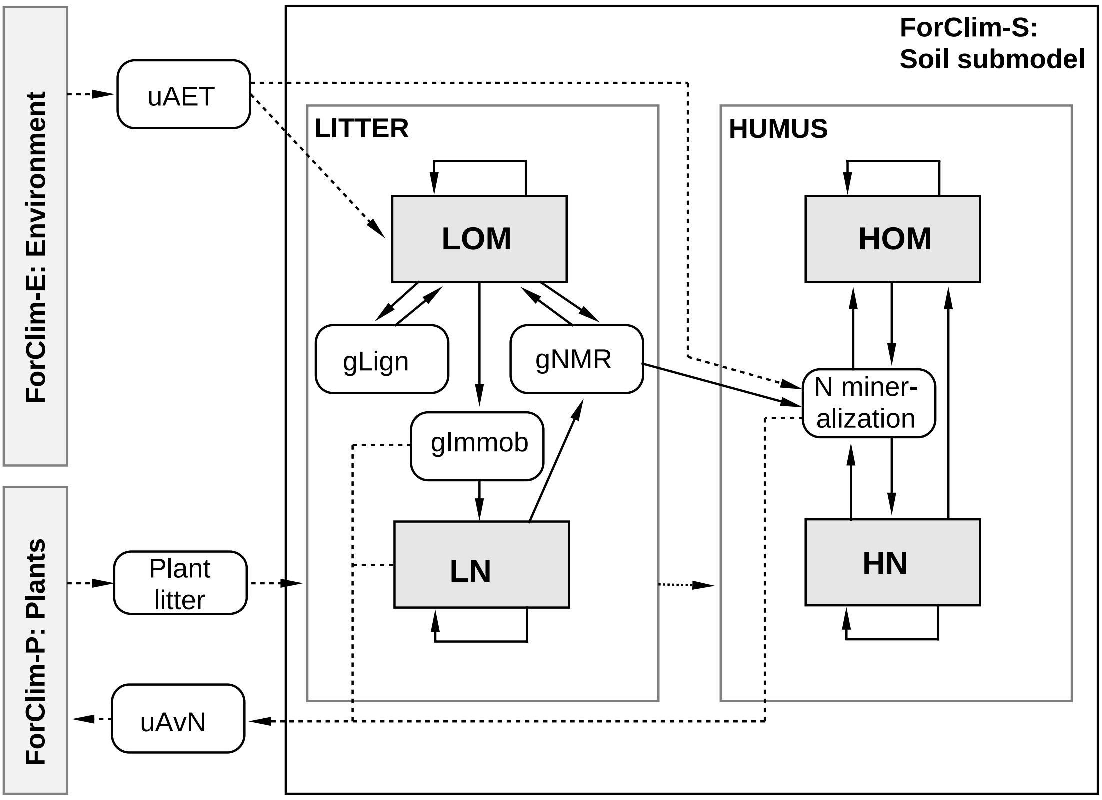


Fig. 3.3: Structure of the soil organic matter submodel ForClim-S. The identifiers are explained in the text.

The litter produced by the trees in a given year loses carbon continuously during decomposition, but the rate of nitrogen uptake by the microbes attacking the tissue is initially greater than the release of nitrogen from the tissue; this results in a net immobilization of nitrogen (e.g. Berg & Staaf 1981, Waring & Schlesinger 1985). Thus, in ForClim-S two state variables are used to characterize litter: its organic matter content (LOM), and its nitrogen content (LN; Fig. 3.3). The litter becomes progressively richer in recalcitrant compounds, and the rate of nitrogen release begins to exceed the uptake, leading to nitrogen mineralization. Pastor & Post (1985) call the material in this stage “humus”. The change from immobilization to mineralization – and thus the transition from “litter” to “humus” – generally happens at nitrogen concentrations of about 2% of weight (Alexander 1977). Similar to the litter, the humus is divided into organic matter (HOM) and nitrogen content (HN, Fig. 3.3).

The basic idea behind the decomposition module in Linkages is to formulate decay rates based directly on the wealth of data obtained from litterbag studies (e.g. Meentemeyer 1978, Melillo et al. 1982, Pastor et al. 1984, Coûteaux et al. 1991). To this end, the decay of each year's litter is tracked through time, thus mimicking many litterbag studies. When the critical nitrogen concentration (Alexander 1977) is reached, the litter is transferred to a common “humus” compartment, and nitrogen mineralization starts. The amount of nitrogen available for plant growth (uAvN) is calculated as the difference between the nitrogen mineralized from the humus pool and the immobilization demand of the litter cohorts (gImmob, Fig. 3.3).

Pastor et al. (1984) and Pastor & Post (1985) found good correlations between litter decay rates, actual evapotranspiration (uAET), litter lignin content (gLign), and the nitrogen to mass ratio of the litter (gNMR); these indices are used to formulate litter decay rates in LINKAGES and FORCLIM (Fig. 3.3). The leaching of nitrate from nitrogen-rich litter is taken into account (Cole & Rapp 1981) as well as a constant atmospheric deposition rate of soluble nitrogen compounds. The more recalcitrant litter types (twigs and wood) are assumed to decay at a constant rate. The hypothesized effects of canopy openings on litter and humus decay rates as incorporated in LINKAGES were not included in the FORCLIM model (Fig. 3.3).

Most of the litterbag studies to date were conducted under boreal conditions and/or in America; only few data are available for central European conditions and species (e.g. Berg & Staaf 1981, Ellenberg 1986, Lüscher 1991). Thus it was necessary to collapse the 17 litter types distinguished in LINKAGES to three types of leaf litter (fast, medium, and slow decay), twig litter, root litter, and stemwood litter.

At least two weaknesses remain in the LINKAGES as well as the FORCLIM-S model: First, there is no compartment with a very slow turnover rate of soil organic matter. It is well known that part of the organic matter is “protected” or “stabilized” and very recalcitrant to decay (e.g. Parton et al. 1987, Verberne et al. 1990); neither the LINKAGES nor the FORCLIM model simulate these processes. Second, Pastor & Post (1985) had to use the N:C ratio of the *litter* to formulate the mineralization rate of the *humus* compartment; while this approach was phenomenologically correct (Pastor et al. 1984), it represents an empirical, not a causal relationship. Lüscher (1991) investigated the dynamics of the forest floor and the humus of many soils in Switzerland; however, this data base does not allow to reformulate the rate of nitrogen mineralization from the humus as a function of abiotic variables on a more mechanistic basis. Thus, the data from Pastor et al. (1984) had to be used again in FORCLIM (Fig. 3.3).

3.2.3 Environment submodel: The abiotic forest environment

The submodels for plant dynamics and soil organic matter turnover are based on abiotic input variables, such as the annual sum of degree-days, which could be calculated best from very detailed weather records, e.g. hourly temperature measurements. However, within an ecosystem model that calculates forest succession over many centuries, such a resolution is hardly feasible. Thus, there arises the need to sacrifice the precision of detailed weather data to allow for general and simple calculations of the abiotic conditions. Monthly weather data capture some of the basic features of the annual weather cycle, and they mediate between the annual time step of the other submodels and more detailed approaches. Thus, monthly temperature and precipitation data seem to be a good compromise and will be used in FORCLIM.

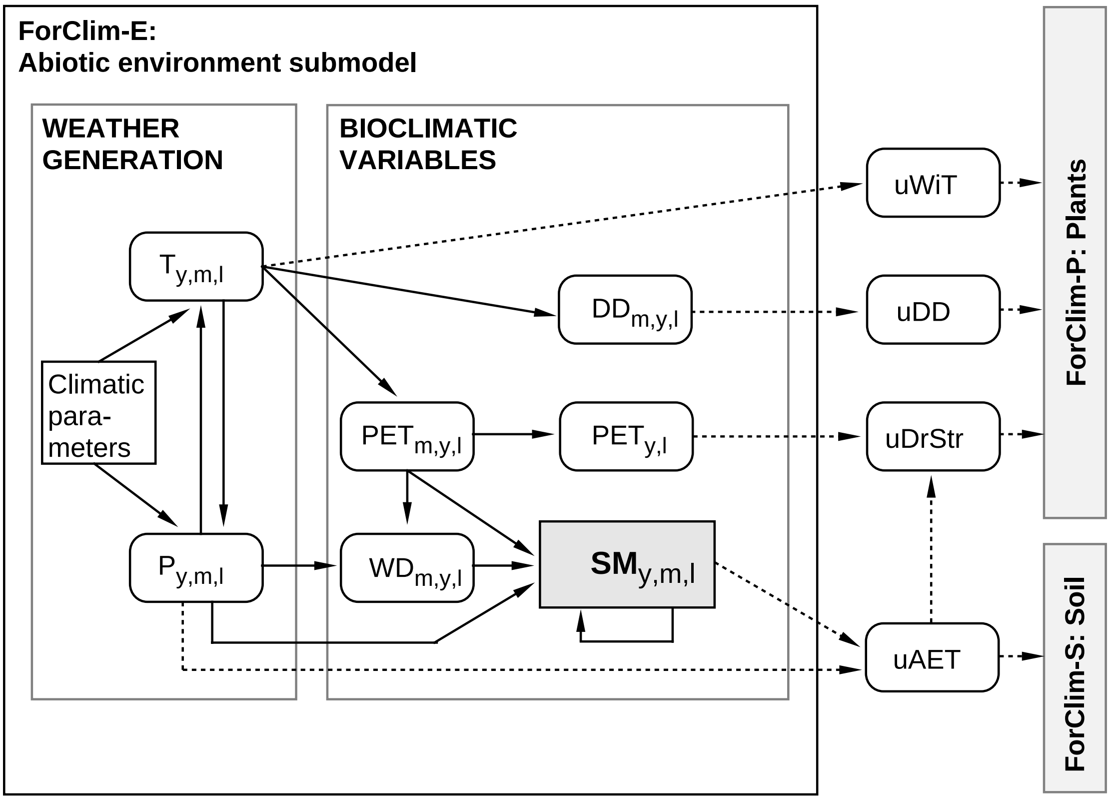


Fig. 3.4: Structure of the submodel of the abiotic environment (FORCLIM-E). The identifiers are explained in the text and in Fischlin et al. (1994).

The environment submodel is divided in two parts (Fig. 3.4): (1) The generation of monthly weather data from the long-term statistical distributions, and (2) the translation of monthly weather data into *bioclimatic variables*, i.e. environmental scalars that influence the establishment and growth of trees and the decomposition of soil organic matter (cf. Prentice & Helmisaari 1991, Prentice et al. 1993).

GENERATION OF WEATHER DATA

The monthly means of temperature ($T_{m,y,l}$) and precipitation ($P_{m,y,l}$) are sampled stochastically from their respective long-term statistics (Fig. 3.4). It is assumed that both variables are distributed normally around their long-term means. This assumption is met better for temperature than for precipitation (Fliri 1974). In principle, a different statistical distribution (such as the γ distribution, Bonan et al. 1990) could be fitted on a site-by-site basis to the precipitation data, and sampling from such a distribution would provide more realistic precipitation data for the current climate. However, there is no evidence that the assumption of normality of monthly precipitation sums falls short relative to the sensitivity of forest gap models; moreover, all the parameters of more complicated distributions probably change with a changing climate, and it is more difficult to generate consistent scenarios for the parameters of complicated distributions than for those of the simple normal distribution. Thus, the assumption of normality is used for sampling both temperature and precipitation data in FORCLIM-E.

Warm, sunny summer months tend to be dry, whereas cool, cloudy ones often are wet. In other words, the temperature and precipitation data are cross-correlated. It may be important to take this phenomenon into account when modelling the water balance of the soil: For example, if the evaporative demand in a given month is large due to high temperatures, then the soil water content will be reduced to a larger extent if there is little rainfall at the same time; this effect is not negligible even if the correlation is moderate ($|r| < 0.64$, cf. Appendix III), which was used as an argument against modelling the cross-correlation (Kräuchi & Kienast 1993). Thus the cross-correlation between monthly temperature and precipitation data is modelled explicitly in FORCLIM (Fig. 3.4).

BIOCLIMATIC VARIABLES

Winter minimum temperature (uWiT)

Based on the global data set by Müller (1982), Prentice et al. (1992) showed that there is a good correlation between the absolute minimum temperature and the average temperature of the coldest month (January). In several models (Pastor & Post 1985, Solomon 1986, Prentice et al. 1992) such correlations were used to estimate the winter minimum temperature from the actual mean January temperature. However, the month with the lowest *long-term* mean temperature is not necessarily the month with the lowest *actual* mean temperature. Therefore the FORCLIM model uses the minimum of the actual mean temperature of the winter months December, January, and February as a proxy for the winter minimum temperature (Fig. 3.4).

Degree-days (uDD)

The concept of degree-days, i.e. a linear dependency of the growth rate on temperature above a threshold temperature, was used in most forest gap models developed to date (Shugart 1984). The tree species native to the European Alps have rather similar threshold temperatures of net photosynthesis (Lyr et al. 1992); it is therefore justified to use a general threshold temperature, which is independent of the single tree species. By doing so, the annual sum of degree-days becomes an abiotic index of the forest environment (Fig. 3.4).

Evapotranspiration (uAET) and drought stress (uDrStr)

There are many models available to calculate evapotranspiration and the water balance (e.g. Penman 1948, Thornthwaite & Mather 1957; see review in Mintz & Serafini 1992). The more accurate methods require many weather variables with a high temporal resolution. The model by Thornthwaite & Mather (1957), although an entirely empirical approach, is especially useful because it is based on monthly mean temperatures ($T_{m,y,l}$) and monthly precipitation sums ($P_{m,y,l}$) only, and it provides a reasonable estimate of potential and actual evapotranspiration (PET and AET, respectively). Correspondingly, it was used in many empirical and modelling studies (e.g. Müller 1982, Meentemeyer et al. 1985, Mintz & Serafini 1992) as well as in most forest gap models (Shugart 1984). In FORCLIM, this approach is used as well.

In the Thornthwaite & Mather model, actual evapotranspiration is assumed to be independent of the vegetation cover and is based on an average leaf area index. Since canopy openings caused by the death of single trees are relatively small (<0.1 ha), their effect on evapotranspiration rates is moderate, which justifies this simplicistic assumption (Fig. 3.4).

3.3 Model equations

For the formulation of the model equations, the following notational conventions are used: First, the symbols used in the mathematical model correspond to the identifiers in the simulation model (section 3.5). Second, the first letter of a mathematical symbol denotes its type (Swartzman & Kaluzny 1987), i.e. u stands for input/output variables (cf. Tab. 3.1), k – model parameters, and g – auxiliary variables. State variables have no prefix. Third, the subscripts s and c are used to denote species-specific and cohort-specific variables, respectively.

Tab. 3.1: Symbols used for input/output variables of the FORCLIM model. “Eq.” denotes the number of the equation where the variables are calculated.

Link	Symbol	Unit	Explanation	Eq.
FORCLIM-E → P	uWiT	°C	minimum of current Dec, Jan, Feb temperatures	3.71
	uDD	°C·d	annual sum of degree-days	3.72
	uDrStr	–	drought stress index	3.75
FORCLIM-E → S	uAET	$mm \cdot yr^{-1}$	actual evapotranspiration	–1)
FORCLIM-P → S	uFL_i	$t \cdot ha^{-1}$	three types of foliage litter (i = 1,2,3)	3.43
	uTL	$t \cdot ha^{-1}$	twig litter	3.44
	uRL	$t \cdot ha^{-1}$	root litter	3.45
	uWL	$t \cdot ha^{-1}$	woody litter	3.46
FORCLIM-S → P	uAvN	$kg \cdot ha^{-1}$	nitrogen availability	3.62

1) the calculation of this variable was described in detail by Fischlin et al. (1994).

3.3.1 FORCLIM-P: A forest gap model of tree population dynamics

FORCLIM-P is formulated as a discrete time model with a time step (Δt) of one year (“Sequential Machine”, Zeigler 1976; cf. section 2.1). Each tree cohort is described by two state variables (Fig. 3.2). The dimension of the state vector of FORCLIM-P varies with time because tree cohorts are established depending on the environmental conditions, and they are removed again when their last member dies. To derive an estimate of the maximum size of the state vector, we generously assume that one cohort of every species is established every 10th year (cf. Eq. 3.7 and Tab. 3.12), and that the life expectancy of tree cohorts is 100 years. Thus the state vector has a dimension of not more than $20 \cdot n$, where n is the number of species incorporated in the model. For European conditions where about 30 species have to be considered, the dimension of the state vector of FORCLIM-P may be as large as 600; however, typically it is less than 100.

TREE ESTABLISHMENT

All the ecological establishment factors are formulated as boolean variables that allow (value = 1) or prevent (value = 0) establishment. The symbols used in the establishment submodel of FORCLIM-P are given in Tab. 3.2.

Winter temperature

The influence of low winter temperatures on sapling establishment rates is formulated according to the descriptions by Ellenberg (1986), Woodward (1987), and Prentice & Helmisaari (1991), i.e. sapling establishment is assumed to be impossible if winter temperature (uWiT) is below a species-specific threshold temperature ($kWiT_S$):

$$gWFlag_S = \begin{cases} 0 & uWiT < kWiT_s \\ 1 & \text{else} \end{cases} \qquad (3.1)$$

Tab. 3.2: Symbols used in the establishment submodel of FORCLIM-P. “Eq.” denotes the number of the equation where state and auxiliary variables are calculated.

Factor	Symbol	Unit	Explanation	Eq.
Winter temperature	$gWFlag_S$	–	boolean auxiliary variable	3.1
	$kWiT_S$	°C	minimum winter temperature tolerated	
Light availability	gLFlag	–	boolean auxiliary variable	3.2
	gAL_0	%/100	light availability at forest floor (height 0 meters)	3.18
	$kThres_S$	%/100	threshold for establishment	3.3
	$kL_{y,s}$	[1..9]	light requirement of tree saplings	
Browsing	$gBFlag_S$	–	boolean auxiliary variable	3.4
	$gBrP_S$	%/100	mortality due to browsing	3.4
	$kBrow_S$	[1..3]	browsing susceptibility	
	kBrPr	[0..10]	browsing intensity	
Degree-day range	$gDFlag_S$	–	boolean auxiliary variable	3.5
	$kDDMin_S$	°C·d	minimum annual degree-day sum	
	$kDDMax_S$	°C·d	maximum annual degree-day sum	
Immigration	$gIFlag_S$	–	boolean auxiliary variable	3.6
	$kImmYr_S$	yr	simulation time of first occurrence of the species	
Establishment	$gP_{Est,s}$	%/100	probability of establishment	3.7
	$kEstP_S$	%/100	establishment probability parameter	
	kEstNr	$\#\cdot m^{-2}\cdot yr^{-1}$	maximum rate of tree establishment	
	kInitDBH	cm	initial diameter at breast height of tree saplings	
	kPatchSize	m^2	size of a forest patch	

Light availability

If available light at the forest floor (gAL_0, calculated according to Eq. 3.18) drops below a species-specific threshold ($kThres_S$) defined as a fraction of full sunlight, sapling establishment is prevented according to Eq. 3.2 & 3.3:

$$gLFlag_S = \begin{cases} 0 & gAL_0 < kThres_S \\ 1 & \text{else} \end{cases} \tag{3.2}$$

where the species-specific threshold $kThres_S$ is calculated according to Ellenberg (1986, Fig. 3.5 left) based on the parameter $kL_{y,s}$, which denotes the light requirements of saplings ("young trees") on a nominal scale in the range [1..9]:

$$kThres_S = \begin{cases} 0.025\cdot(kL_{y,s}-1) & kL_{y,s} < 5 \\ 0.1\cdot kL_{y,s} - 0.4 & \text{else} \end{cases} \tag{3.3}$$

Browsing pressure

The constant browsing intensity simulated in the FORECE model (Kienast 1987) was modified in a simple way which allows to explore the possible effects of varying browsing intensities on sapling establishment rates (Fig. 3.5 right):

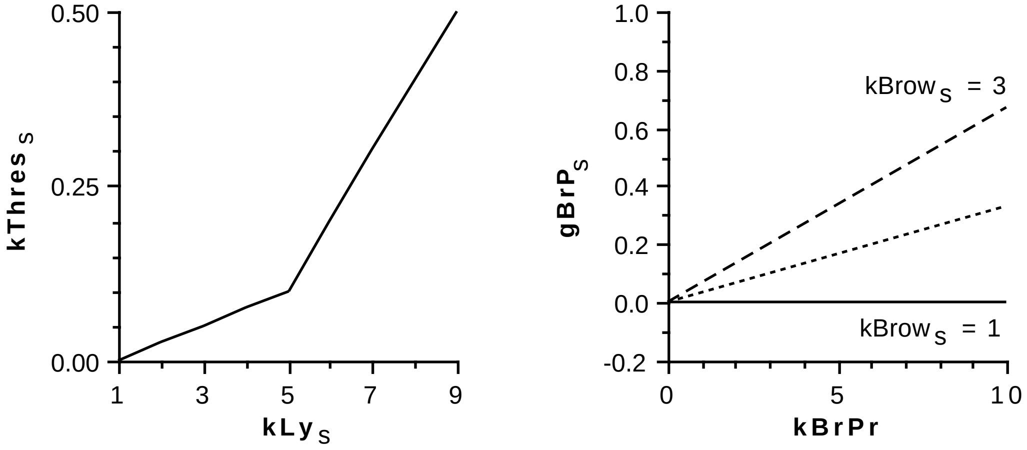


Fig. 3.5: Factors influencing sapling establishment. Left: The threshold parameter $kThres_S$ (% of full sunlight) is a function of the species parameter $kL_{y,S}$ (Eq. 3.3). Right: The probability that establishment is prevented ($gBrP_S$) depends on browsing pressure (kBrPr) and the susceptibility to browsing of the tree species ($kBrow_S$).

$$\mathrm{gBFlag_S} = \begin{cases} 0 & \mathrm{U(0,1)} < \mathrm{gBrP_S} = (\mathrm{kBrow_S} - 1) \cdot \dfrac{\mathrm{kBrPr}}{30} \\ 1 & \mathrm{else} \end{cases} \tag{3.4}$$

where U(0,1) is a random number with uniform distribution in the range [0…1], $\mathrm{kBrow_S}$ is the species-specific browsing tolerance, and kBrPr is browsing pressure on a nominal scale between 0 (no browsing) and 10 (heavy browsing). The sapling mortality ($\mathrm{gBrP_S}$) thus increases linearly with increasing browsing intensity, and the maximum mortality ranges from 0 to 66.7% depending on the parameter $\mathrm{kBrow_S}$ (Fig. 3.5 right). The current quantification of this mortality is entirely speculative because a quantitative basis could not be found in the literature (e.g. Näscher 1979, Eiberle & Nigg 1986, Liss 1988, Albrecht 1989). However, latest research (Rechsteiner 1993, Kräuchi 1994) may allow for a more reliable formulation of this environmental filter controlling sapling establishment. Moreover, the browsing pressure parameter kBrPr could be replaced by an input variable uBrPr, thus providing the link to models of game population dynamics (e.g. Schröder 1976, Buchli 1979).

Degree-days

Sapling establishment is assumed to be impossible when the annual sum of degree-days does not conform to the degree-day requirements of the tree species, which are defined by the parameters $\mathrm{kDDMin_S}$ and $\mathrm{kDDMax_S}$ (Shugart 1984):

$$\mathrm{gDFlag_S} = \begin{cases} 1 & \mathrm{kDDMin_S} < \mathrm{uDD} < \mathrm{kDDMax_S} \\ 0 & \mathrm{else} \end{cases} \tag{3.5}$$

Immigration

The last factor that modifies sapling establishment rates is introduced to simulate simple immigration scenarios of the tree species:

$$\mathrm{gIFlag_S} = \begin{cases} 1 & \mathrm{kImmYr_S} > t \\ 0 & \mathrm{else} \end{cases} \tag{3.6}$$

where $\mathrm{kImmYr_S}$ is a parameter denoting the first simulation year where the species may establish, and t is the current simulation time. The choice of $\mathrm{kImmYr_S}$ depends on the hypothesis to be tested, such as a specific immigration scenario or the complete exclusion of a given species from a simulation experiment.

Overall establishment probability and number of established saplings

The above environmental filters (Eq. 3.1-3.6) are multiplied with each other, so that establishment of saplings is possible only if they all have a value of 1 (Eq. 3.7). The fact that sapling establishment also depends on factors not considered above is taken into account by reducing the establishment probability ($gP_{Est,s}$) by the parameter kEstP:

$$gP_{Est,s} = kEstP \cdot gWFlag_s \cdot gLFlag_s \cdot gBFlag_s \cdot gDFlag_s \cdot gIFlag_s \tag{3.7}$$

The occurrence of sapling establishment is determined by Monte Carlo techniques based on $gP_{Est,s}$. When establishment takes place, the number of saplings is calculated using a random number with uniform distribution in the range [1…kEstNr·kPatchSize], where kEstNr is the maximum sapling establishment rate, and kPatchSize is the size of a forest patch (Shugart 1984, Kienast 1987). The diameter at breast height of new saplings is specified by the kInitDBH parameter.

TREE GROWTH

Derivation of an equation for tree growth under optimal conditions

To derive a difference equation for the diameter growth of trees, most previous forest gap models started from the following simple assumption on tree volume increment (Botkin et al. 1972a,b):

$$\frac{\Delta\left(D_c^2 \cdot gH_c\right)}{\Delta t} = kR \cdot gL_c \cdot \left(1 - \frac{gH_c \cdot D_c}{kHm_s \cdot kDm_s}\right) \tag{3.8}$$

where Δt is the discrete time step (the symbols used in the growth submodel are listed in Tab. 3.3). The structure of this equation implies that volume increment ($\Delta D_C^2 \cdot gH_C$) is a linear function of leaf area (gL_C), and that there is some *“cost associated with tree size that decreases tree growth”* (Shugart 1984, p. 50). From Eq. 3.8 an equation of the annual diameter growth rate can be obtained (for the derivation, see Botkin et al. 1972a,b):

$$\frac{\Delta D_c}{\Delta t} = \frac{kG_s \cdot D_c \cdot \left(1 - \frac{gH_c \cdot D_c}{kHm_s \cdot kDm_s}\right)}{274 + 3 \cdot kB_{2,s} \cdot D_c + 4 \cdot kB_{3,s} \cdot D_c^2} \tag{3.9}$$

In most forest gap models Eq. 3.9 is used to predict optimum diameter growth (Shugart 1984, Botkin 1993). However, the formulation of Eq. 3.8 conceals the assumptions about the *“cost associated with tree size”*, i.e. respiration. It can be hypothesized that maintenance respiration should be proportional e.g. to stem volume or stem surface (Kinerson 1975); reconstructing from Eq. 3.8 an equation where the formulation of respiration is explicit (see Moore 1989), we obtain

$$\frac{\Delta V_c}{\Delta t} = kR \cdot gL_c - kS \cdot V_c \cdot D_c \tag{3.10}$$

Thus, in the conventional growth equation maintenance respiration is assumed to be proportional to a power higher than tree volume, which is not realistic. In view of this limitation, Moore (1989) developed an equation for tree diameter increment from a simple carbon budget of the tree: Considering biomass (volume) increment and assuming that (a) gross photosynthesis is proportional to leaf area gL_c and (b) respiration is proportional to stem volume V_c, we can write

$$\frac{\Delta V_c}{\Delta t} = kR \cdot gL_c - kS \cdot V_c \tag{3.11}$$

Next we assume the following allometric relationships:

(c) $gL_c = k_1 \cdot D_c^2$ (Whittaker & Marks 1975) (3.12)
(d) $gH_c = 137 + kB_{2,s} \cdot D_c + kB_{3,s} \cdot D_c^2$ (Ker & Smith 1955) (3.13)
(e) $V_c = k_2 \cdot D_c^2 \cdot gH_c$ (the volume of a cone) (3.14)

Using these assumptions, the following equation for diameter increment is obtained (for the details of the derivation, see Moore 1989):

$$\boxed{\frac{\Delta D_c}{\Delta t} = \frac{kG_s \cdot D_c \cdot \left(1 - \frac{gH_c}{kHm_s}\right)}{274 + 3 \cdot kB_{2,s} \cdot D_c + 4 \cdot kB_{3,s} \cdot D_c^2} \cdot f(e)_c \qquad (3.15)}$$

where $f(e)_c$ is a multiplier used to reduce maximum growth according to the environmental constraints described below. This equation has a form similar to the conventional equation (Eq. 3.9), but its assumptions conform more to biological expectations. Thus it is used to predict the diameter increment in ForClim-P (Fig. 3.6).

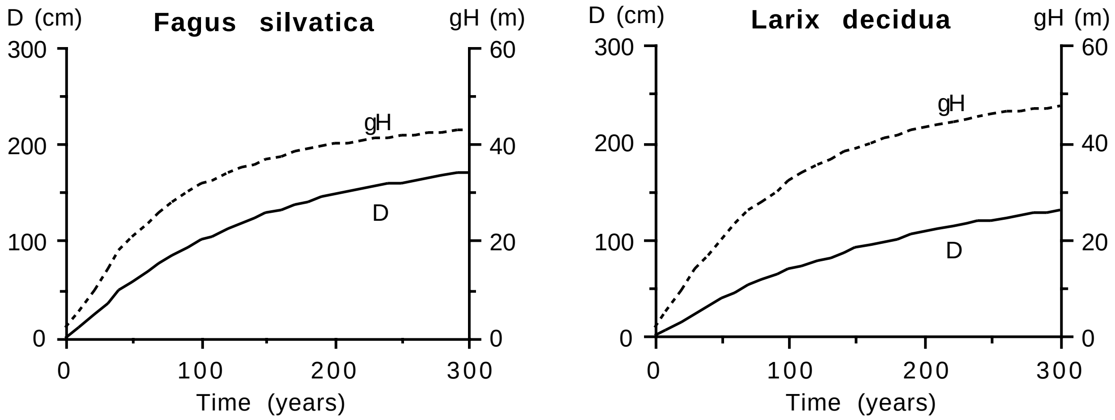


Fig. 3.6: The maximum growth equation (Eq. 3.15) simulated for beech *(Fagus silvatica*, left) with kG_S = 191 cm/year, kHm_S = 45 m, and kDm_S = 225 cm, and larch *(Larix decidua*, right) with kG_S = 170 cm/year, kHm_S = 52 m, and kDm_S = 185 cm. $D_c(0)$ is 1.27 cm, and the discrete time step (Δt) is one year.

Finally, from the evaluation of Eq. 3.13 when $\partial gH_c/\partial D_c = 0$ at $gH_c = kHm_S$ and $D_c = kDm_S$, the parameters $kB_{2,s}$ and $kB_{3,s}$ can be expressed as functions of maximum height and maximum diameter alone:

$$kB_{2,s} = \frac{2 \cdot (kHm_s - 137)}{kDm_s} \tag{3.16}$$

$$kB_{3,s} = -\frac{kB_{2,s}}{2 \cdot kDm_s} \tag{3.17}$$

Light growth factor

The calculation of the light growth factor follows the descriptions by Botkin et al. (1972a,b) and Shugart (1984): Beer's extinction law is used to calculate the available light at the height of cohort c as a function of leaf area index:

$$gAL_{gHc} = e^{-\, kLAtt \cdot gCumLA_{gHc}} \tag{3.18}$$

where $gCumLA_{gHc}$ is the cumulative leaf area index at the height of cohort c (Eq. 3.19), summed over all cohorts based on the relationships given in Eq. 3.20 & 3.21 for calculating the double-sided foliage area ($gFolA_c$) from foliage dry weight ($gFolW_c$) (Burger 1945-1953):

$$gCumLA_{gHc} = \frac{1}{kPatchSize} \cdot \sum_{i \mid gH_i \geq gH_c}^{n} gFolA_i \qquad (3.19)$$

where kPatchSize is the size of the forest patch, and n is the number of trees present on the patch.

Tab. 3.3: Symbols used in the growth submodel of FORCLIM-P. Bold face denotes state variables.

Factor	Symbol	Unit	Explanation	Eq.
Maximum growth equation	$\mathbf{D_c}$	cm	diameter at breast height	3.15
	gH_c	cm	tree height	3.13
	kG_s	$cm\cdot yr^{-1}$	growth rate parameter	
	kHm_s	cm	maximum tree height	
	kDm_s	cm	maximum diameter at breast height	
	$kB_{2,s}$	–	allometric parameter for relating gH to D	3.16
	$kB_{3,s}$	cm^{-1}	allometric parameter for relating gH to D	3.17
	$f(e)_c$	–	effect of environment on max. growth rate	3.28
	$\mathbf{V_c}$	cm^3	tree volume$^{1)}$	3.11
	gL_c	cm^2	foliage area$^{1)}$	
	kR	$cm\cdot yr^{-1}$	photosynthesis rate parameter$^{1)}$	
	kS	yr^{-1}	respiration rate parameter$^{1)}$	
	k_1, k_2	–	constants of proportionality$^{1)}$	
Light growth factor	$gALGF_c$	–	growth factor	3.24
	$gL_{1,c}$, $gL_{9,c}$	–	light response curves	3.22f.
	gAL_H	%/100	light availability at height H	3.18
	$gCumLA_H$	$m^2\cdot m^{-2}$	cumulative leaf area index at height H	3.19
	$gFolW_c$	kg	foliage weight	3.22
	$gFolA_c$	m^2	foliage area	3.20
	kLAtt	–	light attenuation coefficient	
	$kA_{1,s}$	$kg\cdot cm^{-1}$	allometric parameter for foliage weight	
	$kA_{2,s}$	–	allometric parameter for foliage weight	
	$kC_{1,s}$	%/100	dry to wet weight ratio of foliage	
	$kC_{2,s}$	$m^2\cdot kg^{-1}$	foliage area per unit foliage weight	
	$sType_s$	–	grouping parameter (cf. Tab. 3.10)	
	$kL_{a,s}$	[1..9]	shade tolerance of adult trees	
	kPatchSize	m^2	size of a forest patch	
Degree-day growth factor	$gDDGF_s$	–	growth factor	3.25
	$kDDMin_s$	°C·d	minimum annual degree-day sum	
	$kDDMax_s$	°C·d	maximum annual degree-day sum	
Soil moisture growth factor	$gSMGF_s$	–	growth factor	3.26
	$kDrT_s$	[0..1]	drought tolerance parameter	
Soil nitrogen growth factor	$gSNGF_s$	–	growth factor	3.27
	$kN_{1,kNTols}$	–	nitrogen response function parameter	
	$kN_{2,kNTols}$	$kg\cdot ha^{-1}\cdot yr^{-1}$	nitrogen response function parameter	
	$kNTol_s$	[1..3]	nitrogen tolerance parameter	

1) used for the derivation of the maximum growth equation only; not used in the simulation model.

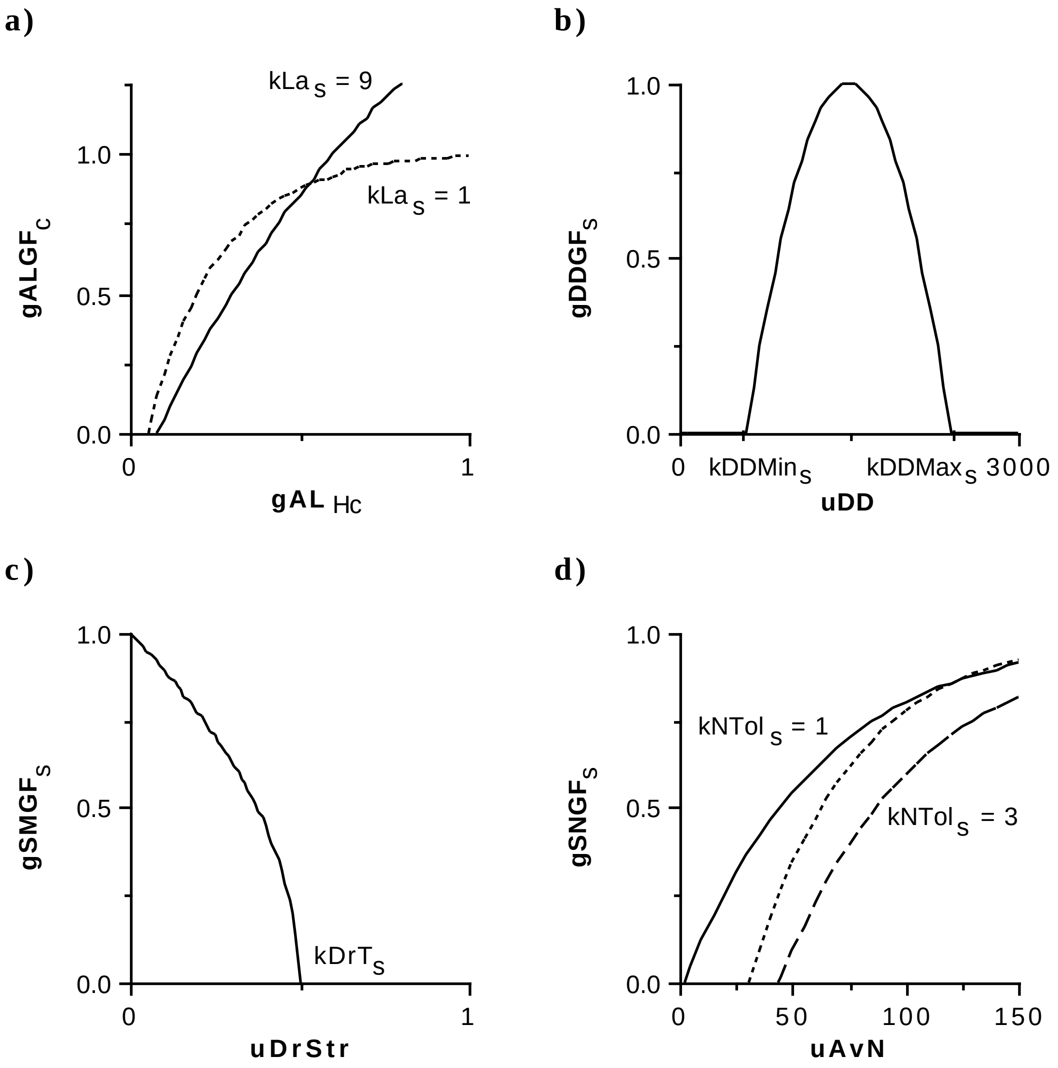


Fig. 3.7: The four growth factors of the FORCLIM-P submodel:
a) available light growth factor ($gALGF_C$); b) degree-day growth factor ($gDDGF_S$);
c) soil moisture growth factor ($gSMGF_S$); d) soil nitrogen growth factor ($gSNGF_S$).

$$gFolA_c = \frac{kC_{2,s}}{kC_{1,s}} \cdot gFolW_c \qquad (3.20)$$

$$gFolW_c = kC_{1,s} \cdot kA_{1,s} \cdot D_c^{kA_{2,s}} \qquad (3.21)$$

where the $kA_{i,s}$ and $kC_{i,s}$ are allometric parameters. Eq. 3.22 & 3.23 describe the light response function of shade-tolerant ($gL_{1,c}$) and shade-intolerant ($gL_{9,c}$) tree species, respectively, as a function of light availability (gAL, Botkin et al. 1972a,b):

$$gL_{1,c} = 1 - e^{-4.64 \cdot (gAL_{gHc} - 0.05)} \qquad (3.22)$$

$$gL_{9,c} = 2.24 \cdot \left(1 - e^{-1.136 \cdot (gAL_{gHc} - 0.08)}\right) \tag{3.23}$$

Finally, the light growth factor of the tree cohort ($gALGF_c$) is calculated by interpolation between the above two functions, depending on $kL_{a,s}$, a parameter denoting the shade tolerance of adult trees (Fig. 3.7a):

$$gALGF_c = MAX\left(gL_{1,c} + (kL_{a,s}-1) \cdot \frac{gL_{9,c} - gL_{1,c}}{8}\ ,\ 0\right) \tag{3.24}$$

Degree-day growth factor

The effect of degree-days on tree growth ($gDDGF_s$) is modelled according to the parabolic equation proposed by Botkin et al. (1972a,b) (Fig. 3.7b):

$$gDDGF_s \ = \ MAX\left(4 \cdot \frac{(uDD - kDDMin_s) \cdot (kDDMax_s - uDD)}{(kDDMax_s - kDDMin_s)^2}\ ,\ 0\right) \tag{3.25}$$

Soil moisture growth factor

Bassett (1964) found that the basal area increment of trees is related linearly to the amount of drought stress they experience; thus diameter increment can be expected to be related to drought stress (uDrStr) by a square root function. The latter relationship was incorporated in many forest gap models in order to represent the influence of drought on tree growth ($gSMGF_S$, e.g. Pastor & Post 1985, Kienast 1987), taking into account the maximum drought tolerance of the species ($kDrT_S$, Prentice & Helmisaari 1991; Fig. 3.7c):

$$gSMGF_s = \sqrt{MAX\left(1 - \frac{uDrStr}{kDrT_s}\ ,\ 0\right)} \tag{3.26}$$

Soil nitrogen growth factor

The equations by Aber et al. (1979), which are based on the fertilizer trials by Mitchell & Chandler (1939), are used to define the influence of nitrogen availability (uAvN) on tree growth rate ($gSNGF_S$, Pastor & Post 1985):

$$gSNGF_s = MAX\left(1 - e^{kN_{1,kNTols} \cdot (uAvN - kN_{2,kNTols})}\ ,\ 0\right) \tag{3.27}$$

where $kN_{1,kNTol_S}$ and $kN_{2,kNTol_S}$ are parameters with different values depending on $kNTol_S$, the nitrogen tolerance class of the tree species (Fig. 3.7d).

Growth reduction by unfavorable environmental conditions

In section 3.1 it was noted that both the multiplication of all the growth factors with each other (e.g. Botkin et al. 1972a,b) as well as “Liebig's Law” (Kienast 1987) are partly unsatisfactory for calculating the overall growth reduction in forest gap models. Ideally, such a procedure should fulfil the following requirements:

1) The numerical value of each single growth factor should affect tree growth, not only the ranking of the growth factors; too much information on the environmental conditions is lost if only the smallest growth factor is considered.

2) Tree growth should not converge to zero when an increasing number of non-zero growth factors is considered.

Neither the multiplicative nor Liebig's approach fulfil both requirements. As an alternative, the geometric mean could be used to combine the growth factors. However, this measure has a strong smoothing effect; specifically, low growth factors are smoothed too much. For example, three growth factors with a value of 0.5 each and one factor with a value of 0.01, i.e. almost zero growth, result in an overall growth factor still amounting to 0.19, which is too high. Thus a modified geometric mean as given in Eq. 3.28 was formulated; it conforms to the above two requirements, but it smoothes the growth factors less than the unmodified geometric mean:

$$f(e)_c = \sqrt[3]{gALGF_c \cdot gDDGF_s \cdot gSMGF_s \cdot gSNGF_s} \tag{3.28}$$

Besides the third root, the square root was evaluated as well. The FORCLIM-P model appeared to be little sensitive to the choice of the square or third root. Thus Eq. 3.28 was used in the model.

TREE MORTALITY

As stated above, FORCLIM-P models the establishment and growth of tree cohorts, not of individual trees. However, the mortality functions described below are evaluated for each member of each tree cohort individually, i.e. the mortality probability does not refer to all the members of a tree cohort simultaneously. The symbols used in the mortality submodel are given in Tab. 3.4.

Age-related mortality

The age-related probability of mortality is calculated by assuming that the annual tree mortality rate ($gP_{m1,s}$) is constant throughout tree life, which corresponds to the negative exponential curve for survivorship (Harcombe 1987, Eq. 3.29):

$$gS_{t,s} = e^{-gP_{m1,s} \cdot t} \tag{3.29}$$

where $gS_{t,s}$ is the percentage of survivors of species s at time t. The value of $gP_{m1,s}$ can be determined by assuming that only a small fraction kP of the population reaches the age kAm_s (Eq. 3.30):

$$gP_{m1,s} = \frac{-Ln(gS_{t,s})}{t} = \frac{-Ln(kP)}{kAm_s} = \frac{kDeathP}{kAm_s} \tag{3.30}$$

Assuming kP = 0.01 yields kDeathP = 4.605, which is the default value of this parameter seen throughout the literature (Botkin et al. 1972a,b, Shugart 1984).

Tab. 3.4: Symbols used in the mortality submodel of FORCLIM-P. Bold face denotes state variables.

Factor	Symbol	Unit	Explanation	Eq.
Age-dependent mortality	$gP_{m1,s}$	%/100	mortality probability	3.30
	kDeathP	–	mortality probability coefficient	
	kAm_s	yr	maximum tree age	
	gS_t	%/100	fraction of population surviving up to time t[1)]	
	kP	%/100	fraction of population that reaches kAm_s[1)]	
Stress-induced mortality	$gP_{m2,c}$	%/100	mortality probability	3.31
	$\mathbf{SGr_c}$	–	number of years a cohort has grown slowly	3.32
	$f(e)_c$	–	effect of environment on max. growth rate	3.28
	kMinAbsInc	$cm \cdot yr^{-1}$	minimum absolute growth requirement	
	kMinRelInc	–	minimum relative growth requirement	
	kSGrYrs	yr	number of years a tree can grow slowly without being subject to stress-induced mortality	
	kSlowGrP	%/100	mortality rate of slow-growing trees	
Extrinsic disturbances	gP_{m3}	%/100	mortality probability	3.33
	kDistP	%/100	probability of occurrence of a disturbance	
Total mortality probability	gP_m	%/100	probability that a tree dies in a given year	3.34

1) used for the derivation of the age-dependent mortality; not used in the simulation model.

Stress-induced mortality

Analogous to the age-related mortality, the increased mortality rate induced by environmental stress ($gP_{m2,c}$) is based on the assumption that only a small fraction of trees will survive a given number of years when they are subject to such stress (Shugart 1984, Pastor & Post 1985, Kienast 1987, Solomon & Bartlein 1993):

$$gP_{m2,c} = \begin{cases} kSlowGrP & SGr_c > kSGrYrs \\ 0 & else \end{cases} \tag{3.31}$$

where SGr_c is the the number of consecutive years the cohort's diameter has increased less than 10% of the maximum diameter increment (kMinRelInc) or less than 0.3 mm (kMinAbsInc). Hence, SGr_c provides a memory for past environmental stress; therefore it is a state variable (Eq. 3.32):

$$SGr_c(t+1) = \begin{cases} SGr_c(t) + 1 & f(e)_c < kMinRelInc \;\vee\; \frac{\Delta D_c}{\Delta t} < kMinAbsInc \\ 0 & else \end{cases} \tag{3.32}$$

where t denotes the discrete time in years.

Disturbance-related mortality

As noted in section 3.1, the disturbance-related mortality is formulated in a simple manner, i.e. the probability that the trees on the patch are killed by a disturbance is regulated by the model parameter kDistP (Eq. 3.33):

$$gP_{m3} = kDistP \tag{3.33}$$

Overall mortality probability

Eq. 3.34 describes the calculation of the overall mortality probability for each tree and each year (gP_m). The trees are subject to the disturbance-related mortality first (gP_{m3}); if they survive, they may die from the age-related mortality ($gP_{m1,s}$) and, finally, from the stress-induced mortality rate ($gP_{m2,c}$). In the simulation model, the overall mortality probability (gP_m) is determined for each tree using Monte Carlo techniques.

$$gP_m = gP_{m3} + (1 - gP_{m3})\cdot(gP_{m1,s} + [1 - gP_{m1,s}]\cdot gP_{m2,c}) \tag{3.34}$$

LITTER PRODUCTION

Two sources of litterfall are distinguished in FORCLIM-P. First, there is the annual production of litter by living trees, i.e. roots, twigs, and leaves. Second, there is the litter accumulating when a tree dies, which includes the above litter categories plus stemwood (Pastor & Post 1985). Litter production constitutes the output variables of the FORCLIM-P model (Fig. 3.2). The symbols used for calculating litter production are listed in Tab. 3.5.

Litter production of living trees

The quantity of foliage litter produced annually by each tree cohort (uFLL) is calculated from tree foliage weight ($gFolW_C$). It is assumed that each species produces leaf litter of one given quality; thus the leaf litter from a tree cohort is assigned to the appropriate group of litter according to the discrete parameter kLQ_S (Pastor & Post 1985):

$$uFLL_{kLQ,\,c} = gFolW_c \cdot \frac{nAlive_c}{kFRT_s} \cdot kAshFree \tag{3.35}$$

where nAlive is the number of trees alive in the cohort, $kFRT_S$ is the average foliage retention time of the species, and kAshFree is a conversion factor to determine the ash-free weight of litter, i.e. its organic dry matter content.

Twig litter (uTLL) is calculated based on a field study by Christensen (1977, as cited in Pastor & Post 1985), assuming that twig litterfall is proportional to basal area:

$$uTLL_c = \frac{\pi}{4} \cdot D_c^2 \cdot kConv \cdot nAlive_c \cdot kAshFree \tag{3.36}$$

where kConv is a factor to convert basal area [cm^2] to twig litter [kg].

Only few measurements are available on the turnover of root litter (uRLL) in forest ecosystems (e.g. Waring & Schlesinger 1985, Kimmins 1987); thus roots were assumed to have a turnover rate proportional to the turnover rate of foliage (Pastor & Post 1985):

$$uRLL_c = kRSR \cdot uFLL_{kLQ,c} \tag{3.37}$$

Tab. 3.5: Symbols used for calculating litter production in FORCLIM-P.

Factor	Symbol	Unit	Explanation	Eq.
General	kAshFree	%/100	organic matter content of dry weight	
	$nAlive_c$	–	number of living trees per cohort	
	$nDead_c$	–	number of dead trees per cohort	
	nTC	–	number of tree cohorts present on a patch	
Leaf litter production	$uFLL_{kLQ,c}$	kg	foliage litter from living trees (kLQ = 1,2,3)	3.35
	$uFLD_{kLQ,c}$	kg	foliage litter from dead trees (kLQ = 1,2,3)	3.38
	$gFolW_c$	kg	foliage weight	3.21
	$sType_s$	–	grouping parameter (cf. Tab. 3.10)	
	$kFRT_s$	yr	average time of foliage retention	
	kLQ_s	[1..3]	leaf litter quality (1 = fast, 3 = slowly decaying)	
Twig litter production	$uTLL_c$	kg	twig litter from living trees	3.36
	$uTLD_c$	kg	twig litter from dead trees	3.39
	kConv	$kg \cdot cm^{-2}$	conversion factor basal area → twig litter	
Root litter production	$uRLL_c$	kg	root litter from living trees	3.37
	$uRLD_c$	kg	root litter from dead trees	3.40
	kRSR	–	root:shoot ratio of litter production	
Wood litter production	$uWLD_c$	kg	wood litter from dead trees	3.41
	$gSBio_c$	kg	dry stemwood biomass	3.42

The data base for European tree species was found to be too small to allow for species-specific root:shoot ratios (kRSR). Hence a common root:shoot ratio was assumed to be valid for all species (Waring & Schlesinger 1985).

Litter from dead trees

The same rationale as above is applied to calculate foliage litter (uFLD), twig litter (uTLD), and root litter (uRLD) of dead trees (Eq. 3.38-3.40):

$$uFLD_{kLQ,\,c} = gFolW_c \cdot nDead_c \cdot kAshFree \tag{3.38}$$

$$uTLD_c = \frac{\pi}{4} \cdot D_c^2 \cdot kConv \cdot nDead_c \cdot kAshFree \tag{3.39}$$

$$uRLD_c = kRSR \cdot uFLD_{kLQ,c} \tag{3.40}$$

where $nDead_c$ is the number of dead trees in cohort c. The amount of woody litter (uWLD) produced by the dead trees of a cohort is calculated from stemwood biomass ($gSBio_c$) based on allometric relationships from Burger (1945-53), Sollins et al. (1973), and Woods et al. (1991):

$$uWLD_c = gSBio_c \cdot nDead_c \cdot kAshFree \quad (3.41)$$

$$gSBio_c = 0.12 \cdot D_c^{2.4} \quad (3.42)$$

Total annual litter production

The total annual litter production is calculated by summing the litter produced by each tree cohort (Eq. 3.35-3.41) over all the cohorts *(nTC* is the number of tree cohorts currently present on the patch):

$$uFL_{kLQ} = \sum_{c=1}^{nTC} uFLL_{kLQ,c} + uFLD_{kLQ,c} \qquad \text{for } kLQ = 1, 2, 3 \quad (3.43)$$

$$uTL = \sum_{c=1}^{nTC} uTLL_c + uTLD_c \quad (3.44)$$

$$uRL = \sum_{c=1}^{nTC} uRLL_c + uRLD_c \quad (3.45)$$

$$uWL = \sum_{c=1}^{nTC} uWLD_c \quad (3.46)$$

OVERVIEW OF STOCHASTIC MODEL COMPONENTS IN FORCLIM-P

The overall behaviour of forest gap models, including FORCLIM, is dominated by its stochastic components (cf. section 2.2.2), although surprisingly few components are formulated in a probabilistic way (Tab. 3.6).

Tab. 3.6: Overview of stochastic components in the FORCLIM-P submodel.

Process	Stochastic component
Establishment	• browsing by game • establishment of tree cohorts • number of saplings to be established
Mortality	• age-related mortality • stress-related mortality • disturbance-related mortality

3.3.2 FORCLIM-S: A model of the turnover of soil organic matter

Both LINKAGES (Pastor & Post 1985) and FORCLIM-S are formulated as difference equation systems with a time step (Δt) of one year. The symbols used in FORCLIM-S are listed in Tab. 3.7.

LITTER INPUT AND CREATION OF NEW LITTER COHORTS

For each of the six types of litter that are accumulated every year (Eq. 3.43–3.46), a litter cohort is created unless the amount of litter for a type is zero. These new litter cohorts are characterized by their initial organic matter content ($\mathrm{LOM_{c,init}}$, Eq. 3.47), which is required to calculate litter lignin content (Eq. 3.50), and by their nitrogen content ($\mathrm{LN_{c,init}}$, Eq. 3.48), which is calculated by assuming an average nitrogen concentration depending on the tissue type (Ellenberg 1986):

$$\mathrm{LOM_{c,init}} = \mathrm{uXL} \tag{3.47}$$

$$\mathrm{LN_{c,init}} = \mathrm{kInitN_X} \cdot \mathrm{LOM_{c,init}} \tag{3.48}$$

where LOM is litter organic matter, LN is litter nitrogen, *X* is a placeholder for F_{kLQ} (three types of foliage litter), *T* (twigs), *R* (fine roots), or *W* (stemwood), and $\mathrm{kInitN_X}$ is the initial nitrogen concentration of litter type *X*. The litter type subsequently influences the calculation of litter decay rates (Eq. 3.49) and nitrogen leaching (Eq. 3.56).

LITTER DECAY AND NITROGEN IMMOBILIZATION

For foliage and root litter, the decomposition of the organic matter (LOM) is predicted from the lignin to nitrogen ratio of the tissue (Melillo et al. 1982) and actual evapotranspiration (uAET, Meentemeyer 1978). Stemwood and twigs are assumed to decay at constant rates (Eq. 3.49). Pastor & Post (1985) derived these empirical relationships from a large body of field data by regression analysis.

$$\frac{\Delta \mathrm{LOM_c}}{\Delta t} = \begin{cases} -\left(\mathrm{k_1 + k_2 \cdot uAET - (k_3 + k_4 \cdot uAET)} \cdot \dfrac{\mathrm{gLign_c}}{\mathrm{gNMR_c}}\right) \cdot \mathrm{LOM_c} & \text{foliage \& roots} \\ -\,\mathrm{kLoss_W} \cdot \mathrm{LOM_c} & \text{stemwood} \\ -\,\mathrm{kLoss_T} \cdot \mathrm{LOM_c} & \text{twigs} \end{cases} \tag{3.49}$$

where $gLign_c$ is litter lignin content predicted according to Eq. 3.50 (Berg et al. 1985), and $gNMR_c$ is the nitrogen to organic matter ratio of the litter (Eq. 3.51).

$$gLign_c = kLignA + kLignB \cdot \frac{LOM_c}{LOM_{c,init}} \tag{3.50}$$

$$gNMR_c = \frac{LN_c}{LOM_c} \tag{3.51}$$

The lignin parameters in Eq. 3.50 are calculated from data compiled by Pastor & Post (1985, p.139):

$$kLignA = 0.4929 + 19.1784 \cdot kNC \tag{3.52}$$

$$kLignB = 0.01558 - 0.673 \cdot kLignA \tag{3.53}$$

Tab. 3.7: Symbols used in FORCLIM-S. Bold face denotes state variables.

Factor	Symbol	Unit	Explanation	Eq.
Litter decay	$\mathbf{LOM_c}$	$t \cdot ha^{-1}$	organic matter content of a litter cohort	3.49
	$\mathbf{LN_c}$	$t \cdot ha^{-1}$	nitrogen content	3.54
	$gLign_c$	%/100	lignin content	3.50
	$gNMR_c$	–	nitrogen:organic matter content ratio	3.51
	$gImmob_c$	$t \cdot ha^{-1} \cdot yr^{-1}$	gross nitrogen immobilization rate	3.55
	$gLeach_c$	$t \cdot ha^{-1} \cdot yr^{-1}$	gross nitrogen leaching rate	3.56
	$gNetImmob_c$	$t \cdot ha^{-1} \cdot yr^{-1}$	net nitrogen immobilization rate	3.54
	$kInitN_X$	%/100	initial N concentration ($X = F_{kLQ}$,T,R,W)	
	k_i		regression parameters	
	$kLoss_W$	%/100	decomposition parameter of wood	
	$kLoss_T$	%/100	decomposition parameter of twigs	
	kLignA	%/100	regression parameter	3.52
	kLignB	–	regression parameter	3.53
	kNC	–	nitrogen immobilization parameter	
	kLeach	%/100	nitrogen leaching parameter	
Humus decay	**HN**	$t \cdot ha^{-1}$	nitrogen content of humus compartment	3.57
	HOM	$t \cdot ha^{-1}$	organic matter content	3.60
	gLNC	–	N:C ratio of litter compartment	3.58
	gAETM	–	AET multiplier	3.59
	k_i		regression parameters	
	kMin	%/100	N mineralization rate in the absence of litter	
	kCM	%/100	carbon:organic matter ratio of litter	
	kAET	$mm \cdot yr^{-1}$	AET multiplier parameter	
Nitrogen availability	gLImmob	$t \cdot ha^{-1} \cdot yr^{-1}$	total net nitrogen immobilization rate of litter	3.61
	kNAtm	$t \cdot ha^{-1} \cdot yr^{-1}$	input rate of atmospheric nitrogen	

where kNC in Eq. 3.52 & 3.55 is the amount of nitrogen immobilized per unit organic matter that is respired. Pastor & Post (1985) used values of this parameter that were specific for each litter type. Since the data base for European conditions did not permit to derive specific values of kNC, simulation studies were conducted to explore the sensitivity of FORCLIM-S to the value of kNC. The model was found to be little sensitive, and therefore one value was used for all litter types in FORCLIM-S.

In the equation for the change in litter nitrogen content (LN, Eq. 3.54), gross nitrogen immobilization and nitrogen leaching are distinguished; the equation thus represents net nitrogen immobilization:

$$\frac{\Delta LN_c}{\Delta t} = gImmob_c - gLeach_c \equiv gNetImmob_c \tag{3.54}$$

where $gImmob_c$ is gross nitrogen immobilization (Eq. 3.55, Melillo et al. 1982), $gLeach_c$ is the amount of nitrogen leaching from the litter (Eq. 3.56, Cole & Rapp 1981), and $gNetImmob_c$ is the net immobilization rate of nitrogen. It should be noted that Pastor & Post (1985, p. 92f.) did not subtract nitrogen leaching in the calculation of the change of LN_c (Eq. 3.54) although they used it to calculate net nitrogen immobilization; thus the nitrogen balance in LINKAGES was disrupted.

$$gImmob_c = -\,kNC \cdot \frac{\Delta LOM_c}{\Delta t} \tag{3.55}$$

$$gLeach_c = \begin{cases} kLeach \cdot LN_c & \text{foliage \& roots} \\ 0 & \text{stemwood \& twigs} \end{cases} \tag{3.56}$$

A litter cohort is transferred to the humus compartment when its current nitrogen concentration ($gNMR_c$, Eq. 3.51) exceeds $kCritN_X$, the critical nitrogen concentration of the corresponding litter type X (Alexander 1977, Ellenberg 1986). In the simulation model, this transfer is implemented as a discrete time approximation, i.e. LOM_c and LN_c are added to the respective humus compartments (HOM and HN) and then are set to zero.

HUMUS DECAY AND NITROGEN MINERALIZATION

The turnover of humus nitrogen (HN) is calculated based on data recalculated from Pastor et al. (1984). These authors determined the amount of nitrogen mineralized per unit of organic matter (HOM) as a function of the N:C ratio of the litter (gLNC). However, the equation developed by Pastor & Post (1985) contains a pole, i.e. the nitrogen mineralization rate tends towards +∞ when the litter N:C ratio approaches 2.984%; moreover, the data in Pastor et al. (1984) do not suggest strongly that there is a nonlinear relationship between the litter N:C ratio and the nitrogen mineralization rate. Thus, for ForClim-S a new, linear equation was developed from the data in Pastor et al. (1984): If there is litter present in the soil, the N:C ratio of the litter (gLNC) and the amount of humus organic matter (HOM) are used to calculate nitrogen mineralization; otherwise, a constant turnover rate (kMin) of humus nitrogen is assumed (Eq. 3.57). In both cases actual evapotranspiration (uAET) influences the turnover (gAETM, Pastor & Post 1985; Eq. 3.59); thus it is assumed that uAET can be used to characterize the humidity as well as the temperature of the organic soil layer:

$$\frac{\Delta HN}{\Delta t} = \begin{cases} -\mathrm{MAX}\left(k_5 + \dfrac{k_6}{gLNC}\ ,\ k_7\right) \cdot gAETM \cdot HOM & \text{gLNC defined (litter present)} \\ -kMin \cdot gAETM \cdot HN & \text{gLNC not defined (no litter present)} \end{cases} \tag{3.57}$$

where

$$gLNC = \frac{\sum_{c=1}^{nLC} LN_c}{kCM \cdot \sum_{c=1}^{nLC} LOM_c} \tag{3.58}$$

$$gAETM = \mathrm{MIN}\left(\frac{uAET}{kAET - uAET}\ ,\ 1\right) \tag{3.59}$$

nLC is the number of litter cohorts currently present in the soil of a patch, and kCM is a parameter to convert litter organic matter to carbon. kAET is a parameter defining the slope of the multiplier curve.

Both in Linkages and in ForClim-S, the turnover of humus organic matter (HOM) is assumed to be proportional to the turnover of nitrogen (HN; Pastor & Post 1985):

$$\frac{\Delta HOM}{\Delta t} = \frac{\Delta HN}{\Delta t} \cdot \frac{HOM}{HN} \tag{3.60}$$

NITROGEN AVAILABILITY FOR PLANT GROWTH

The amount of nitrogen available for plant growth (uAvN, Eq. 3.62) is calculated as an output variable of the FORCLIM-S model from the net nitrogen immobilization of all the *nLC* litter cohorts (Eq. 3.61) and the nitrogen mineralization rate (Eq. 3.57). uAvN is not a state variable because it is assumed that the available nitrogen not used by the plants in a given year leaves the system either by streamflow or as volatile nitrogen compounds. Eq. 3.62 also includes the atmospheric deposition of soluble N compounds (kNAtm).

$$\mathrm{gLImmob} = \sum_{c=1}^{\mathrm{nLC}} \mathrm{gNetImmob}_c \tag{3.61}$$

$$\mathrm{uAvN} = \mathrm{MAX}\left(\frac{\Delta \mathrm{HN}}{\Delta \mathrm{t}} - \mathrm{gLImmob},\ 0 \right) + \mathrm{kNAtm} \tag{3.62}$$

3.3.3 FORCLIM-E: A model of the abiotic environment

All the equations used in the submodel FORCLIM-E were described previously in our analysis of the sensitivity of forest gap models to climate parametrization schemes (Fischlin et al. 1994). Thus, only the modifications made to these equations are presented and discussed here, using the same notational conventions as in Fischlin et al. (1994).

GENERATION OF WEATHER DATA

Cross-correlated variates of monthly mean temperature (T) and monthly precipitation sum (P) are generated using the following method: First, we note that the long-term means (μ) and standard deviations (σ) of these variables may be written as vectors (Eq. 3.63), and their cross-correlations (r) as a matrix (Eq. 3.64):

$$\underline{\mu}_{\,m,l} = \begin{pmatrix} \mu_{T,m,l} \\ \mu_{P,m,l} \end{pmatrix} \qquad \underline{\sigma}_{\,m,l} = \begin{pmatrix} \sigma_{T,m,l} \\ \sigma_{P,m,l} \end{pmatrix} \tag{3.63}$$

$$R_{\,m,l} = \begin{pmatrix} r_{TT,m,l} & r_{TP,m,l} \\ r_{PT,m,l} & r_{PP,m,l} \end{pmatrix} = \begin{pmatrix} 1 & r_{TP,m,l} \\ r_{PT,m,l} & 1 \end{pmatrix} \tag{3.64}$$

where the subscript m stands for a given month, and l for a location. The covariance matrix of the two variables is given in Eq. 3.65 (Flury & Riedwyl 1983):

$$COV_{m,l} = \begin{pmatrix} \sigma^2_{T,m,l} & r_{TP,m,l} \cdot \sigma_{T,m,l} \cdot \sigma_{P,m,l} \\ r_{PT,m,l} \cdot \sigma_{T,m,l} \cdot \sigma_{P,m,l} & \sigma^2_{P,m,l} \end{pmatrix} \tag{3.65}$$

The loadings of the principal component factors of the covariance matrix are calculated next (i.e. its denormalized Eigenvectors $\underline{E}_1$ and $\underline{E}_2$, Eq. 3.66; Flury & Riedwyl 1983). Like this it is possible to obtain cross-correlated variates of temperature and precipitation according to Eq. 3.67 & 3.68:

$$\underline{E}_1 = \text{eig}(COV)_1 = \begin{pmatrix} E_{11} \\ E_{12} \end{pmatrix}, \qquad \underline{E}_2 = \text{eig}(COV)_2 = \begin{pmatrix} E_{21} \\ E_{22} \end{pmatrix} \tag{3.66}$$

$$T_{m,y,l} = \mu_{T,m,l} + cl_{T,m,y,l} \tag{3.67}$$

$$P_{m,y,l} = \mu_{P,m,l} + cl_{P,m,y,l} \tag{3.68}$$

where $X_{m,y,l}$ is the actual mean monthly value of the variable ($X \in \{T,P\}$), and $cl_{X,m,y,l}$ is a linear combination of two independent normal variates v ($v \sim N(0,1)$) multiplied by the components of the Eigenvectors (Eq. 3.69 & 3.70):

$$cl_{T,m,y,l} = v_1 \cdot E_{11} + v_2 \cdot E_{21} \tag{3.69}$$

$$cl_{P,m,y,l} = v_1 \cdot E_{12} + v_2 \cdot E_{22} \tag{3.70}$$

CALCULATION OF BIOCLIMATIC VARIABLES

Winter minimum temperature

The approach presented by Fischlin et al. (1994) is used in FORCLIM-E (Eq. 3.71).

$$uWiT \equiv Tw_{y,l} = MIN(T_{Dec,y-1,l} , T_{Jan,y,l} , T_{Feb,y,l}) \tag{3.71}$$

Annual sum of degree-days

In our analysis of climate-dependent factors in forest gap models (Fischlin et al. 1994) we compared the conventional method for calculating the annual degree-day sum (Botkin et al 1972a,b) with the more precise sine-wave method by Allen (1976), and we conjectured that the difference between the two methods increases the closer the mean monthly temperature is to the threshold temperature used for the summation. In the subsequent analysis, this hypothesis was tested, and a correction formula for obtaining more accurate estimates of the annual degree-day sum was developed.

The estimates of monthly degree-days as produced by the approximation developed by Botkin et al. (1972a,b) and the more precise sine-wave method by Allen (1976) were compared at the sites Bern, Bever, Locarno, Davos, Basel, and Sion (cf. Appendix III). The former three sites were used to develop a model for the degree-day correction, and the latter three were used to validate it.

The error in the estimation of the monthly sum of degree-days showed a remarkably similar pattern across all six sites (cf. Fig. 3.8 with the site Bern as an example). The hypothesis that the largest error can be found in the vicinity of the development threshold of 5.5 °C seems to be the main cause for the site-specific bias. Thus for FORCLIM-E an empirical correction formula was developed based on these data. To reveal the pattern underlying the data more clearly, the differences between Allen's and Botkin's estimation methods (Fig. 3.8) were averaged in temperature windows having a width of 1 °C, centered around every 0.5 °C (Fig. 3.9). Three separate regressions were fitted to these data, yielding an error function of the monthly degree-day estimation according to the conventional method (Fig. 3.9).

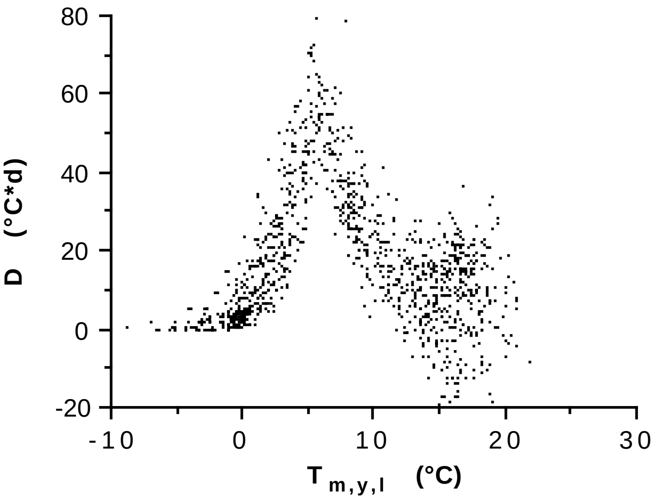


Fig. 3.8: Difference (D) between the estimation method for the monthly degree-day sum used in conventional forest gap models (Botkin et al. 1972a,b) and the more precise sine-wave method by Allen (1976) as a function of the monthly mean temperature ($T_{m,y,l}$). Data from the site Bern (Appendix III).

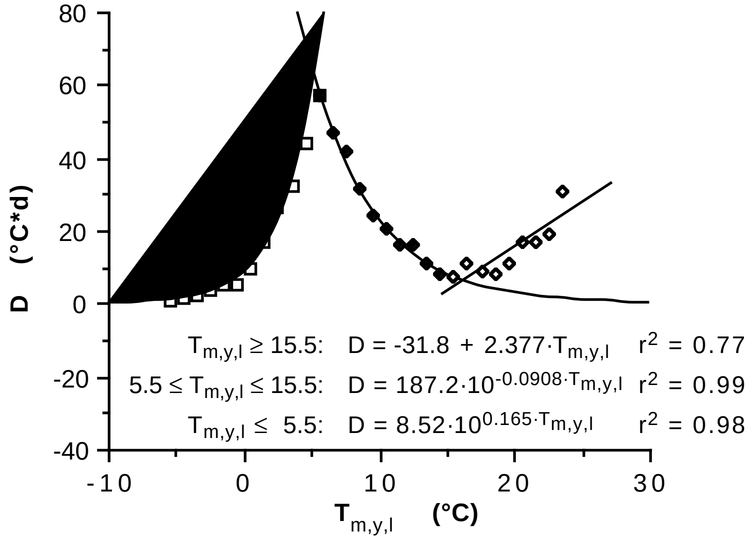


Fig. 3.9: Average difference (D) of estimated monthly degree-days between the more precise estimation method by Allen (1976) and the formula used in conventional forest gap models (Botkin et al. 1972a,b) as a function of monthly mean temperature ($T_{m,y,l}$). The data are from the sites Bern, Bever, and Locarno.

Next, the monthly degree-day sums were recalculated taking into account the error terms given in Fig. 3.9. A verification test for the site Bern and a validation test for the site Basel are shown in Fig. 3.10. It can be concluded that the correction formula provides an accurate estimate of Allen's monthly degree-day sums.

Finally, the effects of the correction formula on the annual sum of degree-days were evaluated at all six sites (Fig. 3.11). The new formula provides estimates of the annual sum

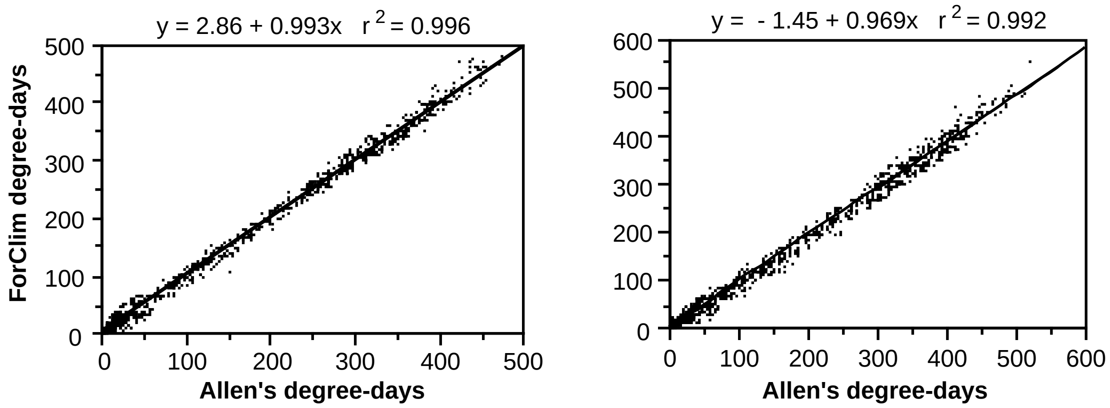


Fig. 3.10: Performance of the empirical correction formula for estimating the monthly sum of degree-days from monthly mean temperature. Left: Verification test for the site Bern. Right: Validation test for the site Basel.

of degree-days that are not significantly ($\alpha = 5\%$) different from the results of Allen's (1976) method (Tab. 3.8). Thus, the annual sum of degree-days is estimated in the FORCLIM-E model according to Eq. 3.72:

$$uDD \equiv DD_{y,l} = \sum_{m = Jan}^{Dec} MAX\,(T_{m,y,l} - kDTT,\quad 0\,) \cdot kDays \cdot gCorr\,(T_{m,y,l}) \qquad (3.72)$$

where kDTT is the development threshold temperature, kDays is a parameter denoting the average number of days per month, and gCorr is the empirical correction formula shown in Fig. 3.9, which was defined in FORCLIM-E as a table function (Fischlin et al. 1990; Tab. 3.9).

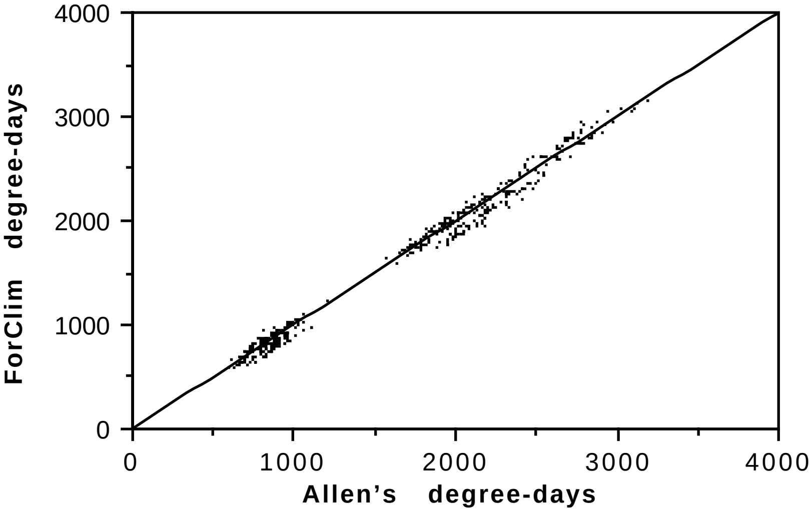


Fig. 3.11: Estimated annual sums of degree-days according to the empirical correction formula used in FORCLIM (Fig. 3.9) versus the more precise method by Allen (1976). Data from six sites in the European Alps (cf. Tab. 3.8).

Tab. 3.8: Regressions of the form y = a + b·x, where x is the annual sum of degree-days according to Allen (1976), and y is the annual sum of degree-days according to the two approximation methods discussed in the text. F-test according to Riedwyl (1980). The critical F value at $\alpha = 5\%$ is 3.84.

Approximation method	a	b	r^2	F (a=0)	F (b=1)
conventional (Botkin et al. 1972a,b)	-186.44	0.963	0.989	417.7	53.5
new correction formula (this study)	-16.5	1.0001	0.990	3.43	0.0004

Tab. 3.9: Values of the empirical degree-day correction function gCorr (Eq. 3.72, Fig. 3.9) used to define a table function in the FORCLIM-E model. T is in [°C], and gCorr is in [°C·d].

T	-20.0	-10.0	-5.0	-2.5	0.0	2.5	5.24	7.5	10.0	12.5	16.11	17.5
gCorr	0.0	0.0	1.28	3.3	8.52	22.02	62.56	39.0	23.12	13.71	6.45	9.76

Evapotranspiration and drought stress

The model of the soil moisture balance according to Thornthwaite & Mather (1957) was described in detail by Fischlin et al. (1994). It is used with two minor modifications in the FORCLIM-E model:

First, soil moisture content is not reset to field capacity at the beginning of every simulation year, but the soil water content of the previous December is used as a starting point for the soil water balance in the next year. Thus, soil moisture content (SM, Fig. 3.4) is a true state variable in FORCLIM-E. While this change may be insignificant in the European Alps under current climate because the soil is recharged to field capacity in most places during the winter, it still is important because it relaxes the implicit assumption that climate does not change: In a changing climate with decreasing winter precipitation or increasing winter temperatures, the new formulation tracks soil moisture content more realistically and has the potential to produce more and earlier drought stress.

Second, it is well known that slope and aspect of the terrain have a considerable effect on the amount of incident radiation. Evapotranspiration rates depend not only on air temperature and precipitation (Thornthwaite & Mather 1957), but also on the incoming solar radiation (Penman 1948, Mintz & Serafini 1992). In a study comparing north and south slopes, Running et al. (1987) found that radiation was 8-34% higher on southern slopes than on northern slopes, which affected potential evapotranspiration rates (cf. Schädler 1980). Thus, the calculation of the potential evapotranspiration ($\mathrm{PET}_{m,y,l}$) described in Fischlin et al. (1994) was modified according to Eq. 3.73.

$$\mathrm{PET}'_{m,y,l} = \mathrm{kPMod} \cdot \mathrm{PET}_{m,y,l} \tag{3.73}$$

$$\mathrm{kPMod} = \begin{cases} 1 + \mathrm{kSlAsp} \cdot 0.125 & \mathrm{kSlAsp} > 0 \\ 1 + \mathrm{kSlAsp} \cdot 0.063 & \text{else} \end{cases} \tag{3.74}$$

where kPMod is the fractional change in PET with increasing (or decreasing) incident solar radiation, and kSlAsp is a parameter describing this change on a qualitative basis in the range [-2…+2]. The parameter kPMod thus causes $\mathrm{PET}_{m,y,l}$ to decrease by a maximum of 12.5% on steep northern slopes (kSlAsp = -2), and to increase by a maximum of 25% on steep southern slopes (kSlAsp = +2) as compared to flat terrain (where kSlAsp = 0) (Running et al. 1987). It is acknowledged that this formulation is purely empirical; however, it provides a tool to explore the sensitivity of the FORCLIM model to microclimatic differences, which may be especially important in the subalpine zone where direct radiation is considerably higher than at lower altitudes.

Finally, drought stress (uDrStr) is calculated in FORCLIM-E according to Eq. 3.75; the calculation of $uAET_{y,l}$ and $PET_{y,l}$ were described in detail by Fischlin et al. (1994).

$$uDrStr = 1 - \frac{uAET_{y,l}}{PET_{y,l}} \tag{3.75}$$

3.4 Parameter estimation

3.4.1 FORCLIM-P

The 30 tree species present in the model under European conditions were chosen based on Hess et al. (1980) and Kienast (1987). The derivation of the species-specific parameter values for these species required a major effort, which is documented in Appendix II. The values finally obtained are given in Tab. 3.11, while the other parameter values are listed in Tab. 3.12 & 3.13. Some of the species-specific parameters in FORCLIM-P were simplified by defining species groups: A new species-specific parameter called sType (species type) was introduced (Tab. 3.10). It serves the following purposes:

- First, it separates evergreen (coniferous) from deciduous species. This distinction is possible because all the species of a type behave similar in various respects: (1) the foliage area per unit foliage weight (parameter $kC_{2,s}$, Tab. 3.3), (2) the dry to wet weight ratio of foliage ($kC_{1,s}$, Tab. 3.3), and (3) the average retention time of foliage ($kFRT_s$; Tab. 3.5).

- The second information contained in the sType parameter is the type of relationship between diameter at breast height and foliage weight, thus replacing the parameters $kA_{i,s}$ (Tab. 3.3). Five species types were derived from an extensive analysis of the data by Burger (1945-1953).

The rationale for the grouping of the species and the estimation procedure for these parameters are described in Appendix II.

Tab. 3.10: Definition of the sType parameter (cf. Tab. 3.11). The syntax of sType is "X*n*", where X ∈ {C,D} and *n* ∈ {1,2,3,4,5}. C denotes coniferous (evergreen) and D deciduous trees, respectively; *n* denotes the type of relationship between diameter at breast height and foliage weight (cf. Appendix II).

Parameter & Unit		C	D	1	2	3	4	5
kC_1	[%/100]	0.45	0.35					
kC_2	$[m^2 \cdot kg^{-1}]$	6	12					
kFRT	[yr]	5	1					
kA_1	$[kg \cdot cm^{-1}]$			0.08	0.10	0.06	0.17	0.23
kA_2	[–]			1.43	1.43	1.70	1.40	1.56

Tab. 3.11: Default values of the species-specific parameters in FORCLIM-P. N denotes no sensitivity to low winter temperatures. For the derivation, see Appendix II.

Species	sType	Dm	Hm	Am	G	DDMin	DDMax	WiT	DrT	NTol	Brow	Ly	La	LQ
Abies alba	C5	215	6000	700	117	641	4491	-6	0.18	2	3	3	1	2
Larix decidua	D2	185	5200	850	170	323	2325	-11	0.12	1	2	8	9	3
Picea abies	C5	210	5800	930	171	385	2325	N	0.06	2	2	5	5	3
Pinus cembra	C5	180	2600	1050	115	323	1124	-11	0.3	1	3	6	5	3
Pinus montana	C5	50	2300	300	138	436	1925	N	0.3	1	2	8	9	3
Pinus silvestris	C4	155	4500	760	119	610	2777	N	0.3	1	2	7	9	3
Taxus baccata	C5	355	2200	2110	47	1011	4491	-5	0.24	2	3	4	3	2
Acer campestre	D2	80	2300	170	156	1062	4491	N	0.24	2	1	5	5	2
Acer platanoides	D3	170	3200	380	142	1042	4768	-17	0.18	2	1	2	4	2
Acer pseudoplatanus	D3	215	3700	550	125	898	4491	N	0.18	2	1	2	4	2
Alnus glutinosa	D2	130	3100	240	250	898	5230	-16	0.06	2	2	5	5	1
Alnus incana	D2	160	2200	150	266	610	4204	N	0.06	2	2	6	7	1
Alnus viridis	D2	20	400	100	531	272	1237	N	0.12	2	2	7	7	1
Betula pendula	D1	115	2900	220	278	610	4655	N	0.12	1	1	7	9	2
Carpinus betulus	D3	110	2700	220	177	898	4655	-9	0.18	2	3	4	3	1
Castanea sativa	D3	355	3300	1510	142	1237	4778	N	0.24	1	2	5	5	2
Corylus avellana	D3	70	1000	70	95	898	4655	-16	0.24	2	3	6	6	1
Fagus silvatica	D3	225	4500	430	191	723	4655	-4	0.12	1	3	3	1	2
Fraxinus excelsior	D2	190	4200	350	177	980	4491	-17	0.12	3	2	4	6	1
Populus nigra	D2	190	3600	280	285	662	5405	N	0.06	3	3	5	5	2
Populus tremula	D2	125	3000	140	310	610	4655	N	0.18	1	3	6	7	2
Quercus petraea	D3	285	4500	860	195	785	4655	-5	0.18	1	2	6	7	2
Quercus pubescens	D3	90	2500	500	148	1011	4655	N	0.24	2	2	7	7	2
Quercus robur	D3	320	5200	1060	195	1042	4655	-17	0.3	1	2	7	9	2
Salix alba	D1	100	2700	170	278	1062	5405	N	0.06	3	1	5	5	2
Sorbus aria	D2	55	2200	180	82	898	5343	N	0.24	2	2	6	7	1
Sorbus aucuparia	D1	65	1900	110	167	498	4204	N	0.24	1	2	6	7	1
Tilia cordata	D3	230	3000	940	114	1339	4491	-19	0.24	2	2	5	5	2
Tilia platyphyllos	D3	405	3900	960	110	1339	4491	N	0.18	2	2	4	3	2
Ulmus scabra	D3	195	4300	480	153	1062	5230	-16	0.18	3	1	4	3	1

References for Tab. 3.11 (cf. Appendix II):

sType	Burger (1945-53), Ellenberg (1986), Kienast (1987)
kDm, kHm, kAm	Amann (1954), Fenaroli & Gambi (1976), Brosse (1977), Polunin (1977), Bernatzky (1978), Phillips (1978), Krüssmann (1979), Mitchell (1979), Hess et al. (1980), Edlin & Nimmo (1983), Marcet & Gohl (1985), Godet (1986), Prentice & Helmisaari (1991), Leibundgut (1991)
kG	Anonymous (1983), Kienast (1987), Schober (1987)
kDDMin, kDDMax	Meusel et al. (1965, 1978), Rudloff (1981), Müller (1982), Kienast (1987)
kWiT	Ellenberg (1986), Kienast (1987), Prentice & Helmisaari (1991)
kNTol	Landolt (1977), Ellenberg (1986), Jahn (1991), Prentice & Helmisaari (1991)
kDrT	Bernatzky (1978), Ellenberg (1986), Jahn (1991), Prentice & Helmisaari (1991)
kBrow	Amann (1954), Ellenberg (1986), Kienast (1987), Dengler et al. (1990)
kLy, kLa	Landolt (1977), Ellenberg (1986), Jahn (1991), Prentice & Helmisaari (1991)
kLQ	Berg & Staaf (1981), Ellenberg (1986)

Tab. 3.12: Default values of the general parameters in the FORCLIM-P model. The parameters of the nitrogen response function are given in Tab. 3.13.

Parameter	Value	Unit	Reference
kBrPr	5	–	Kienast (1987)
kEstP	0.1	yr^{-1}	Kienast (1987)
kEstNr	0.006	$\#\cdot m^{-2}\cdot yr^{-1}$	Shugart (1984)
kInitDBH	1.27	cm	Botkin et al. (1972a)
kPatchSize	833.3	m^2	Shugart & West (1977, 1979)
kLAtt	0.25	–	Wang et al. (1991), Smith et al. (1991)
kDeathP	4.605	–	Botkin et al. (1972a), Shugart (1984)
kMinRelInc	10	%	Kienast (1987), Solomon & Bartlein (1993)
kMinAbsInc	0.03	cm	Kienast (1987)
kSGrYrs	2	yr	Solomon & Bartlein (1993)
kSlowGrP	0.368	yr^{-1}	Shugart (1984), Kienast (1987)
kDistP	0	%/100	–
kAshFree	0.92	%/100	Pastor & Post (1985)
kConv	0.0025	$kg\cdot cm^{-2}$	Christensen (1977)
kRSR	4.0	–	Waring & Schlesinger (1985)

Tab. 3.13: Parameter values for the nitrogen response function (Eq. 3.27) in the growth submodel of FORCLIM-P. Data recalculated from Aber et al. (1979) and Pastor & Post (1985).

$kNTol_S$	kN_1 [–]	kN_2 [$kg\cdot ha^{-1}\cdot yr^{-1}$]
1	-0.016	2.245
2	-0.022	30.605
3	-0.016	43.973

3.4.2 FORCLIM-S

The parameters that are specific for each litter type in the FORCLIM-S model are documented in Tab. 3.14; the other parameters of FORCLIM-S are listed in Tab. 3.15.

Tab. 3.14: Parameters describing the initial (kInitN) and the critical (kCritN) nitrogen concentration of the six litter types in the FORCLIM-S model.

Litter type	kInitN [%/100] (Ellenberg 1986)	kCritN [%/100] (Bosatta & Ågren 1985)
Foliage “fast” ($kLQ_S = 1$)	0.016	0.020
Foliage “medium” ($kLQ_S = 2$)	0.010	0.017
Foliage “slow” ($kLQ_S = 3$)	0.006	0.015
Twigs	0.003	0.009
Roots	0.0093	0.015
Stemwood	0.003	0.020

Tab. 3.15: General parameters of the FORCLIM-S model.

Parameter	Value	Unit	Reference
k_1	$9.804 \cdot 10^{-3}$	–	Pastor & Post (1985)
k_2	$9.352 \cdot 10^{-4}$	$yr \cdot mm^{-1}$	Pastor & Post (1985)
k_3	$-4.956 \cdot 10^{-3}$	–	Pastor & Post (1985)
k_4	$1.93 \cdot 10^{-5}$	$yr \cdot mm^{-1}$	Pastor & Post (1985)
$kLoss_W$	0.03	yr^{-1}	Pastor & Post (1985)
$kLoss_T$	0.2	yr^{-1}	Pastor & Post (1985)
kNC	0.005	–	Melillo et al. (1982)
kLeach	0.16	yr^{-1}	Cole & Rapp (1981)
k_5	$7.9702 \cdot 10^{-3}$	–	Pastor et al. (1984)
k_6	$-1.317 \cdot 10^{-4}$	–	Pastor et al. (1984)
k_7	0.005	–	Pastor et al. (1984)
kMin	0.035	yr^{-1}	Pastor & Post (1985)
kCM	0.48	–	Pastor & Post (1985)
kAET	1200	$mm \cdot yr^{-1}$	Pastor & Post (1985)
kNAtm	0.005	$t \cdot ha^{-1} \cdot yr^{-1}$	Pastor & Post (1985)

3.4.3 FORCLIM-E

The generation of weather data in FORCLIM-E does not require any parameters besides the site-specific climatic data given in Appendix III. The minimum winter temperature is directly calculated from the weather data and does not require any model parameters either. The two parameters required for calculating the annual sum of degree-days are given in Tab. 3.16.

Tab. 3.16: Default parameter values in the FORCLIM-E model.

Parameter	Description	Value	Unit	Reference
kDTT	development threshold	5.5	°C	Botkin et al. (1972a)
kDays	average length of months	30.5	d	–
kSlAsp	slope & aspect parameter	0	–	–
kFC	soil field capacity	30.0	cm	Richard et al. (1978)

Tab. 3.17: Results from the linear regression analysis of the parameter kLatPtr against latitude (kLat, Eq. 3.76). Raw data from Pastor & Post (1985).

Month	a	b	r^2
Jan	1.1226	$-7.31 \cdot 10^{-3}$	0.977
Feb	0.9859	$-3.87 \cdot 10^{-3}$	0.987
Mar	1.0454	$-4.92 \cdot 10^{-4}$	0.640
Apr	0.9708	$3.52 \cdot 10^{-3}$	0.988
May	0.9605	$7.15 \cdot 10^{-3}$	0.988
Jun	0.9185	$8.47 \cdot 10^{-3}$	0.990
Jul	0.9669	$7.64 \cdot 10^{-3}$	0.986
Aug	0.9892	$4.94 \cdot 10^{-3}$	0.981
Sep	0.9900	$1.20 \cdot 10^{-3}$	0.860
Oct	1.0600	$-2.63 \cdot 10^{-3}$	0.957
Nov	1.0815	$-6.37 \cdot 10^{-3}$	0.987
Dec	1.1444	$-8.66 \cdot 10^{-3}$	0.982

The parameters of the soil moisture balance model are fully documented in Thornthwaite & Mather (1957) and Pastor & Post (1984, 1985); they are used in the FORCLIM-E model with a few exceptions: First, the default values of the site-specific slope/aspect parameter (kSlAsp) and of the soil field capacity, which is site-specific as well, are listed in Tab. 3.16. Second, the parameters required to correct the potential monthly evapotranspiration according to geographical latitude and sun angle (kLatPtr) are given in Pastor & Post (1985, pp. 113f.) as one large data matrix. Equations of the form

$$\mathrm{kLatPtr} = a + b \cdot \mathrm{kLat} \tag{3.76}$$

were fitted to the data for each month, where kLat is northern latitude in the range [25 °N…50 °N]. They fit the data very closely (Tab. 3.17) and are used in FORCLIM-E to determine the latitude and sun angle correction of potential evapotranspiration.

3.5 Model implementation

3.5.1 Modelling and simulation tools

For the implementation of the FORCLIM model system, the modelling and simulation environment RAMSES (Fischlin 1991) was used. RAMSES is designed to support interactive modelling and simulation. It allows modular modelling, i.e. to split complex (ecosystem) models into several submodels, and supports the coupling of models with different model formalisms. RAMSES is based on the DialogMachine (Fischlin 1986, Fischlin & Ulrich 1987), which provides an open and flexible user interface, and on the high-level programming language Modula-2 (Wirth 1985). It was implemented with the Modula-2 language system MacMETH (Wirth et al. 1992). The simulation session of RAMSES uses the simulation environment ModelWorks (Fischlin et al. 1990); it offers both interactive and batch-oriented simulations as well as full access to the DialogMachine and Modula-2, providing the flexibility for programming any additional routines, e.g. for the statistical analysis of simulation results at runtime of the model.

Fig. 3.12 gives an overview of the software used for the implementation of the FORCLIM model. Most of the simulation experiments in the present study were performed using a pre-release of version 2.2 of the RAMSES software, version 2.2 of ModelWorks, version 2.2 of the DialogMachine, and version 3.2.1 of the MacMETH language system.

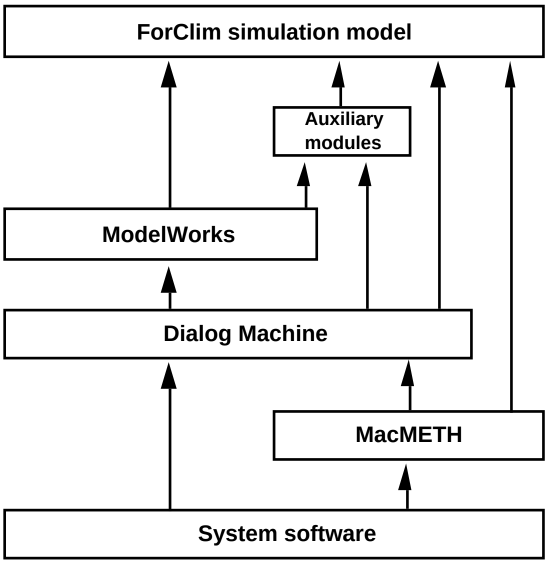


Fig. 3.12: Software used for the implementation of the FORCLIM simulation model. Arrows denote Modula-2 imports.

All the simulation studies with the FORCLIM model were run on Apple Macintosh computers, using the computer models SE/30 (CPU Motorola 68030, FPU Motorola 68882), IIfx (68030/68882) and Quadra 700 (68040, with integrated FPU). For efficiency reasons, the object code of all the models was generated using the Compile20 option of the MacMETH environment (Wirth et al. 1992), which produces code that addresses the mathematical coprocessor directly, thus bypassing the much slower Standard Apple Numerical Environment (SANE).

3.5.2 Coupling the submodels

The three submodels FORCLIM-E, FORCLIM-P, and FORCLIM-S each were implemented as ModelWorks models of their own (Fischlin et al. 1990). One important aim of the model implementation was that the behaviour of each of the three submodels can be studied irrespective of whether one or both of the other submodels are present. Thus, if one of the submodels is not present, there must be a mechanism that provides a constant parametrization of its output variables. To this end the module ForestBase was introduced, which contains always a pseudo-model. At the startup of FORCLIM, this pseudo-model declares all the input/output variables of all the potential FORCLIM submodels as model parameters. Every submodel that is declared in ModelWorks subsequently removes the parameters corresponding to its output variables and supplies their values based on its dynamics. In case the user removes a submodel, ForestBase declares the respective parameters in the pseudo-model again. Thus all the variables coupling the FORCLIM submodels have always well-defined values (Fig. 3.13).

The module structure of the FORCLIM system is shown in Fig. 3.14, and the matrix of module dependencies is given in Tab. 3.18. FORCLIM-E and FORCLIM-S are implemented as one single module each. The six modules making up FORCLIM-P serve the following purposes:

FCPBase provides a dynamic list of Modula-2 records with variables describing the tree species, i.e. the species-specific growth factors and parameters. A list of tree cohorts is attached to each tree species. Again, each tree cohort is described by a Modula-2 record containing the cohort-specific state and auxiliary variables. FCPBase also offers procedures for adding species and cohorts to and deleting them from these lists. Moreover, a procedure for the interactive editing of the species parameters is exported.

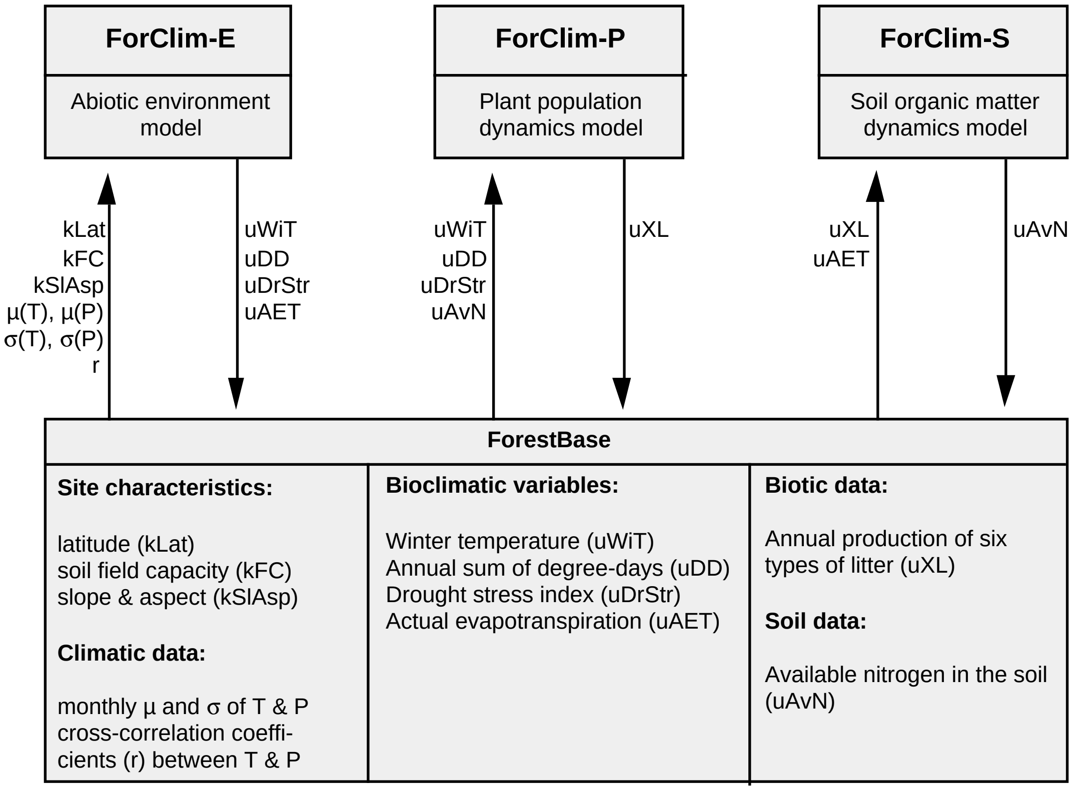


Fig. 3.13: Architecture of the FORCLIM model. The three submodels FORCLIM-E, FORCLIM-P, and FORCLIM-S exchange data via the base module ForestBase, which warrants that all the output variables have a well-defined value all the time.

FCPMon exports the procedures necessary for the monitoring of stem density distributions (histograms) and tree ring chronologies, plus the animation of tree growth.

FCPFileIO contains routines that perform file input and output tasks, such as reading of files with species parameters, writing of a matrix of limiting factors for tree establishment and growth, and the reading and writing of the state vector of FORCLIM-P.

FCPGrFact: Calculation of the three species-specific growth factors (gDDGF, gSMGF, gSNGF) and of total leaf area index, total biomass, and total tree number.

FCPDynamic: This module contains the equations describing tree establishment, growth (except for three growth factors, cf. module FCPGrFact), mortality, and litter production. Moreover, it also contains the update procedure of the state vector.

ForClimP: model declaration in ModelWorks; it contains the ModelWorks procedures for model dynamics and maintains the user interface.

The master module ForClim (Fig. 3.14) provides a menu command for configuring the FORCLIM simulation model and a message displayed at the startup of FORCLIM.

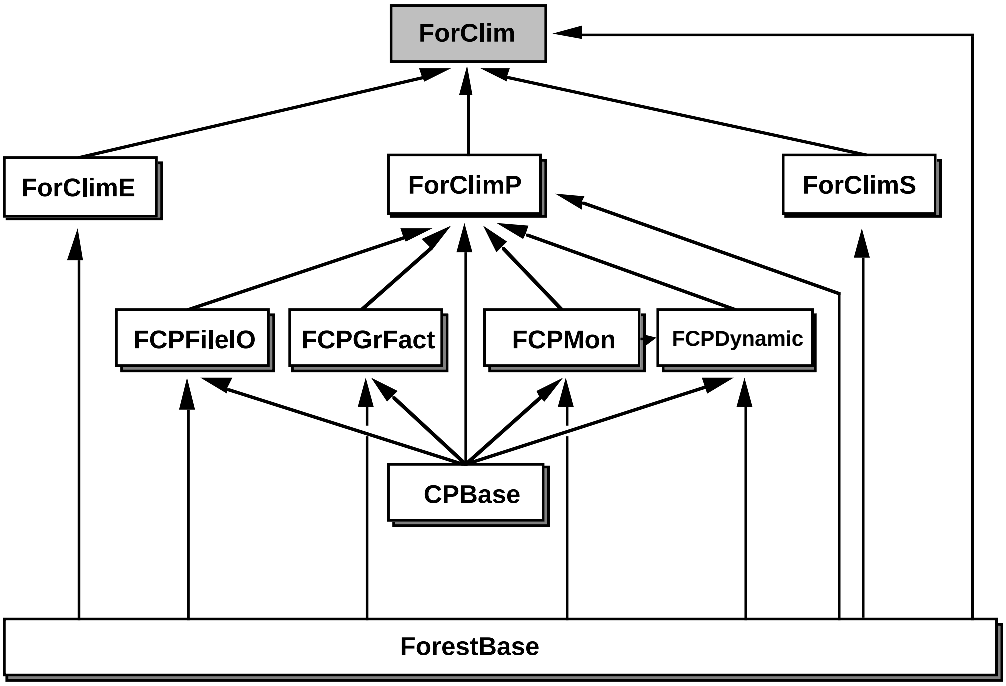


Fig. 3.14: Module structure of the FORCLIM model. Arrows denote Modula-2 imports; white boxes are definition modules, shadowed boxes are implementation modules.

Tab. 3.18: Imported modules (top row) and importing modules (leftmost column) used in the FORCLIM simulation system. • = import in definition module; o = import in implementation module. Module numbers (#):

1	ForClim	11	Histograms
2	ForClimE	12	Lists
3	ForClimP	13	MultiNormal
4	FCPDynamic	14	Jacobi
5	FCPFileIO	15	Random Number Generators (RandGen, RandNormal)
6	FCPGrFact	16	ReadData
7	FCPMon	17	StochStat
8	FCPBase	18	TabFunc
9	ForClimS	19	DialogMachine Library modules (DM)
10	ForestBase	20	ModelWorks Library modules (MW)

	FORCLIM modules										Auxiliary Library modules								DM	MW
#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	•	o	o						o	o									o	o
2		•								o			o	o	o		o	o	o	o
3			•	o	o	o	o	o		o					o		o		o	o
4				•			o	o		o					o					o
5					•			o		o						o			o	o
6						•		o		o										
7							•	o		o	o								o	
8								•			o	o			o		o		o	o
9									•	o							o		o	o
10										•			o	o	o	o	o		o	o

The module ForestBase provides mechanisms for coupling all the submodels, for changing climatic parameters, and for reading files with site-specific data. Moreover, it is also used to administer the statistics calculated by the submodels and for various technical aspects of the simulation model. The data exchange between submodels via a common base module such as ForestBase provides another advantage: For example, if the submodels were to import their input variables directly from those submodels providing the variables, it would be impossible to avoid a circular dependency between FORCLIM-P and FORCLIM-S (cf. Fig. 3.1).

3.5.3 The concepts of sites and species

Forest gap models have always been implemented to run for a specific site (Botkin et al. 1972a,b), which is defined by its geographical location, climatic parameters, and other site-specific parameters, such as the field capacity of the soil, plus a set of tree species. In FORCLIM, the ForestBase module provides the parameters specific for the currently chosen site, which may be used by any of the submodels. A different site may be chosen either by pull-down menu commands at the user interface or under program control; however, it is not possible to be in a state where no site is defined. Similarly, FORCLIM-P runs for a specific set of tree species, which may also be replaced by another set of species interactively or under program control. It should be noted that site and species data are separated into different files in FORCLIM; thus it is possible to perform experiments with any combinations of sites and species via the user interface.

3.5.4 Other implementational aspects

The size of the source and object code of all the modules of the FORCLIM model are given in Tab. 3.19. The total disk space occupied by the model may appear to be rather high; however, it should be noted that the actual model structure requires only 13% of the code of all the implementation modules (24 KBytes). The vast majority of the code was introduced to provide the possibility that the user can perform extensive monitoring of many model properties at runtime, such as stem density distributions, tree-ring chronologies, and animations of tree growth. It is also possible to calculate the statistical properties of *n* simulation runs at runtime. Thus only the summary statistics are written to an output file instead of megabytes of simulation results. Moreover, a summary matrix of the limiting factors for tree establishment and tree growth is provided, and the state vector of

FORCLIM-P can be read from and written to a text file. Most fundamentally, it is possible to change both the site and the set of species and to choose another setup of the submodels of FORCLIM from within the ModelWorks simulation environment.

The uniformly distributed random variates required by FORCLIM-P are generated according to Wichmann & Hill (1982, 1987); the normally distributed variates required by FORCLIM-E are generated with the acceptance-rejection method by Box & Muller (1958). Both routines are contained in the RAMSES Auxiliary Library (Tab. 3.18).

Tree and litter cohorts in the models FORCLIM-P and FORCLIM-S are simulated as dynamic lists of Modula-2 records (Wirth 1986), allocating the memory required for a new record in the computer's heap memory when a tree or litter cohort is to be created, and deallocating it when the last member of the tree cohort dies or the litter cohort is transferred to the humus compartment, respectively. For efficiency reasons, the update mechanism for state variables offered by ModelWorks (Fischlin et al. 1990) was not used in the model implementation. Thus both FORCLIM-P and FORCLIM-S have their own update procedures which are called in the Output procedure of the respective model (Fischlin et al. 1990). The Modula-2 source code of the FORCLIM model is given in Appendix IV.

The current version of the FORCLIM model requires at least 1.5 MBytes of Random Access Memory (RAM), which is mainly used as heap space. If the additional monitoring facilities are to be used extensively, it may be desirable to have up to 2.5 MB of RAM.

Tab. 3.19: Size of the modules in the FORCLIM model. DEF: Modula-2 definition source code; MOD: implementation source code; SBM: symbol file code; OBJ: executable object code. Lines of source code include neither comments nor empty lines.

	DEF		**MOD**		**SBM**	**OBJ**
	bytes	lines	bytes	lines	bytes	bytes
ForClim	–	–	4217	86	–	1'752
ForClimS	1'476	4	21'537	480	77	8'944
ForClimP	1'532	4	26'248	525	77	12'070
FCPDynamic	2'215	10	11'940	187	1'777	5'098
FCPMon	1'999	11	13'882	335	1'824	6'266
FCPGrFact	1'919	10	4'302	81	1'774	1'788
FCPFileIO	2'479	16	20'225	464	1'916	11'258
FCPBase	5'169	76	12'793	320	2'110	5'836
ForClimE	1'657	4	24'167	568	77	11'636
ForestBase	8'013	99	45'632	1'075	2'446	19'628
TOTAL	**26'459**	**234**	**184'943**	**4'035**	**12'078**	**84'276**

4. Behaviour of FORCLIM along a transect in the European Alps

The modular structure of FORCLIM makes it possible to examine the behaviour of each submodel in isolation before considering combinations of the three submodels. This allows to quantify e.g. the effects of FORCLIM-E on FORCLIM-P, and to evaluate the feedback mechanisms between FORCLIM-P and FORCLIM-S. Thus, in a first step each submodel will be run on its own, either for all or a selection of the sites given in Appendix III (sections 4.1 – 4.3.1). Second, two interesting combinations of submodels will be examined: (1) FORCLIM-E/P, a setup corresponding to many other forest gap models (section 4.3.2), and (2) the full FORCLIM-E/P/S model, a setup coming closer to a true ecosystem model (section 4.3.3). Finally, a method for estimating efficiently the steady state species composition of FORCLIM will be developed (section 4.4).

4.1 FORCLIM-E

The FORCLIM-E model was run for the time window 0…5000 years at all 12 sites (Tab. 4.1). These sites correspond to an ecological gradient from cool to warm and from ecologically wet to dry (cf. the variables uDD and uDrStr, Cleuson – Sion in Tab. 4.1). There is an emphasis on sites around uDD = 1900 °C·d (Huttwil – Basel) because these conditions are typical for a large part of the Swiss Plateau.

It is evident from Tab. 4.1 that these sites do not correspond to a smooth gradient of the drought stress index. For example, there are no sites with $0.06 < uDrStr < 0.2$. In fact, drought gradients are very steep in the European Alps. In central alpine valleys precipitation decreases from around 800 mm to 600 mm over distances as small as 30 km (e.g. from Martigny to Sion; Martigny has similar climatic parameters as Basel, Tab. 4.1); yet this corresponds to a strong increase of drought stress. These gradients will be explored in more detail in chapter 5.

The cross-correlation coefficients between monthly temperature means and monthly precipitation sums affect both the actual evapotranspiration (uAET) and the drought stress index (uDrStr). The effect on uAET itself is negligible (Tab. 4.1): at average this variable is only 0.25% higher if cross-correlations are neglected, and the distributions are not significantly different. The distributions are slightly left-skewed at all sites (Fig. 4.1). The drought stress index responds strongly to small increases of uAET when the actual is close to the potential evapotranspiration, and this explains the pattern evident from Tab. 4.1: The strongest increase of drought stress occurs at sites where drought stress is low, which leads to significant differences in the distributions of uDrStr (Fig. 4.2); at the other extreme, simulated drought stress remains essentially the same at the site with the highest stress (Sion, Fig. 4.3). At average, drought stress decreaes by 9.6% if the cross-correlation between monthly mean temperature and monthly precipitation sum is disregarded (Tab. 4.1). Thus it can be concluded that it has a considerable effect on simulated drought stress at many sites in the European Alps.

While the analysis of simulated actual evapotranspiration and drought stress may reveal interesting patterns, the realism and precision of the Thornthwaite & Mather model of soil moisture remains to be determined. The variable uDrStr itself can not be measured in the field, and actual evapotranspiration rates are difficult to determine. However, soil moisture content, the state variable of the soil moisture balance model, can be measured more

Tab. 4.1: Averages of the output variables of FORCLIM-E at the 12 test sites estimated from simulation experiments covering 5001 years. uDD – degree-days; uWiT – winter temperature; uAET – actual evapotranspiration; uDrStr – drought stress. Asterisks (*) denote values that have been calculated without taking into account the cross-correlation between monthly temperature means and precipitation sums.

Site	uDD [°C·d]	uWiT [°C]	uAET [mm/yr]	uAET* [mm/yr]	uDrStr [%]	uDrStr* [%]	uAET*/ uAET	uDrStr*/ uDrStr
Cleuson	566.9	-7.313	390.1	391.6	1.955	1.593	1.0038	0.815
Bever (north)[1]	773.0	-10.189	373.4	373.8	1.351	1.243	1.0011	0.920
Bever (south)[2]	773.0	-10.189	518.6	519.9	4.182	3.962	1.0025	0.947
Davos	900.6	-7.497	453.4	454.1	0.877	0.723	1.0015	0.824
Montana	1309.8	-3.711	493.6	496.0	5.236	4.812	1.0049	0.919
Adelboden	1203.0	-3.146	504.9	505.6	0.629	0.512	1.0014	0.814
Huttwil	1862.9	-2.178	587.0	587.8	1.466	1.362	1.0014	0.929
Bern	1933.4	-2.17	591.9	593.6	2.347	2.105	1.0029	0.897
Schaffhausen	1993.5	-2.3	588.6	590.9	4.321	3.998	1.0039	0.925
Basel	2096.1	-1.148	595.5	597.6	5.431	5.152	1.0035	0.949
Sion	2285.1	-1.441	514.1	514.3	20.612	20.643	1.0004	1.002
Airolo	1399.3	-3.372	519.7	521.0	2.322	2.108	1.0025	0.908
Locarno	2777.0	2.0	688.3	690.3	2.606	2.355	1.0029	0.904
average							**1.0025**	**0.904**

[1] north-facing slope, kSlAsp = –2

[2] south-facing slope, kSlAsp = +2

easily. Thus, soil moisture data were gathered from the literature, and FORCLIM-E was used to simulate these independent data as a small validation study.

A considerable body of data on soil moisture content was found for sites close to Basel, which are characterized by considerable drought occurrence (Tab. 4.1). Monthly temperature and precipitation data for the years where measurements of soil moisture had been made were obtained from the climate station Rheinfelden (SMA 1971-1984). The field capacity parameter (kFC) required by FORCLIM-E was calculated from the data in Tab. 4.2. It should be noted that the extremely large rooting depths at two sites lead to values of kFC that probably are exaggerated; yet the FORCLIM-E model is little sensitive to the value of kFC unless it is below 25 cm.

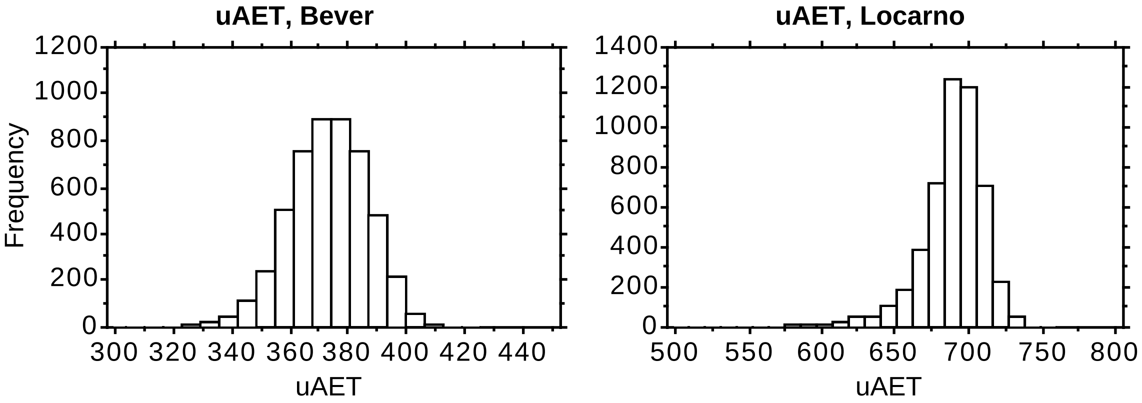


Fig. 4.1: Frequency distribution of simulated annual actual evapotranspiration rates (uAET, mm·yr^{-1}) at the sites Bever (north-facing slope, left) and Locarno (right), taking into account the cross-correlation between temperature and precipitation.

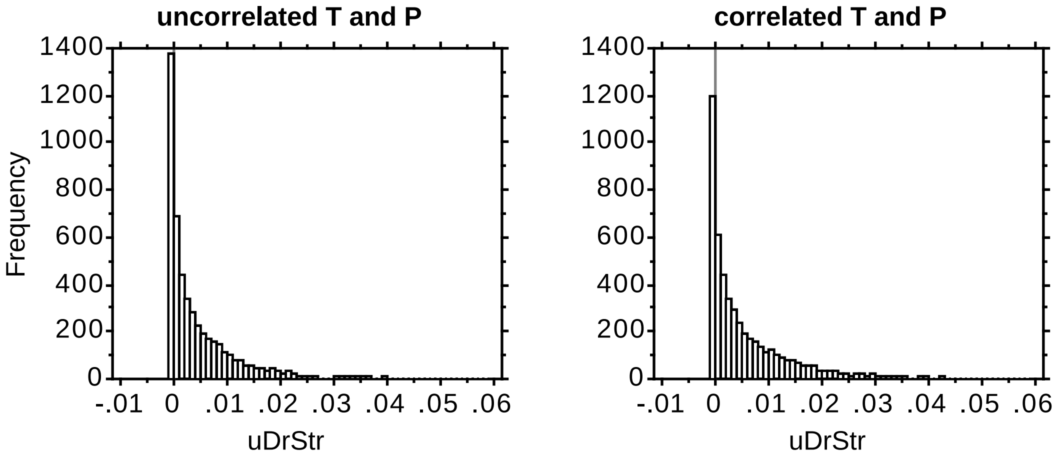


Fig. 4.2: Frequency distribution of simulated drought stress (uDrStr) at the site Adelboden, where the largest differences occur (cf. Tab. 4.1). Although they look similar, the distributions are significantly different at p = 0.0031 (Kolmogorov-Smirnov test, Zar 1984).

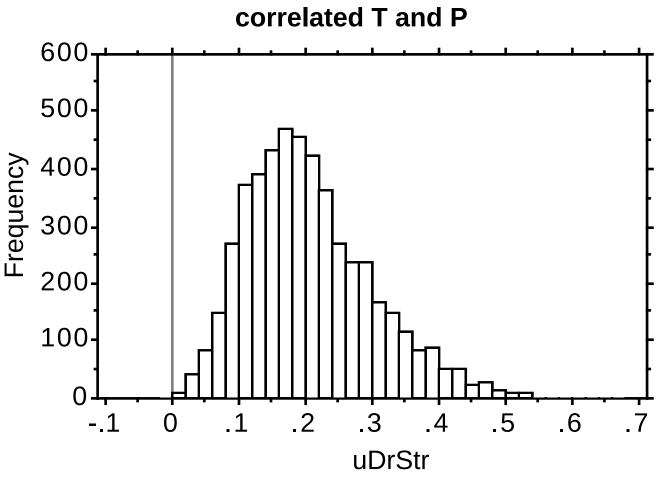


Fig. 4.3: Frequency distribution of simulated drought stress (uDrStr) at the site Sion.

The time series of soil water content as simulated by FORCLIM-E at these sites (Tab. 4.2) are shown in Fig. 4.4. The Thornthwaite & Mather (1957) model tracks measured soil moisture fairly well. The deviations from the measurements should be interpreted considering both the accuracy of the measurements and their representativeness: The measured soil moisture content is influenced considerably by the water demand of the trees surrounding the measuring devices, whereas the simulated water content corresponds to the average over a larger area. Moreover, it should be kept in mind that the FORCLIM-E model has a monthly time step only, whereas the measurements have a much finer resolution that can not be produced by the model. Generally speaking, FORCLIM-E appears to be capable of simulating realistic time series of soil moisture under conditions of moderate drought. It can be expected that results of a similar quality would be obtained for other sites on the Swiss Plateau because they are characterized by similar drought stress (Tab. 4.1). However, the precision of the calculation for sites with much more drought (e.g. Sion) can not be inferred from the above experiments and would have to be assessed separately.

Tab. 4.2: Derivation of the field capacity parameter (kFC) at the sites used for testing the behaviour of the soil water balance model.

Site	Rooting depth [cm]	Field capacity [%]	kFC [cm]	Observation years	Reference
Wallbach-Möhlin	350	38	132.3	1971, 1972	Germann (1976)
Möhlin	300	38	114.0	1975, 1976	Borer (1982)
Kaisten	150	25	37.5	1978, 1979	Vogelsanger (1986)
Eiken-Laufenburg	150	25	37.5	1982–1984	Hurst (1988)

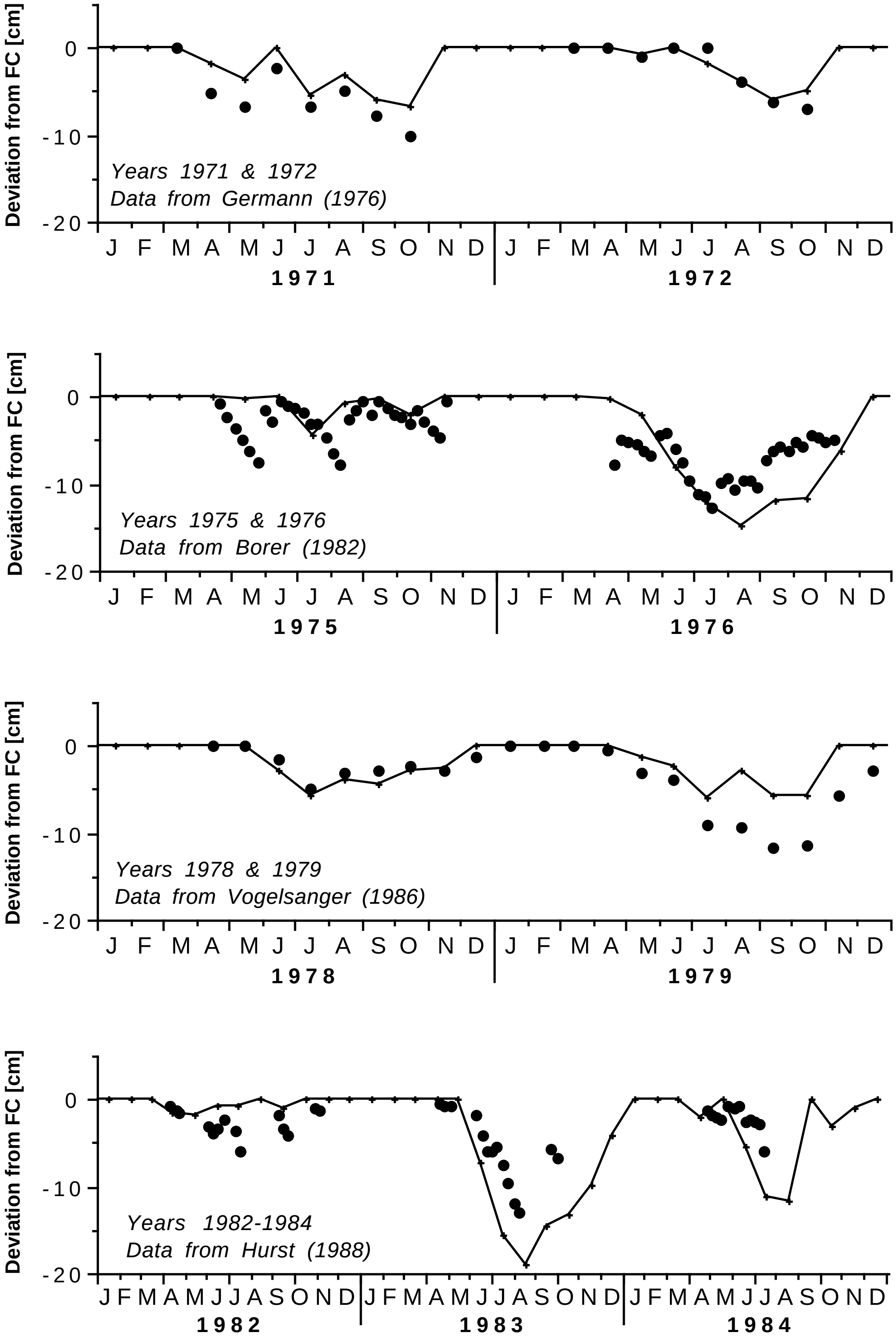


Fig. 4.4: Comparison of simulated (solid lines) and measured (dots) soil moisture content at various sites on the Swiss Plateau (Tab. 4.2).

4.2 FORCLIM-S

The buildup of soil organic matter was evaluated at six sites along a gradient of increasing actual evapotranspiration (Bever, north-facing slope; Davos; Sion; Bever, south-facing slope; Bern; Locarno; cf. Tab. 4.1). It was assumed that there is no organic material at the beginning of the simulations and that there is a constant annual input of litter into the system (Tab. 4.4). The simulations were run until the steady state of soil organic matter was reached.

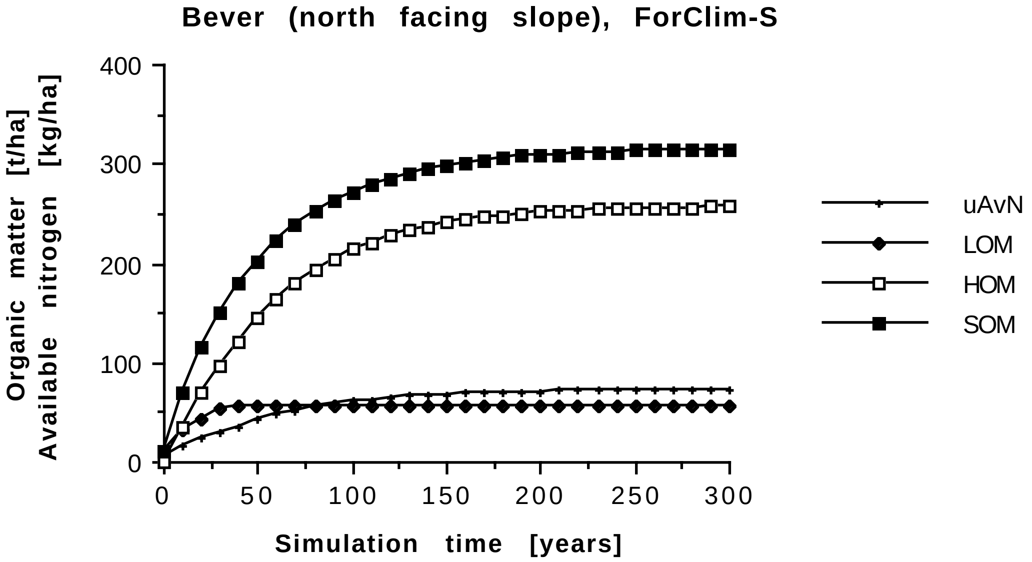


Fig. 4.5: Buildup of soil organic matter content on a north-facing slope at the site Bever as simulated by FORCLIM-S. LOM: litter organic matter; HOM: humus organic matter; SOM: total soil organic matter, SOM = LOM + HOM; uAvN: nitrogen available for plant growth. Litter input is from Tab. 4.4, and actual evapotranspiration is from Tab. 4.1.

Fig. 4.5 shows typical simulation results obtained from FORCLIM-S for a northern slope at the site Bever. The steady state of belowground organic matter is reached within 200-250 years, and Tab. 4.3 gives an overview of the steady-state results obtained at the six sites.

As mentioned in the section on the assumptions of FORCLIM-S, both LINKAGES and FORCLIM-S lack a carbon pool with a turnover rate in the order of 1000 years (Parton et al. 1987, Verberne et al. 1990). Hence the steady state of belowground organic matter is reached too fast and is slightly too low in these models (cf. Fig. 4.5). A hypothesized “slow” compartment would be small and would react much more slowly to climatic change than the species composition. Moreover, within the next few hundred years the main impact of climatic change would be on those pools of soil organic matter that have turnover rates in the order of centuries or less. These pools are modelled explicitly in FORCLIM-S, and the model thus appears to be appropriate for studying the effects of climatic change on belowground carbon storage during a few centuries.

Tab. 4.3: Available nitrogen (uAvN, kg·ha^{-1}), organic matter in the litter (LOM, t·ha^{-1}) and humus compartments (HOM, t·ha^{-1}), and their sum (SOM, t·ha^{-1}). All values refer to the steady state as calculated by FORCLIM-S run in isolation. The input variables are taken from Tab. 4.1 & 4.4.

Site	uAvN	LOM	HOM	SOM
Bever N	72.6	57.7	256.8	314.5
Davos	77.6	62.4	98.2	160.6
Sion	94.1	110.9	48.0	158.9
Bever S	66.2	41.6	81.7	123.3
Bern	130.6	114.5	76.0	190.5
Locarno	138.3	124.3	75.7	200.0

While the simulated ratios of litter to humus mass are difficult to ascertain, it is possible to compare the simulated total amount of soil organic matter with measurements compiled by Richard et al. (1978; D. Perruchoud, pers. comm.): For the Swiss Plateau (elevation <700 m.a.s.l.), the measured amount of organic matter averages to 242 t/ha, ranging from 127 to 423 t/ha; the “Parabraunerde” sites, which are typical of the Swiss Plateau, have a soil organic matter content of some 180 t/ha. These figures compare favourably with the data in Tab. 4.3 (site Bern, cf. also Sion and Locarno). At higher elevations (>700 m.a.s.l.) the average soil organic matter content calculated from the data in Richard et al. (1978) is 359 t/ha, ranging from 152 to 793 t/ha. If the podzols are excluded from the calculation, the average is 257 t/ha. Again, the amount of soil organic matter simulated by FORCLIM-S falls within that range (Bever, Davos).

Another important index of soil organic matter is its residence time, which can be estimated as the ratio of total soil organic matter to the annual litter input in the steady state. The simulated residence times range from 11.15 years at Locarno to 32.86 years at northern slopes in Bever. These figures are considerably lower than those by Raich & Schlesinger (1992), which give 29 years for temperate and 91 years for boreal forests; the residence time simulated by FORCLIM-S is roughly three times less. Given that the estimates of litter production by FORCLIM-P were correct (cf. next section), this would mean that FORCLIM-S underestimates the amount of soil organic matter by a factor three, which appears unprobable when considering the data in Richard et al. (1978). Further research is required to address this issue.

4.3 Model variants including FORCLIM-P

According to the descriptions of near-natural forest communities in the central part of the European Alps (Ellenberg & Klötzli 1972, Ellenberg 1986), four sites typical of today's vegetation zones were selected to study the behaviour of FORCLIM-P (cf. Appendix III):

First, a south-facing slope at Bever, where the near-natural vegetation is formed by larch-Swiss stone pine forests *(Larici-Pinetum cembrae* Ellenberg & Klötzli 1972). The dominating species in this association is *Pinus cembra*; subdominant species are *Larix decidua* and *P. montana*, while *Picea excelsa* occurs only rarely.

Second, the site Davos with larch-spruce forests *(Larici-Piceetum* Ellenberg & Klötzli 1972). *Picea excelsa* is the most abundant species in this association, followed by *L. decidua*, *P. cembra,* and *P. silvestris*.

Third, the site Bern where a variety of communities dominated by beech *(Fagus silvatica)* and oak species *(Quercus robur, Q. petraea)* forms the near-natural vegetation (Ellenberg & Klötzli 1972, Ellenberg 1986). Many other deciduous species occur in these forests, such as *Acer spp.*, *Fraxinus excelsior*, and *Ulmus scabra*. Coniferous species like *P. excelsa* and *Abies alba* do not have a dominant role in these near-natural forests.

Finally, forest succession is simulated at the site Sion, which is close to the dry timberline. Oak species *(Quercus spp.)* and Scots pine *(Pinus silvestris)* should prevail there (Ellenberg & Klötzli 1972).

In a first step, the FORCLIM-P model was run in isolation, assuming constant weather and constant soil fertility. Next, the importance of FORCLIM-E was evaluated by coupling it to FORCLIM-P, yielding the model FORCLIM-E/P. Then the feedbacks between FORCLIM-S and FORCLIM-P were examined in the complete FORCLIM-E/P/S model. All simulations were run for 1200 years and 200 patches, starting with a bare patch as the initial condition both for FORCLIM-P and FORCLIM-S.

4.3.1 FORCLIM-P

The constant values of the bioclimatic variables degree-days (uDD), winter temperature (uWiT), and drought stress (uDrStr) were taken from Tab. 4.1. A nutrient-rich soil with a nitrogen availability (uAvN) of 100 kg/ha was assumed at all sites. The simulation results of the FORCLIM-P model are shown in Fig. 4.6 & 4.7. They will be discussed for each site in turn:

At the site Bever (Fig. 4.6), the FORCLIM-P model simulates a larch *(Larix decidua)* – spruce *(Picea excelsa)* forest. Swiss stone pine *(Pinus cembra)* is of minor importance only, although it should dominate according to Ellenberg & Klötzli (1972). The same happens at the northern slope (not shown), so that forests in Bever according to FORCLIM-P exclusively belong to the *Larici-Piceetum*.

At Davos (Fig. 4.6), FORCLIM-P correctly simulates a larch-spruce forest with some Swiss stone pine *(P. cembra)* as well as Scots pine *(Pinus silvestris)*. The occurrence of black poplar *(Populus nigra)* may represent an anomaly; this species should be competitive on wet soils only (Hess et al. 1980). In the FORECE model, *P. nigra* was excluded by the static soil moisture indicator concept (Kienast 1987), which was omitted in FORCLIM (cf. section 2.3.1).

Simulation results at the site Bern (Fig. 4.7) are characterized by a strong dominance of beech *(Fagus silvatica)*, accompanied by silver fir *(Abies alba)*, Norway spruce *(P. excelsa)*, maple *(Acer spp.)*, and black poplar *(P. nigra)*. Especially during early succession, oak *(Quercus petraea, Q. robur)* are important species. This pattern conforms more to the descriptions by Ellenberg & Klötzli (1972) than the forest simulated by FORECE, which was dominated by beech, silver fir, maple, and linden *(Tilia spp.)*. In the FORECE simulations, oak was not present at all, and maple (especially *A. platanoides)* was too abundant (Kienast 1987). In FORCLIM-P, silver fir may be too abundant, but it is less so than in FORECE.

Tab. 4.4: Litter production [$t \cdot ha^{-1} \cdot yr^{-1}$] of the FORCLIM-P model simulated in isolation, averaged from the model output between the simulation years 1000 and 1200 (200 patches). Symbols: uFL – foliage litter (1 = fast, 2 = medium, 3 = slow decay); uTL – twig litter; uWL – stemwood litter; a.g. – aboveground; uRL – fine root litter.

Site	uFL_1	uFL_2	uFL_3	uTL	uWL	total a.g.	uRL
Bever N	0.02	0.05	1.3	0.8	1.9	4.1	5.5
Bever S	0.02	0.06	1.2	0.8	1.4	3.5	5.0
Davos	0.02	0.3	1.1	0.8	2.1	4.3	5.8
Bern	0.22	2.0	0.05	1.0	4.4	7.7	9.2
Sion	0.02	1.5	0.04	0.6	4.4	7.7	9.2
Locarno	0.23	2.2	0	1.0	4.8	8.2	9.7

The results obtained from FORCLIM-P at the site Sion do not correspond to phytosociological expectations (Fig. 4.7): Although this site is very xeric, an extremely high biomass is attained; while the occurrence of *Q. robur* is plausible (Ellenberg 1986), the co-dominance of chestnut *(Castanea sativa)* may be questionable, and the considerable biomass of yew *(Taxus baccata)* is unrealistic as well.

The litter production simulated by FORCLIM-P is summarized in Tab. 4.4. In coniferous forests, leaf litter of low quality is produced (uFL_3), whereas deciduous forests are characterized by more easily degradable leaf litter (uFL_2). There is some literature data to evaluate the simulated pattern of total aboveground litterfall: For boreal forests (comparable to the sites Davos and Bever), Ajtay et al. (1979) give 5.5–6 $t \cdot ha^{-1} \cdot yr^{-1}$, while their value for temperate forests (Bern, Sion, Locarno) is 8.5 $t \cdot ha^{-1} \cdot yr^{-1}$; the rates simulated by FORCLIM-P are slightly lower. On the other hand, Cox et al. (1978) found only 3.3 $t \cdot ha^{-1} \cdot yr^{-1}$ in a *Liriodendron* forest in Tennessee. For coarse woody debris (corresponding roughly to uWL), Harmon et al. (1986) list a range of 0.17–7 $t \cdot ha^{-1} \cdot yr^{-1}$ in coniferous forests, and up to 14.5 $t\ ha^{-1} \cdot yr^{-1}$ in deciduous forests. The simulated aboveground litter production (Tab. 4.4) agrees with the range of data from these sources (cf. also Vogt et al. 1986).

4.3.2 FORCLIM-E/P

In this model setup, the abiotic environment is stochastic; thus, it is not restricted to average conditions but includes some of the natural variability of the weather and the habitat. As in section 4.3.1, available nitrogen is kept constant at 100 kg/ha. The results of these simulations are shown in Fig. 4.8 & 4.9.

At the site Bever (Fig. 4.8), the spruce forest simulated by FORCLIM-P (Fig. 4.6) is replaced by the *Larici-Pinetum cembrae*, where *P. cembra* dominates (Ellenberg & Klötzli 1972). *Picea excelsa* is not competitive any more due to the occurrence of summer droughts. On northern slopes at Bever (Fig. 4.12), a larch-spruce forest is simulated, corresponding to the pattern observed in the area (Ellenberg & Klötzli 1972).

The forest simulated at the site Davos (Fig. 4.8) does not differ much from the one simulated by FORCLIM-P (Fig. 4.6); it still belongs to the *Larici-Piceetum* (Ellenberg & Klötzli 1972). Silver fir *(Abies alba)* occurs now because winter temperature in some years is high enough to enable establishment of the species. Its presence at elevations such as Davos agrees with descriptions of other near-natural forests of the area (e.g. *Melico-Piceetum* Ellenberg & Klötzli 1972; cf. also Ellenberg 1986).

Similar to the site Bever, the stronger occurrence of summer drought causes shifts of the species composition at the site Bern (Fig. 4.9): Spruce *(P. excelsa)* loses importance. On the other hand, the biomass of *A. alba* increases considerably, and that of *Quercus robur* increases slightly. *Abies* clearly is overrepresented now, which is due to its large maximum height and the formulation of asymmetric competition, as discussed already by Kienast & Kuhn (1989b). The rest of the community remains virtually unchanged.

At the site Sion, radical changes are observed when the abiotic environment is stochastic (Fig. 4.9): Total biomass decreases to about one third, *Tilia* and *Taxus* disappear, and *Castanea* is reduced to very low biomass. The forest simulated by FORCLIM-E/P is an oak-pine forest close to the arid timberline, which corresponds better to phytosociological expectations (Ellenberg & Klötzli 1972, Burnand 1976). It should be noted that small changes of the drought tolerance parameters (kDrT) of *P. silvestris*, *Q. robur*, and *Q. pubescens* can lead to strong changes in the relative proportions of these species at the site Sion; the simulated species composition therefore should be interpreted with caution.

The simulation time required to simulate 1200 years of successional dynamics on one patch with FORCLIM-E/P is 40 seconds (Macintosh Quadra 700); for the same run on the same machine, the FORTRAN version of the FORECE model requires 226 seconds. In other words, simulation time with FORCLIM-E/P is less than one fifth of FORECE (19.4%). Most of the increased efficiency is attributable to the model simplifications (section 2.3) and not to the different programming and simulation environment. Hence large-scale simulation experiments can be performed more efficiently with FORCLIM than with FORECE (cf. chapter 5).

4.3.3 FORCLIM-E/P/S

In this model version, neither the weather nor the availability of nitrogen are kept constant, and it is also possible to evaluate the amount of belowground organic matter. Fig. 4.10 & 4.11 show the results obtained from FORCLIM-E/P/S at the four sites. A common pattern is visible at all sites: the accumulation of biomass is slower in the E/P/S than in the E/P model because nitrogen availability limits tree growth markedly as long as soil organic matter is accumulating (cf. section 4.2). Moreover, even if the average nitrogen availability in the steady state of FORCLIM-E/P/S is higher than the 100 kg/ha assumed in the previous sections, there are prolonged periods where N availability drops to low values, e.g. when a large fallen log immobilizes large amounts of nitrogen. During such phases, species which are tolerant of these conditions (i.e. those which have a low kNTol parameter) have a competitive advantage. Hence, these species may be expected to increase their abundance in the FORCLIM-E/P/S model as compared to the variant E/P.

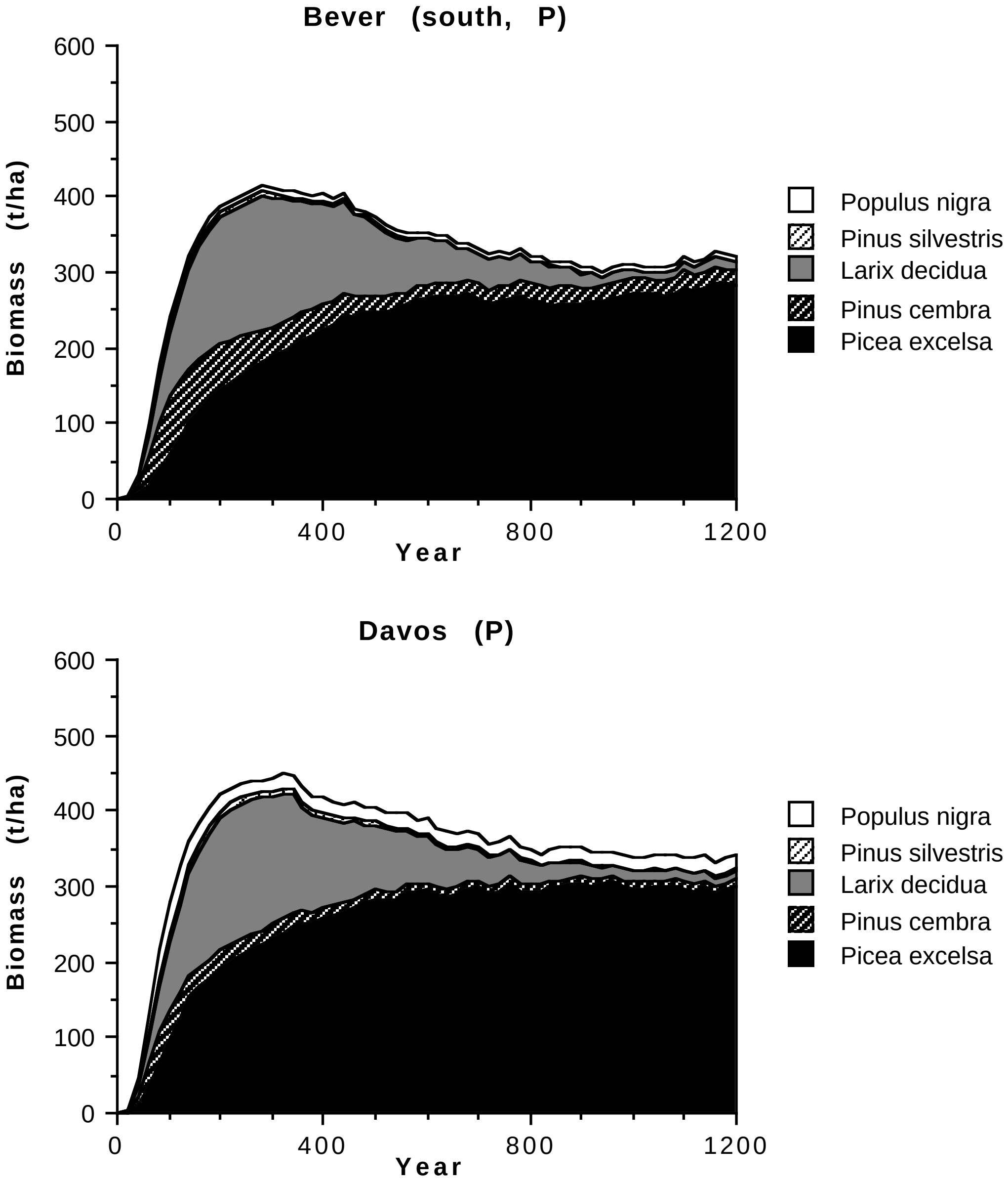


Fig. 4.6: Average species composition from 200 forest patches simulated by the FORCLIM-P model in isolation, assuming a nutrient-rich soil and a constant abiotic environment (i.e. no year-to-year variability in the weather). Top: A south-facing slope at the site Bever; bottom: Davos. The graphs show cumulative species-specific biomass values.

At the site Bever (Fig. 4.10) no strong changes occur as compared to the E/P model. *L. decidua* is somewhat more abundant; considering the abundance of larch in the current forests on southern slopes of the area, this increase is quite plausible.

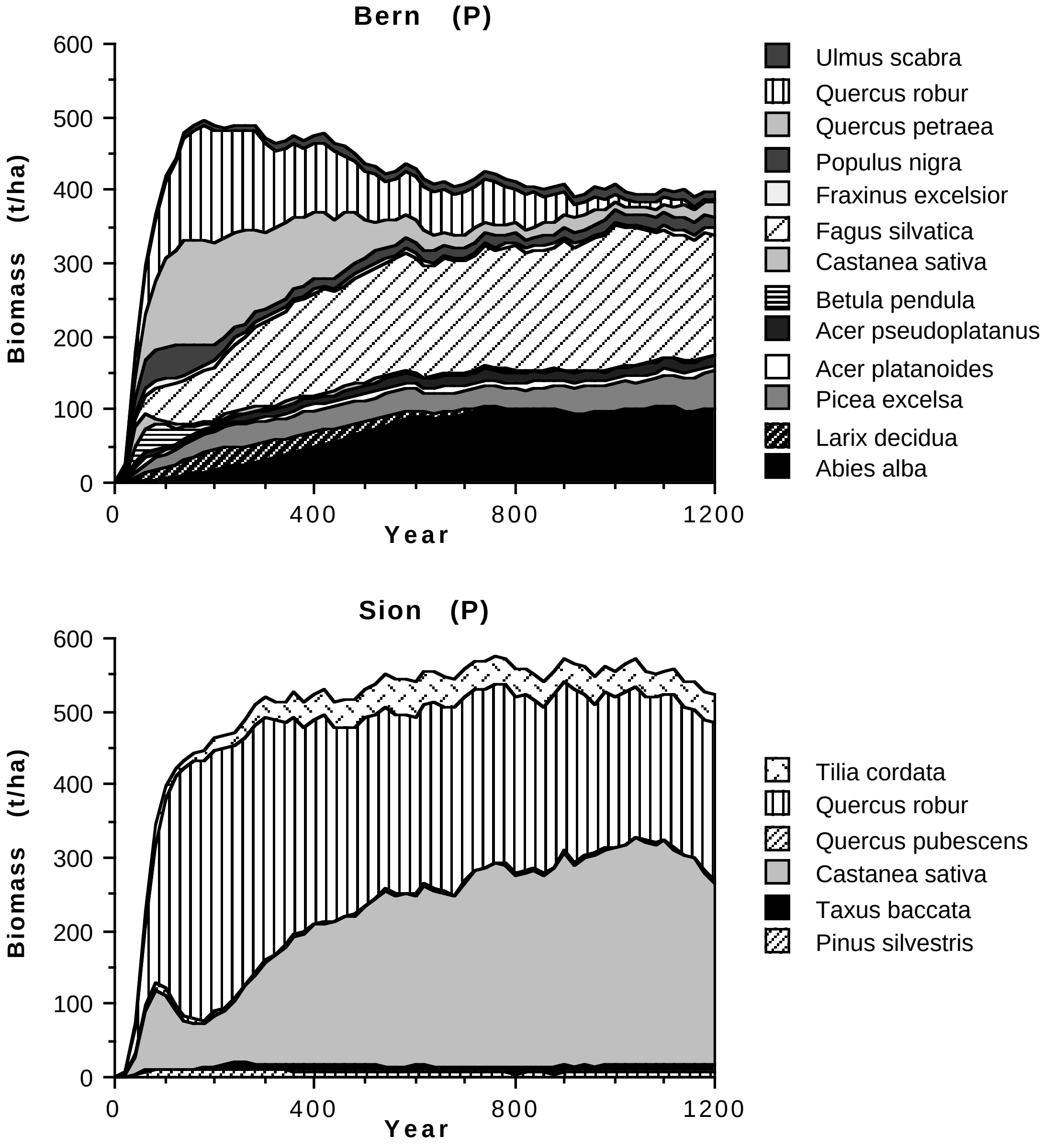


Fig. 4.7: Average species composition from 200 forest patches simulated by the FORCLIM-P model in isolation, assuming a nutrient-rich soil and a constant abiotic environment at the sites Bern (top) and Sion (bottom).

An interesting effect is visible at the site Davos (Fig. 4.10): Due to its nitrogen tolerance, *L. decidua* has a competitive advantage over *P. excelsa*. Moreover, *L. decidua* does not have a dense crown, and self-shading is not as important as for other species; consequently, larch reaches a high biomass peak around the year 350 in the FORCLIM-E/P/S model and is outcompeted only later by spruce. For the same reason larch does not disappear but is able to contribute 15-20% of the total biomass in the late successional stage.

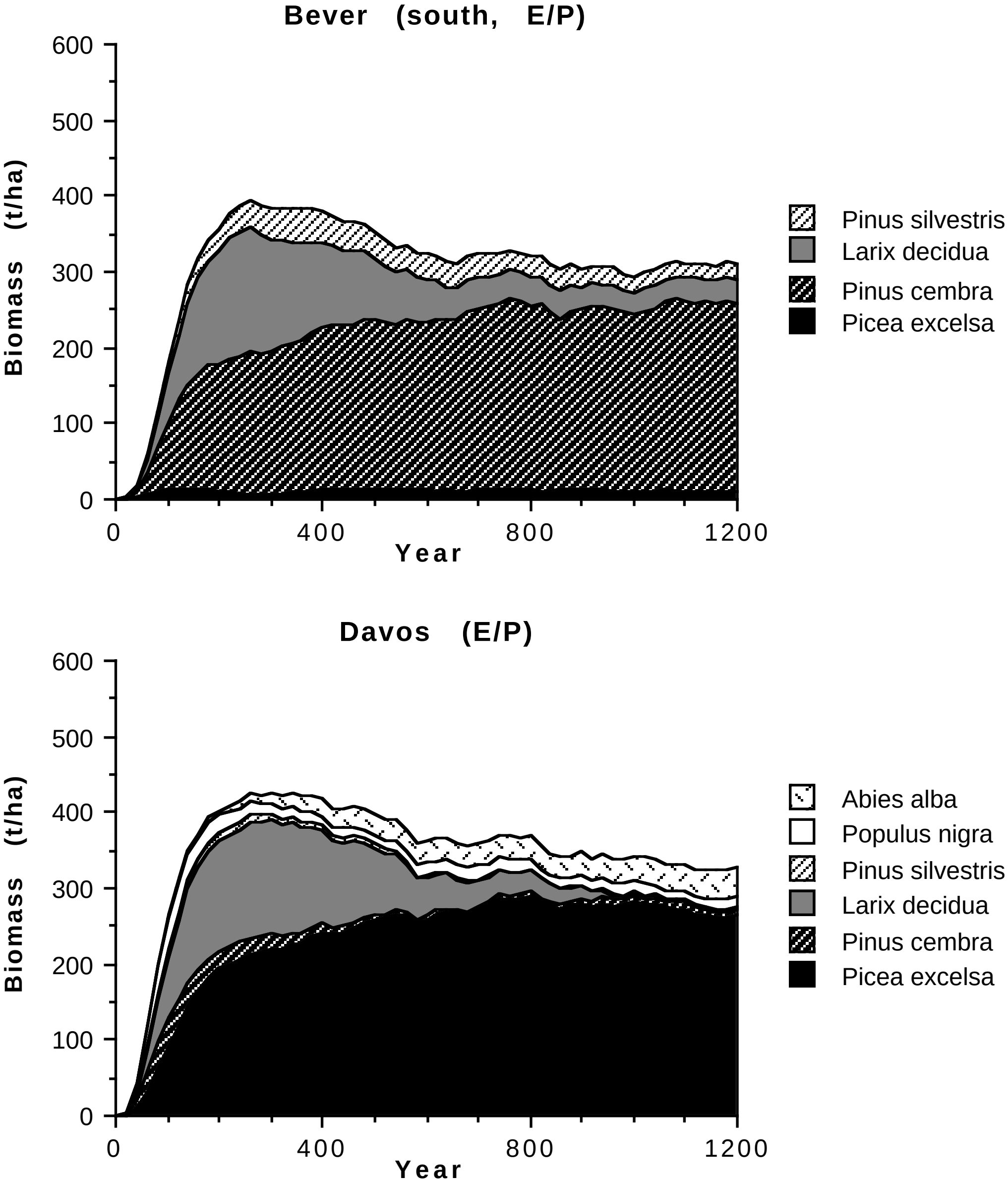


Fig. 4.8: Average species composition from 200 forest patches simulated by the combined FORCLIM-E/P model, assuming a nutrient-rich soil at the sites Bever (southern slope, top) and Davos (bottom).

At the site Bern (Fig. 4.11) oak becomes more important because it is tolerant of low nitrogen concentrations; on the other hand, the abundance of *A. alba* and *P. excelsa* decreases. The oak species *(Q. robur, Q. petraea)* may be too abundant in this model variant as compared to the descriptions by Ellenberg & Klötzli (1972) and Ellenberg (1986).

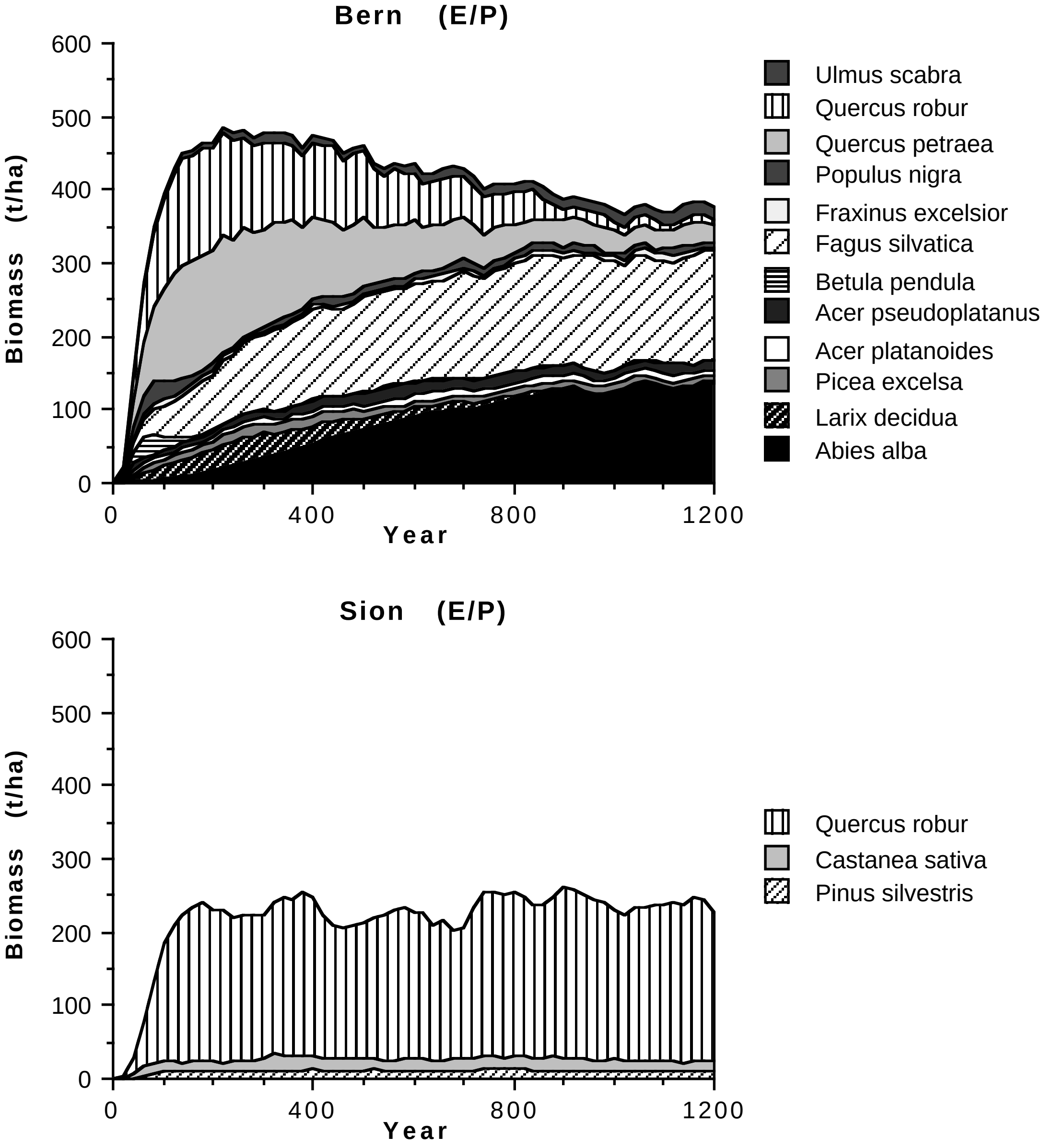


Fig. 4.9: Average species composition from 200 forest patches simulated by the combined FORCLIM-E/P model, assuming a nutrient-rich soil at the sites Bern (top) and Sion (bottom).

At the site Sion (Fig. 4.11), no obvious changes are evident as compared to FORCLIM-E/P, although nitrogen availability is lower (Tab. 4.5). The reason for this is twofold: (1) all three species are tolerant of low nitrogen concentrations; thus none of them gets a competitive advantage over the others; (2) drought stress is of paramount importance at this site, and all the other environmental influences are marginal.

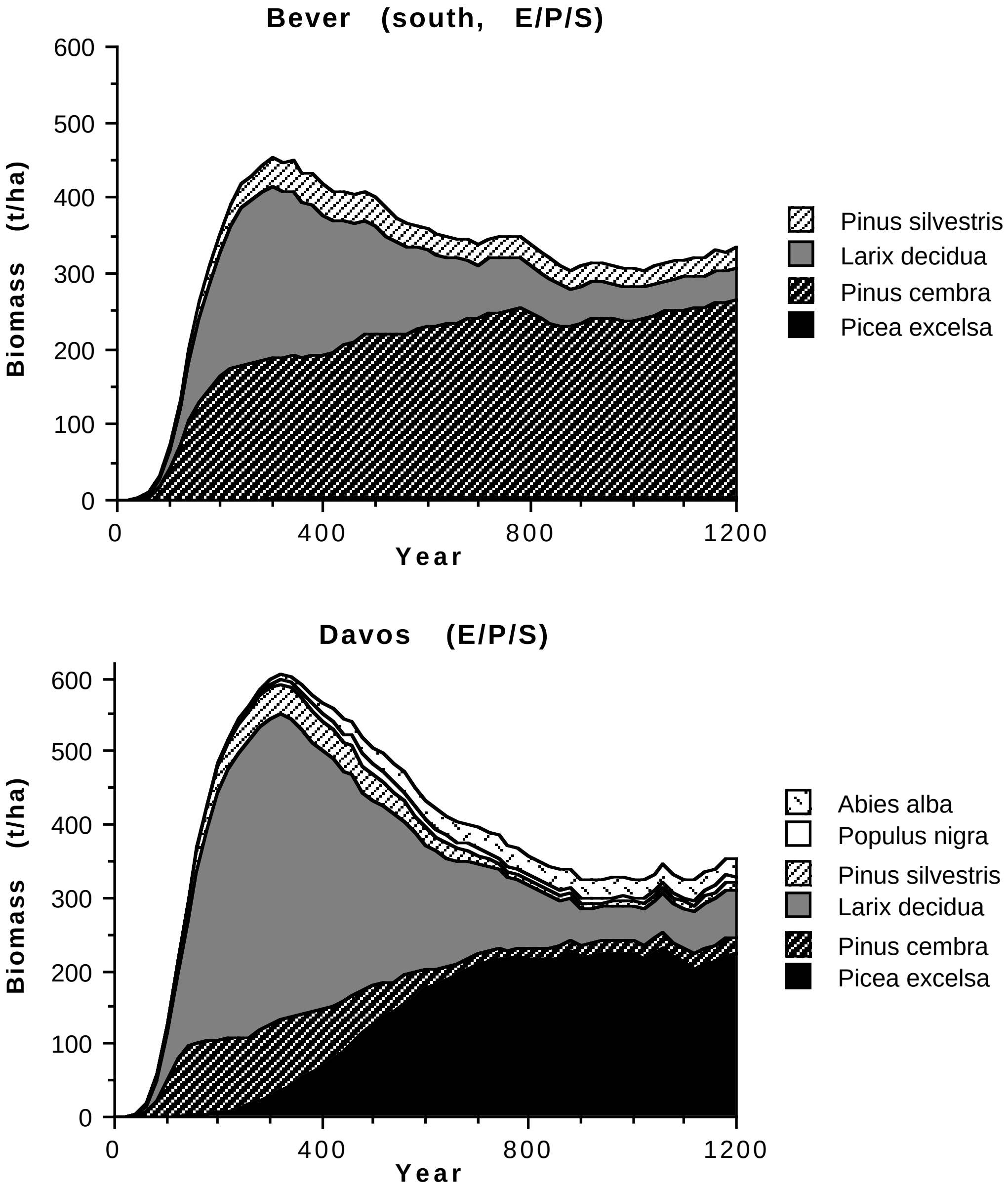


Fig. 4.10: Average species composition from 200 forest patches simulated by the full FORCLIM-E/P/S model at the sites Bever (southern slope, top) and Davos (bottom).

When comparing the amounts of organic matter simulated by FORCLIM-S in isolation (Tab. 4.3) with those produced by the coupled E/P/S model (Tab. 4.5), it may be concluded that the explicit coupling of the plant and the soil submodel does not have large effects on simulated soil organic matter dynamics; however, the species composition is affected considerably by the temporal variability of nitrogen availability, which favours tree species that are tolerant of these conditions.

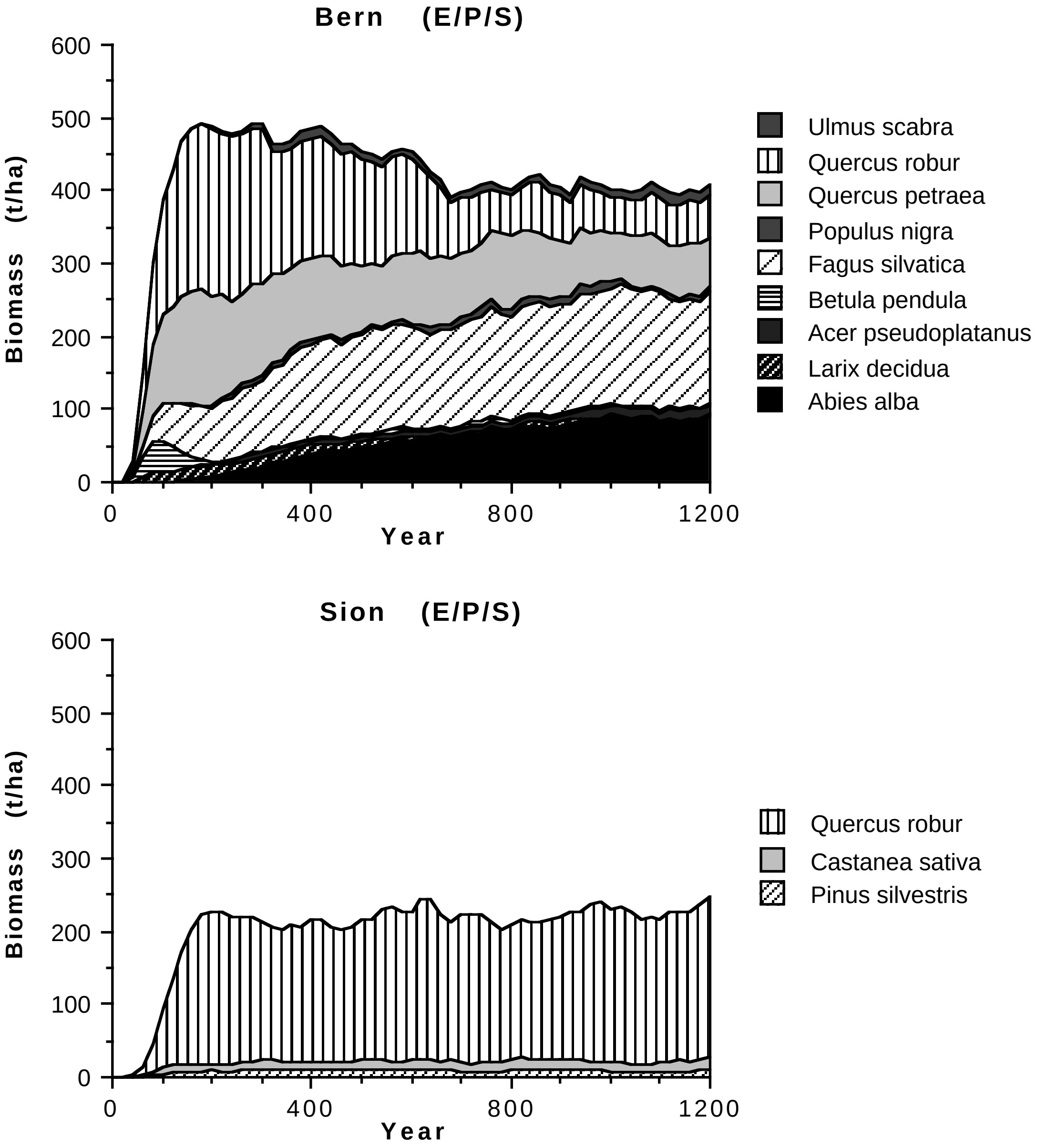


Fig. 4.11: Average species composition from 200 forest patches simulated by the full FORCLIM-E/P/S model at the sites Bern (top) and Sion (bottom).

Tab. 4.5: Organic matter in the litter (LOM, t/ha) and humus compartments (HOM, t/ha), total soil organic matter (SOM, t/ha), and total available nitrogen (uAvN, kg/ha) as calculated by FORCLIM-E/P/S in the steady state. Cf. Tab. 4.3 with the same results from the FORCLIM-S model simulated in isolation.

Site	uAvN	LOM	HOM	SOM
Bever N	72.7	57.0	260.1	317.1
Davos	80.5	67.4	113.4	180.9
Sion	88.3	87.6	56.3	143.9
Bever S	68.0	52.4	92.3	144.7
Bern	137.0	111.3	85.1	196.3
Locarno	142.0	119.8	81.0	200.8

4.3.4 Discussion & conclusion

The simulation studies with various combinations of submodels, all including FORCLIM-P, reveal the following:

The FORCLIM-P model driven by constant weather (section 4.3.1) produces plausible species compositions for some sites (Davos, Bern). However, under circumstances of strong environmental stress, such as close to the alpine and the dry timberline (Bever, Sion), average weather conditions do not suffice to characterize the effects of the abiotic environment on the trees. It may be concluded that the variability of the abiotic environment is at least as important as its averages (cf. Katz & Brown 1992), and that it is necessary to couple FORCLIM-E with FORCLIM-P explicitly (section 4.3.2).

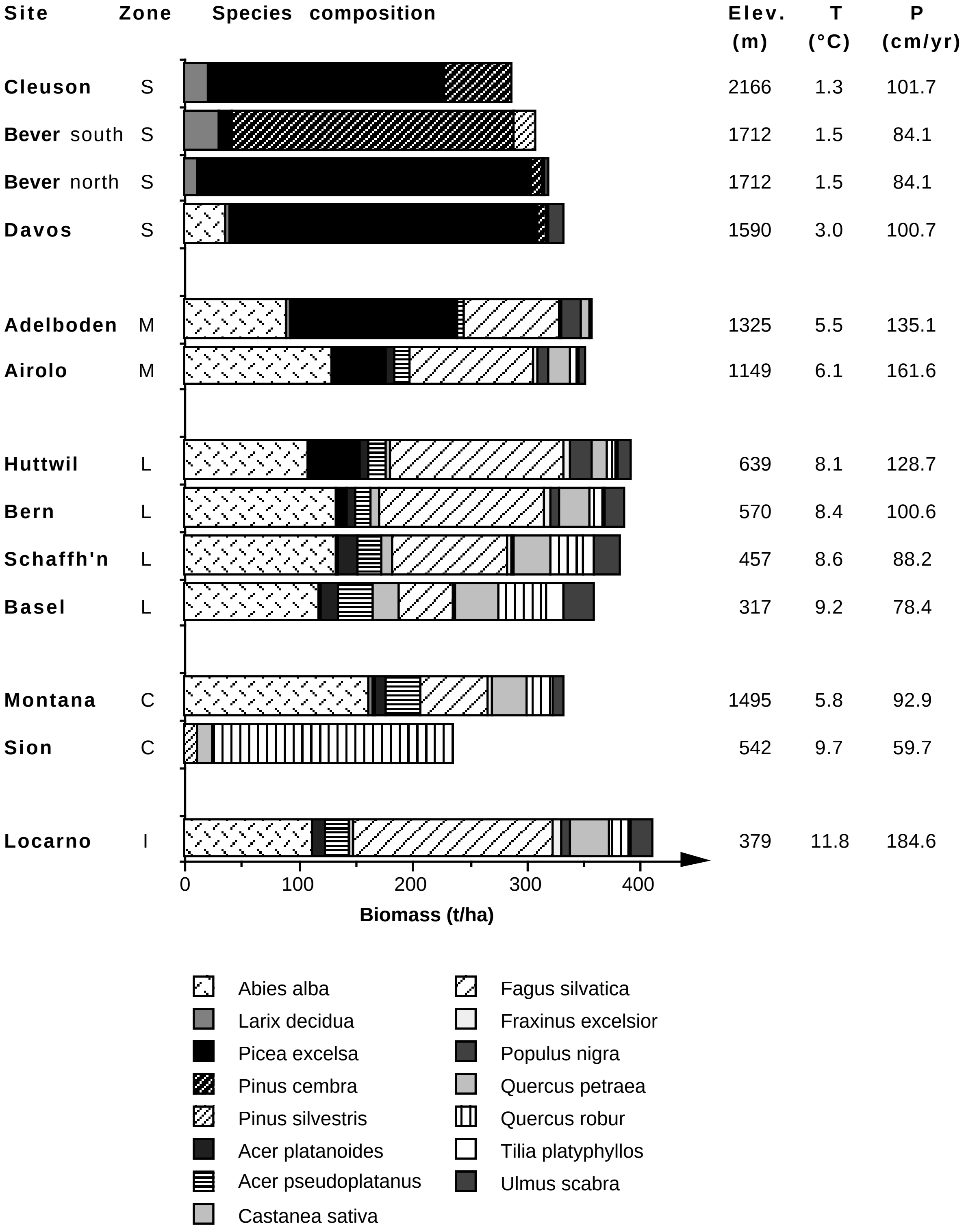
The nitrogen availability simulated by the submodel FORCLIM-S when coupled to FORCLIM-P changes strongly through time. This may have a considerable effect on the simulated species compositions. On the other hand, the amount of soil organic matter simulated by FORCLIM-S does not change much if the FORCLIM-P model is used to simulate litter production instead of assuming a constant production. Thus, the behaviour of FORCLIM-S is influenced only weakly by FORCLIM-P, but FORCLIM-P is influenced more strongly by FORCLIM-S.

The simulation results at the four sites (Fig. 4.6 – 4.11) suggest that the coupling between FORCLIM-S and FORCLIM-P is weaker than the one between FORCLIM-E and FORCLIM-P. The strength of these couplings may be used to explain why the large majority of forest gap models constructed so far have been successful although they ignore the dynamics of nutrients and soil organic matter (Botkin et al. 1972a,b, Shugart 1984, Botkin 1993), but most of them include a stochastic weather generator (one prominent exception is FORSKA-2, Prentice et al. 1991, 1993).

At the sites Bever and Sion, the availability of nitrogen simulated by FORCLIM-S does not have a strong influence on the simulated species composition. At the other two sites, the simulated effect of nitrogen availability on forest succession is debatable: At Davos, the biomass peak of 600 t/ha, which is made up mainly of *L. decidua,* appears little plausible for a subalpine site that should be characterized by low-biomass forests (Fig. 4.10). At the site Bern, the simulated nitrogen availability leads to a considerable increase of the biomass of *Quercus spp.* (Fig. 4.11), which may be questionable because *Quercus spp.* should reach large biomass only under warm and dry conditions, for which the site Bern is not characteristic (Ellenberg & Klötzli 1972).

Based on these considerations it is concluded that the model variant FORCLIM-E/P/S is not more trustworthy than the model variant FORCLIM-E/P and does not offer clear advantages over the variant E/P. Thus, in the subsequent investigations the variant FORCLIM-E/P will be used as the standard model setup. The steady-state species compositions simulated by this model variant at all the sites along the transect in the European Alps are given in Fig. 4.12. Typical examples of the transient behaviour of FORCLIM-E/P at subalpine sites are given in Fig. 4.8 (Bever, Davos). Fig. 4.13 shows the transient behaviour of the model at the montane site Airolo, which will be used in the sensitivity analysis of FORCLIM. The behaviour typical of low-elevation sites is given in Fig. 4.9 (Bern) together with that of a dry central alpine site (Sion, Fig. 4.9). The steady-state species composition simulated at the insubrian site Locarno (Fig. 4.12) does not differ strongly from the one simulated at the site Bern, which may be questionable (Ellenberg 1986). The same goes for the species composition simulated at the site Montana (Fig. 4.12). The reasons for this behaviour will be elaborated in detail in section 5.3.

Finally, it may be concluded that the FORCLIM model produces species compositions that are as plausible as the ones obtained from its predecessor model FORECE (Kienast 1987). At low-elevation sites (e.g. Bern), the FORCLIM simulation results are even more plausible (Ellenberg & Klötzli 1972, Ellenberg 1986). Further tests of the performance of both models will be conducted in section 5.3.



Site	Zone	Elev. (m)	T (°C)	P (cm/yr)
Cleuson	S	2166	1.3	101.7
Bever south	S	1712	1.5	84.1
Bever north	S	1712	1.5	84.1
Davos	S	1590	3.0	100.7
Adelboden	M	1325	5.5	135.1
Airolo	M	1149	6.1	161.6
Huttwil	L	639	8.1	128.7
Bern	L	570	8.4	100.6
Schaffh'n	L	457	8.6	88.2
Basel	L	317	9.2	78.4
Montana	C	1495	5.8	92.9
Sion	C	542	9.7	59.7
Locarno	I	379	11.8	184.6

Fig. 4.12: Steady-state species composition as simulated by the model FORCLIM-E/P along a transect in the European Alps. Zones are S – subalpine, M – upper montane, L – colline (Swiss Plateau), C – central alpine, I – insubrian (Ellenberg 1986). "Elev." denotes the elevation of the sites, "T" stands for the long-term annual mean temperature, and "P" for the long-term annual precipitation sum at the sites. The steady states were calculated by averaging the output from 200 patches between the years 1000 and 1200.

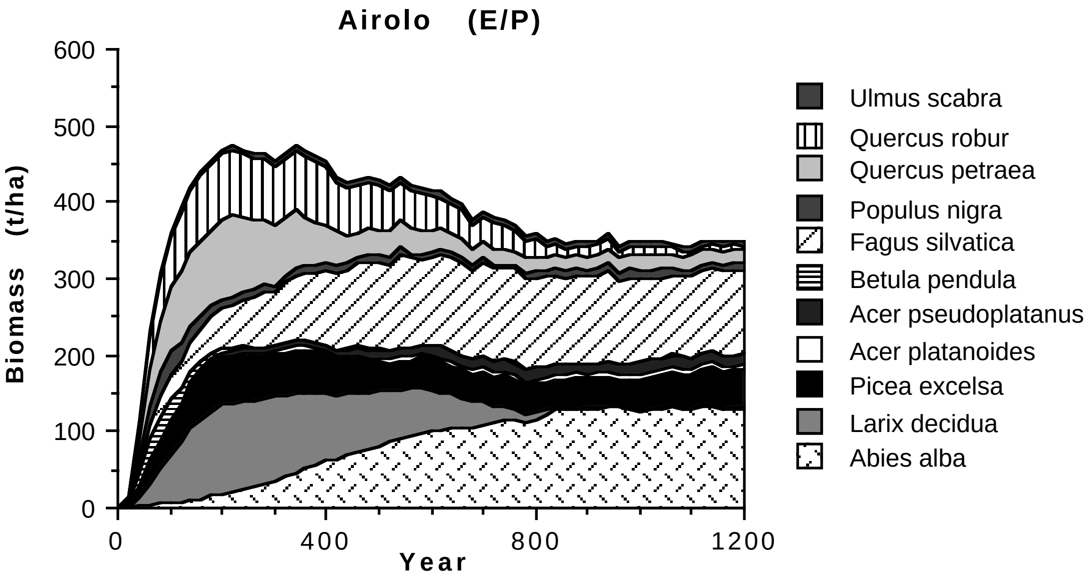


Fig. 4.13: Average species composition from 200 forest patches simulated by the combined FORCLIM-E/P model, assuming a nutrient-rich soil at the site Airolo.

4.4 A new method for estimating the equilibrium species composition

In many studies using forest gap models, it is more important to evaluate the steady state species composition than to know the transient behaviour of the model starting from the highly unrealistic initial condition of a bare patch. Under these circumstances, it would be desirable to have a method for estimating the steady state species composition that avoids the need to simulate the transient behaviour on many patches. A way to achieve this is the following: Instead of simulating many patches (say, 200) over a comparably short time (say, 1200 years), one can simulate just one patch over a much longer time span. Discarding the first centuries of transient behaviour, the average species composition over time will be the same as the average species composition across many patches, because the stochastic process underlying forest gap models appears to be stationary.

The species composition of two points in time of one patch is autocorrelated (section 2.2); hence the distance between the samples (Δt) should be chosen so that autocorrelation becomes negligible. On the other hand, the number of samples *(n)* should be sufficiently large. If the required Δt and n fulfil the inequality $\Delta t \cdot n < 200 \cdot 1200$, then this estimation procedure is more efficient than the conventional method of simulating many patches.

There are two fundamental questions to be addressed within this context:

1) How close to the “true” equilibrium state are the estimates as a function of *n* and Δt? In addition to theoretical reasoning, simulation experiments can yield quantitative information on the precision of such estimates.

2) How similar to each other are two estimates of the same steady state, using a given *n* and Δt? This question is especially important if two model variants are to be compared, e.g. for assessing the effect of climatic change on species composition. Moreover, is it possible to develop a threshold for significant differences between steady states for a given *n* and Δt?

4.4.1 Material & methods

To answer the above two questions, two sets of simulation experiments were conducted with the FORCLIM-E/P model. From the analysis in section 2.2.1, it can be hypothesized that temporal autocorrelation is important at lags up to more than 100 years, and the data from section 2.2.2 suggest that the sample size should be larger than 100. Thus, to answer question 1, a factorial design was used with *n* = 50, 100, 200, 400, 1000, and Δt = 100, 150 years. This yielded a total of 10 experimental setups. For each setup, 20 simulation runs were performed, and a steady state was estimated from each run. The first 1000 years of each simulation were discarded (transient behaviour, cf. chapter 4). The “true” equilibrium was assumed to be the average of the 20 steady states estimated with *n* = 1000 and Δt = 150, thus corresponding to 20'000 points. The percentage similarity coefficient (PS) introduced in Eq. 2.3 was used for comparing the steady states, and simulations were conducted for the site Bern (cf. Appendix III).

From these results, the combination of *n* = 200 and Δt = 150 years was chosen for further study, i.e. to answer question 2. It may be hypothesized that it is easier – both in a forest gap model and in reality – to estimate the composition of a species-poor forest with one dominating species than that of a diverse forest with many co-dominating species. Moreover, the abundance of a species that is always present on a patch but has low biomass is easier to estimate than that of a species with episodic occurrence, but that attains large biomass when it is present. Thus, the PS between independent estimates of the same steady state at a given site should depend on the number of species and their roles at that site (cf. Shugart 1984). To test this hypothesis, 400 steady states were estimated at three sites along a gradient of altitude and species diversity (Bern, Airolo, Davos; Fig. 4.12), and the distributions of the PS coefficients calculated from 200 pairs of independent steady states were analysed statistically.

4.4.2 Results & discussion

SIMILARITY TO THE "TRUE" STEADY STATE SPECIES COMPOSITION

Fig. 4.14 shows the averages and standard deviations of the 20 PS coefficients as a function of *n* and Δt. There is a strong increase of the PS up to *n* ≈ 200; with higher values of *n*, the increase of precision becomes comparably small. It is interesting to note that about the same increase of precision is achieved when Δt is increased by 50% (from 100 to 150 years) as when *n* is doubled, i.e. increasing Δt is more efficient. However,

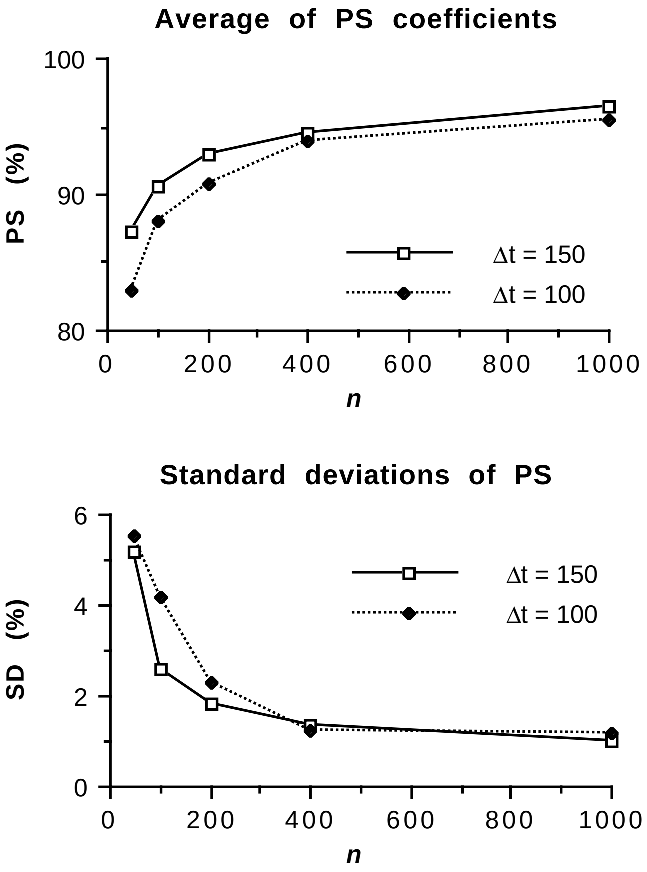


Fig. 4.14: Convergence of the percentage similarity coefficient between estimated equilibrium states and a conjectured "true" equilibrium state at the site Bern in function of the number of points (*n*) and the point-to-point distance (Δt) used.

this would not be true for much larger Δt where autocorrelation becomes negligible. The choice of *n* = 200 and Δt = 150 seems to provide a good compromise between the simulation time needed and the accuracy of the estimation; moreover, these data conform to the considerations in the sections 2.2.1 (autocorrelation) and 2.2.2 (sample size).

SIMILARITY OF INDEPENDENT ESTIMATES OF THE SAME STEADY STATE

The histograms of the distribution of the 200 PS coefficients obtained from 400 simulation runs at the three sites conform to the hypothesis formulated above (Fig. 4.15, Tab. 4.6): In the species-poor *Larici-Piceetum* at Davos (Ellenberg & Klötzli 1972), the PS coefficients are considerably higher than in the diverse forests of Airolo and Bern.

The reason for the decreasing PS coefficients with increasing species diversity can be explained by considering the averages of the estimated species-specific biomasses and their coefficients of variation (CV, Zar 1984) from the 400 steady states estimated at each site.

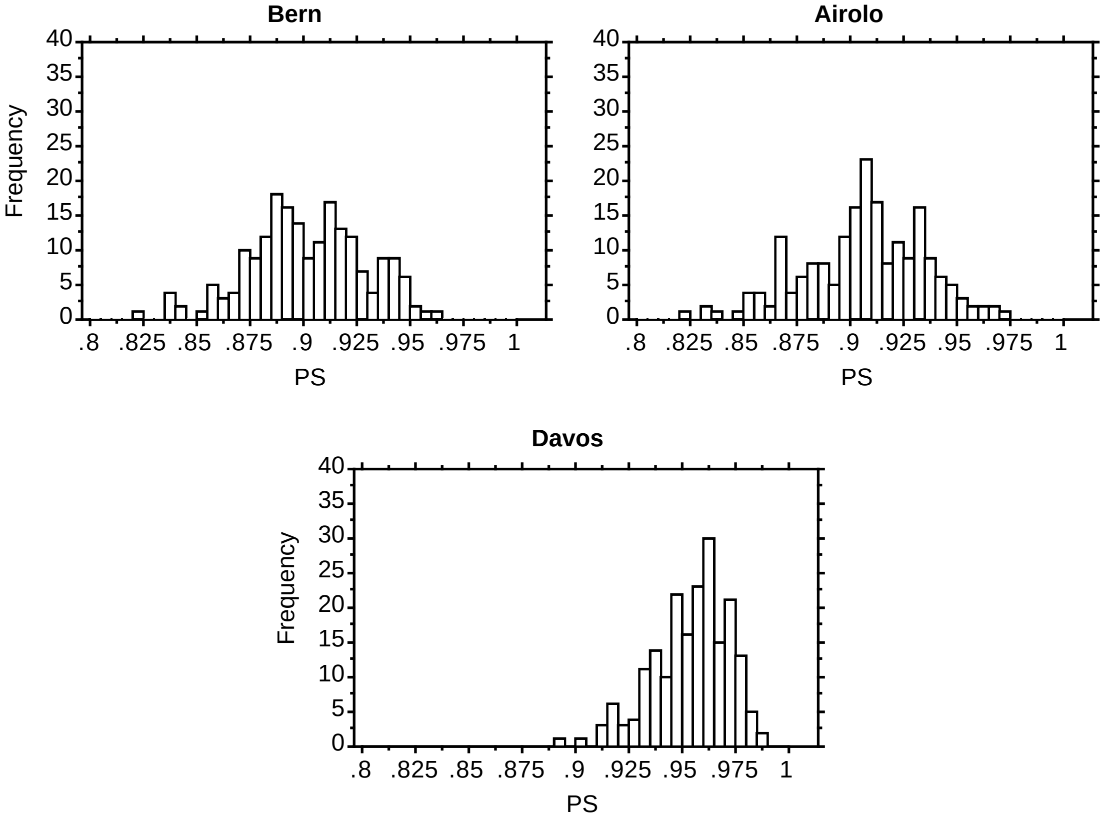


Fig. 4.15: Frequency distribution of the percentage similarity coefficients (PS) from 200 pairs of equilibrium states estimated at the sites Bern, Airolo, and Davos, using *n*=200 and Δt=150 years. The distributions at the sites Bern and Airolo are not significantly different from each other (p = 0.12, Kolmogorov-Smirnov test, Zar 1984).

Tab. 4.6: Statistics of the distribution of the PS coefficients at the three test sites. CI denotes the lower and upper 95% confidence interval of PS. The arcsine transformation is according to Zar (1984).

	Bern		Airolo		Davos	
	un-transformed	arcsine transformed	un-transformed	arcsine transformed	un-transformed	arcsine transformed
CI_{upper}	0.955	0.950	0.963	0.957	0.989	0.983
$\mu(PS)$	0.902	0.903	0.907	0.909	0.954	0.956
CI_{lower}	0.849	0.844	0.850	0.844	0.920	0.916

It is evident from Tab. 4.7 & 24 that the coefficient of variation tends to increase with decreasing species-specific biomass (e.g. *P. excelsa* vs. *L. decidua* at Davos, Tab. 4.7). Moreover, the species role (Shugart 1984) is important as well: For example, *L. decidua* and *P. cembra* have similar biomass at Davos; yet, since *P. cembra* is shade tolerant and usually present with low biomass, its CV is considerably smaller than that of *L. decidua*, which is usually absent except after the formation of a large gap, when it can establish and grow to a considerable size; afterwards, it disappears again.

Similar reasoning can be applied to the results from the site Bern: The biomass estimates of the two dominant species, *F. silvatica* and *A. alba*, have small coefficients of variation (Tab. 4.8). On the other hand, species with similar and low biomass such as *Acer pseudoplatanus* and *Quercus petraea* have coefficients of variation that differ considerably, again due to their different roles: *Q. petraea* is much less shade tolerant than *A. pseudoplatanus*. Obviously the species “roles” defined by Shugart (1984) provide a useful framework for this analysis.

Thus it may be concluded that the statistical properties of the PS coefficient between two independent estimates of the same steady state can not be stated generally. They depend

Tab. 4.7: Averages (μ) and coefficients of variation (CV) of 400 species-specific steady-state biomass estimates at the site Davos ($n = 200$, $\Delta t = 150$).

Variable	μ [t/ha]	CV
total biomass	340.8	2.4%
Picea excelsa	269.7	3.8%
Abies alba	34.5	16.2%
Populus nigra	13.8	16.6%
Larix decidua	8.9	61.3%
Pinus cembra	6.5	36.3%

both on the number of species participating in the succession as well as the specific role of those species (Shugart 1984).

The forest simulated by FORCLIM-E/P at the site Bern is among those with the highest species diversity (Fig. 4.12). Since the average value of the PS coefficients tends to increase with decreasing diversity, this site may be considered as a “worst case” of the statistical properties of the PS coefficients. Hence, two steady states of low-elevation, species-rich forests that are estimated using $n = 200$ and $\Delta t = 150$ years are significantly (95%) different from each other if $PS < 0.85$ (Tab. 4.6). The less species are present, the more the lower confidence limit increases; for species-poor forests (typically at higher elevations such as Davos), the lower end of the confidence interval (95%) increases to ≈0.92 (Tab. 4.6). Thus, also with respect to the size of this confidence limit the design of simulation experiments with $n = 200$ points and $\Delta t = 150$ years appears to be appropriate.

The simulation time required on a Macintosh Quadra 700 computer for simulating 200 patches of 1200 years each with the FORCLIM-E/P model is 133 minutes. On the other hand, estimating the steady state with $n = 200$ and $\Delta t = 150$ years and discarding the first 1000 years of the simulation requires to simulate one patch during 31'000 years, which corresponds to 17 minutes of simulation time, or 12.8% of the time necessary for the transient experiment. Thus, the method presented above is quite efficient if one desires to estimate the steady-state species composition of forest gap models.

Tab. 4.8: Averages (μ) and coefficients of variation (CV) of 400 species-specific steady-state biomass estimates at the site Bern ($n = 200$, $\Delta t = 150$).

Variable	μ [t/ha]	CV
total biomass	392.6	2.4%
Fagus silvatica	151.1	8.8%
Abies alba	128.9	9.5%
Acer pseudoplatanus	17.8	26.3%
Ulmus scabra	17.3	24.1%
Quercus petraea	17.3	59.8%
Picea excelsa	11.3	35.1%
Acer platanoides	10.4	20.0%
Populus nigra	9.6	26.4%
Fraxinus excelsior	6.5	30.3%
Quercus robur	5.6	122.7%

5. Parameter sensitivity & model validation

5.1 Sensitivity of species parameters in FORCLIM

There are various aims of a sensitivity analysis: It may be used for model corroboration, to provide guidelines for future research, or even for parameter estimation (Swartzman & Kaluzny 1987, p. 217). The former two aspects are especially important in the present study: First, little confidence can be placed in the predictions from a model that is extremely sensitive to parameter changes unless the real system has a similar sensitivity to these parameters. Second, since the values of most parameters in ecological models can not be determined with sufficient certainty, it is important to indicate which of them have a large influence on model behaviour; these findings then can provide guidelines for further research.

So far, only few sensitivity studies have been conducted with forest gap models (Kercher & Axelrod 1984, Dale et al. 1988, Leemans 1991). Due to the large parameter space of these models and the long simulation time required to run them, such analyses were restricted to a limited number of parameters (Kercher & Axelrod 1984, Dale et al. 1988), or they dealt with species-poor forests (Leemans 1991). The FORCLIM model has a comparably small parameter space (420 species parameters, cf. chapter 3), and it is apt for performing large-scale simulation studies (cf. chapter 4). Thus with FORCLIM it becomes possible to evaluate the sensitivity of all 420 species parameters.

Two major questions shall be addressed in the present sensitivity analysis:

1) How sensitive is the simulated species composition to the uncertainty inherent in the species parameters? Would the abundance of the dominating species change strongly if their parameters were altered? Would new, previously suppressed species become abundant if they had different parameter values?

2) Which species parameters are most important for determining the successional properties of the simulated forests? What are the most urgent research needs for narrowing the plausibility range of these parameters?

To answer these questions it is necessary to determine the plausibility range of each species parameter. In the following, both the response of the species composition as well as the simulated biomass of selected species will be evaluated.

5.1.1 Range of plausibility for species parameters

The uncertainty inherent in the estimation of the parameters describing maximum tree diameter (kDm), maximum height (kHm), and maximum age (kAm) was quantified from the data assembled during parameter estimation (Appendix II). For the parameters denoting the tolerance of the species on a nominal scale in the range [1…3] or [1…5], such as nitrogen (kNTol) and browsing tolerance (kBrow), as well as for the parameters describing the species type (sType) and its leaf litter quality (kLQ), the uncertainty was assumed to be ±1. Correspondingly, the uncertainty of the shade tolerance parameters (kL_a, kL_y), which are in the range [1…9], was assumed to be ±2 classes. The growth scaling constant (kG), which had turned out to be difficult to determine (Appendix II), was assigned the relatively large uncertainty of ±30%.

The uncertainty of the parameters determining the response to climate was set as follows: While the lower limit of the degree-day range (kDDMin) may be determined with adequate precision (assumed to be ±20%), the determination of the upper limit (kDDMax) has been shown to be more difficult (Prentice & Helmisaari 1991); its uncertainty there-

Tab. 5.1: Uncertainty inherent in the estimation of the species parameters of the FORCLIM-P model.

Parameter	Uncertainty	Parameter	Uncertainty
sType	±1, C/D not varied	kWiT	±2 °C
kDm	[1]	kDrT	±0.1
kHm	[1]	kNTol	±1
kAm	[1]	kBrow	±1
kG	±30%	kL_y	±2
kDDMin	±20%	kL_a	±2
kDDMax	±40%	kLQ	±1

[1] according to the range limits from the literature review (Appendix II).

fore was assumed to be twice as high as for the kDDMin parameter, i.e. ±40%. The uncertainty associated with the winter temperature parameter (kWiT) is also large and was assumed to be ±2 °C. Since drought gradients in the landscape are steep, the drought tolerance parameter (kDrT) is difficult to determine. Its uncertainty was assumed to be ±0.1. Please note that an absolute uncertainty was used since small kDrT values are not more precise than large ones, rather the reverse is true. Tab. 5.1 gives an overview of the plausibility range of each species parameter. Two tables with the minima and maxima for all parameters may be found in Appendix V.

5.1.2 Simulation experiments

The site Airolo (Appendix III) was chosen for the sensitivity analysis because it is located in the transition zone between subalpine coniferous and mixed deciduous forests, where the simulated community may be especially sensitive to parameter changes. Each species parameter was set to the lower and the upper end of its plausibility interval, and the steady state species composition of the FORCLIM-E/P/S model was estimated for each parameter change, thus resulting in $2 \cdot 420 = 840$ samples. The steady states were estimated using $n = 200$ points and $\Delta t = 150$ years (cf. section 4.4). Two types of analyses were performed:

1) To quantify the robustness of the simulated *species composition* to changes of species parameters, the simulated steady states were compared to a conjectured standard steady state calculated with the default parameter set given in Tab. 3.11 ($n = 20'000$ points, $\Delta t = 150$ years). For these comparisons, the percentage similarity coefficient (PS, Eq. 2.3) was used. A sample steady state is significantly different from the standard steady state if $PS < 0.871$ ($\alpha = 5\%$, determined from an investigation for FORCLIM-E/P/S at the site Airolo similar to the ones performed in section 4.4).

2) To quantify the response of *particular species* to changes of their parameters, it was tested whether the average biomass (μ) of the corresponding species is significantly different from the standard biomass (μ^*) of that species. Since the sampling distribution of the mean tends to normality with increasing sample size (and here, $n = 200$; Zar 1984), the range $\mu^* \pm 1.96 \cdot SE$ includes μ at a confidence level (α) of 5%, where SE is the standard error of the mean. For the species with significant differences, the percentage change was calculated.

5.1.3 Results & discussion

The detailed results of all the simulation experiments are listed in Appendix V; they are summarized here, and their statistical properties are presented and discussed as well.

ROBUSTNESS OF THE SIMULATED SPECIES COMPOSITION

The percentage similarity coefficients between the sample steady states and the standard steady state are generally high (PS > 0.72 except for kDrt with *Fagus silvatica;* Tab. 5.2). The overall species composition appears to be little sensitive to changes of single parameters within the plausibility range. This is a distinct difference to the FORECE model: For example, with an ITENO indicator parameter of *F. silvatica* of 5 (Kienast 1987), this species attains almost 40% of the total biomass simulated by FORECE at Airolo. However, when ITENO is increased by just one class (to 6), *F. silvatica* disappears completely (cf. the simulations with ITENO = 6 in Kienast 1991). Similar phenomena can be observed in FORECE for other species at Airolo (e.g. *Larix decidua)* as well as at other sites, such as with the IMST parameter of *Quercus spp.* at Sion.

Tab. 5.2 suggests that the FORCLIM-E/P/S model is sensitive mainly to the parameters of the most abundant species. Thus, their relative proportions are subject to considerable uncertainty: note for example that the lowest PS coefficients occur with *F. silvatica*, the most abundant species. On the other hand, the set of dominating species produced with the default parameter set seems to be rather robust to errors of parameter estimation, i.e. there are no species that turn up or disappear completely and alter the species composition qualitatively when their species parameters are changed within the plausibility range.

WHICH SPECIES PARAMETERS ARE MOST SENSITIVE?

According to Tab. 5.3 and considering the lower end of the plausibility interval of species parameters, the model appears to be most sensitive to the nitrogen tolerance parameter (kNTol), followed by the species type (sType) and the growth scaling constant (kG). For the upper end of the plausibility interval, the ranking is kNTol > kL_a (shading tolerance of adult trees) > kG and kDrT (drought tolerance). The effects of the uncertainty inherent in kNTol on the simulated species composition suggest that there is a strong coupling between FORCLIM-S and FORCLIM-P, as hypothesized earlier (cf. section 4.3.4).

However, I am not aware of a sensitivity analysis that deals with a forest gap model including soil organic matter dynamics; thus it is currently not possible to compare this finding with results from other research.

The importance of the sType parameter corresponds to the results from Kercher & Axelrod (1984), who found that their model is quite sensitive to changes of the allometric parameters determining leaf weight. The growth scaling constant (kG) is treated as an

Tab. 5.2: Sensitivity of species composition at the site Airolo to changes of species parameters, summarized for each species. p – percentage of all species parameters that lead to significant changes of the species composition (α=5%, PS<0.871); μ – average PS coefficient from all parameter changes; min – smallest PS coefficient of all parameters. The subscripts “low” and “up” denote the parameter values corresponding to the lower and the upper end of the plausibility range. Bold face is used to denote the most abundant species at the site Airolo. Insignificant changes are marked by italic face.

Species	p_{low}	μ_{low}	min_{low}	p_{up}	μ_{up}	min_{up}
Abies alba	46	0.850	0.732	33	*0.894*	0.758
Larix decidua	23	*0.885*	0.805	17	*0.898*	0.845
Picea excelsa	23	*0.882*	0.807	36	*0.888*	0.775
Pinus cembra	0	*0.916*	*0.871*	0	*0.913*	*0.873*
Pinus montana	0	*0.920*	*0.887*	13	*0.924*	0.861
Pinus silvestris	0	*0.914*	*0.872*	9	*0.910*	0.827
Taxus baccata	7	*0.914*	0.870	8	*0.909*	0.852
Acer campestre	8	*0.918*	0.848	0	*0.923*	*0.905*
Acer platanoides	0	*0.916*	*0.875*	7	*0.901*	0.862
Acer pseudoplatanus	17	*0.901*	0.858	8	*0.911*	0.866
Alnus glutinosa	0	*0.914*	*0.888*	7	*0.921*	0.868
Alnus incana	0	*0.918*	*0.878*	0	*0.914*	*0.889*
Alnus viridis	0	*0.917*	*0.886*	0	*0.917*	*0.880*
Betula pendula	0	*0.910*	*0.880*	0	*0.924*	*0.893*
Carpinus betulus	8	*0.916*	0.862	23	*0.897*	0.837
Castanea sativa	0	*0.929*	*0.878*	0	*0.929*	*0.883*
Corylus avellana	0	*0.910*	*0.874*	0	*0.921*	*0.875*
Fagus silvatica	67	0.837	0.641	46	0.851	0.722
Fraxinus excelsior	0	*0.923*	*0.881*	8	*0.905*	0.850
Populus nigra	8	*0.910*	0.864	9	*0.916*	0.868
Populus tremula	0	*0.915*	*0.880*	0	*0.916*	*0.878*
Quercus petraea	38	*0.893*	0.849	29	*0.890*	0.784
Quercus pubescens	8	*0.905*	0.870	17	*0.903*	0.815
Quercus robur	8	*0.904*	0.859	23	*0.894*	0.776
Salix alba	0	*0.915*	*0.876*	9	*0.920*	0.866
Sorbus aria	8	*0.922*	0.864	8	*0.902*	0.866
Sorbus aucuparia	0	*0.911*	*0.872*	15	*0.907*	0.806
Tilia cordata	21	*0.912*	0.858	0	*0.913*	*0.882*
Tilia platyphyllos	0	*0.919*	*0.877*	15	*0.912*	0.834
Ulmus scabra	17	*0.909*	0.836	8	*0.905*	0.864

auxiliary variable in the Kercher & Axelrod model and is calculated as a function of maximum tree age (kAm); thus the high sensitivity to kAm found in their study corresponds to the results given in Tab. 5.3. Unfortunately, they did not include the light response parameters (kL_a) in their sensitivity analysis.

The results from the sensitivity analysis by Dale et al. (1988) are not directly comparable with the present data because they expressed kG as a function of maximum tree diameter (kDm), kAm, and maximum height (kHm). Their finding that the sensitivity is kDm > kAm > kHm thus is difficult to compare with the results from Tab. 5.3. At the site Airolo, FORCLIM appears to be least sensitive to changes of kDm, which does not conform to the results by Dale et al. (1988). However, this finding is quite important for FORCLIM because data for determining the kDm parameter are scarce (cf. Appendix II).

In a sensitivity study of the FORSKA model, Leemans (1991) found that FORSKA is most sensitive to changes of the growth scaling constant (corresponding to kG), an allometric parameter for determining leaf area as a function of diameter at breast height (corresponding to sType), and parameters of the light response function (kL_a). Since the version of FORSKA used by Leemans (1991) included neither nitrogen availability (kNTol) nor drought stress (kDrT) nor the effects of low winter temperatures (kWiT), it can be concluded that his results conform to the findings of the present study (Tab. 5.3).

Tab. 5.3: Sensitivity of species composition at the site Airolo to changes of species parameters, summarized for each parameter. p – percentage of the number of species that show significant changes of the species composition (α=5%, PS<0.871); for the other symbols see Tab. 5.2. The parameters are listed according to decreasing number of significant changes (sum of $p_{low} + p_{up}$).

Parameter	p_{low}	μ_{low}	min_{low}	p_{up}	μ_{up}	min_{up}
kNTol	21	0.896	0.789	35	0.883	0.806
kG	17	0.902	0.775	17	0.895	0.765
kDrT	13	0.895	0.641	17	0.904	0.775
kWiT	14	0.902	0.834	14	0.896	0.722
kL_a	7	0.905	0.848	20	0.907	0.849
kAm	10	0.904	0.732	14	0.910	0.834
sType	19	0.908	0.770	4	0.919	0.868
kL_y	10	0.912	0.853	13	0.905	0.758
kDDMin	7	0.906	0.854	13	0.908	0.815
kBrow	8	0.915	0.870	5	0.919	0.827
kHm	3	0.913	0.770	7	0.913	0.861
kDDMax	10	0.906	0.805	0	0.912	0.872
kLQ	10	0.910	0.836	0	0.919	0.876
kDm	4	0.916	0.846	4	0.911	0.866

The large sensitivity to kDrT (Tab. 5.3) found in the present study is primarily a consequence of the large plausibility range of this parameter; it points to the need for further research on the drought tolerance of the tree species and their response to drought stress.

RESPONSE OF PARTICULAR SPECIES TO PARAMETER CHANGES

The data from this analysis (cf. Appendix V) also suggest that the parameters kNTol, kG, kL_y, and kL_a are most important for shaping species performance. Other parameters such as kDm, kAm, kDDMin, and kDDMax were found to be important for some species that have low abundance. However, even if the relative change of their biomass was positive and high, they did not attain considerable biomass; for example, the biomass of *Tilia platyphyllos* increased by 8510.6% (!) when its kDDMin parameter was lowered, yet it reached a biomass of 1.6 t/ha only. Thus, it may be concluded that the biomass estimates of minor species are not robust to parameter changes, and the simulated abundance of those species should not be interpreted quantitatively.

5.1.4 Conclusion

The analysis of the sensitivity of FORCLIM to the values of its species parameters revealed the following:

The species composition simulated by FORCLIM appears to be quite robust to changes of species parameters. Specifically, there are no suppressed species that attain large biomass when one of their species parameters is changed. On the other hand, in some instances the biomass of the most abundant species may decrease considerably, but they still remain characteristic of the simulated forest.

The abundance of the species may vary markedly depending on the parameter values used. Thus the simulated quantity of a given species should be interpreted cautiously. This may be interpreted in the context of the scheme proposed by Levins (1966): Forest gap models may be general and realistic, but the precision of the simulated species composition is rather low.

The FORCLIM model appears to be most sensitive to the values of the kNTol parameter, pointing to the need for further research on soil organic matter dynamics and nutrient availability. Other important parameters are those shaping the maximum growth equation (kG), followed by those describing the response of the species to drought (kDrT), winter temperature (kWiT), and light availability (kL_y, kL_a, sType).

Even though it was possible to perform a sensitivity analysis that included all species-specific parameters in FORCLIM, this does not mean that a generalized statement about the sensitivity of the model to the values of these parameters can be derived: First, the sensitivity of the model to the value of a certain parameter is a function of the abiotic environment and can not be stated generally from the analysis at one single site (Airolo). Second, only the effects on the steady-state species composition were evaluated. Kercher & Axelrod (1984) showed that the relative sensitivity of the SILVA model varies along the time axis; ecologically speaking, the sensitivity of a model during the transient phase may be just as important as in its steady state. Moreover, the percentage similarity coefficient used to compare the species compositions is an aggregated index which is little sensitive to the biomass of species with low abundance, thus concealing part of the effects of the changed parameters. It may be concluded that further studies on the parameter sensitivity of forest gap models would be desirable.

The results from the present study agree to a large extent with those from earlier, partial sensitivity analyses (Kercher & Axelrod 1984, Dale et al. 1988, Leemans 1991), suggesting that the same ecological factors govern the dynamics in the various forest gap models. Moreover, the robustness of the species composition simulated by the FORCLIM model increases our confidence that these results are not arbitrary and that the model produces reliable hypotheses about the near-natural forest vegetation.

5.2 Choice of data and experiments for model validation

The term “model validation” is used with various meanings in ecology. Swartzman & Kaluzny (1987) note that “validation” in the strict sense is a misnomer: It is impossible to assess the truth of a model. We can simply design experiments to increase our confidence that a model meets its objectives; Swartzman & Kaluzny (1987) term this “model corroboration”. However, because it is widespread, the term “validation” will be used in the present study as well with the following definition: In a validation procedure, the performance of a model is tested on its agreement with a set of observations that are independent of those observations used to structure the model and to estimate its parameters (Shugart 1984).

The FORCLIM model was developed to allow for projections of forest dynamics in a changing climate; thus its validation should deal with its behaviour along climatological gradients. There is a wealth of observations on past and current forests in central Europe that potentially could be used to validate various aspects of forest gap models, such as

- Yield tables (e.g. Anonymous 1983, Schober 1987)
- Forest inventories (Zingg & Bachofen 1988, Mahrer 1988)
- Forest reserves (Leibundgut 1978, Broggi & Willi 1993)
- Tree-ring chronologies (Schweingruber et al. 1984, Briffa et al. 1990)
- Pollen records (Huntley & Birks 1983, Ammann & Tobolski 1983, Lotter 1988, Birks 1990, Huntley 1992)
- Remotely sensed data (Guyenne & Calabresi 1989, Blasco & Achard 1990, Runkel 1990, Roughgarden et al. 1991, Hall et al. 1991, Treviño Garza 1992)
- Phytosociological descriptions of the potential near-natural forest types (Schmid 1949, Ellenberg & Klötzli 1972, Ellenberg 1986)

The advantages and deficiencies of these data sources are summarized in Tab. 5.4. It becomes evident that there is no “ideal” source of data for the validation of FORCLIM. Most of the criteria in Tab. 5.4 are met by data from forest reserves and by phytosociological descriptions. While the former are available at a few sites only and thus hardly allow to study climatological gradients, the latter do not cover the temporal aspects of forest dynamics. However, Rehder (1965) and Ellenberg (1986) developed an interesting approach that was based on a large body of phytosociological data: They developed a scheme that presents the dominating species of near-natural forests of central Europe in a climatological space spanned by the annual mean temperature and the annual precipitation sum (Fig. 5.1). A simulation study of these forests could provide detailed information about the changes of the species composition along climatic gradients under current climate and the agreement of the simulated forests with those hypothesized by the two authors. These advantages outweigh the static nature of these descriptions; hence section 5.3 shall deal with such an analysis.

FORCLIM was constructed using an altitudinal gradient in the European Alps (chapter 4). Thus, another transect in the same area would not be really independent of the first one. However, a similar transect in another continent, i.e. with a set of species and climatic

Tab. 5.4: Advantages and deficiencies of various data sources for a model validation study. The following ranking is used for the criteria: Spatial and temporal coverage: + high, – low; Climatological gradient: + data contain a climatological gradient in time or space; – no climatological gradient can be derived from the data; Management: + low, – high; Mapping: + data can be mapped easily to an output of the model, – data can not be mapped directly to model output; Correspondence: + data corresponds to the output of a mixed-age, mixed-species forest gap model of unmanaged stands, – data is from another type of forest or another scale; Effort required: + effort for providing data and simulating these conditions is low, – major effort is required.

Criterion	Yield tables	Ivento-ries	Forest reserves	Tree rings	Pollen data	Remote sensing	Phytosociol. descriptions
Spatial coverage	?	+	–	–	–	++	+
Temporal coverage	+	–	(+)	++	++	–	–
Climatological gradient	–	+	(+)	++	++	+	+
Management	–	–	+	?	+	–	+
Mapping	++	+	+	+	–	–	+
Correspondence	–	+	+	–	–	–	+
Effort required	–	–	–	+	–	–	+

conditions that the model has not been developed for, would constitute a truly independent source of data; the forests simulated by FORCLIM could be compared to those simulated by other forest gap models and to descriptions of the near-natural forests of the area. Therefore, in a second validation experiment the performance of FORCLIM shall be examined along a latitudinal gradient in eastern North America (section 5.4).

5.3 Behaviour of FORCLIM in central Europe

5.3.1 Derivation of input data

The scheme developed by Rehder (1965) and Ellenberg (1986) on the dominating species in near-natural forests of central Europe is redrawn in Fig. 5.1. The climatological space spanned by annual mean temperature and annual precipitation sum in Fig. 5.1 ranges from the alpine timberline (bottom) to insubrian and mediterranean forests (top) and from the dry timberline (left) to humid forests (right).

This climatological space with the associated forests presents a challenge to the FORCLIM model: FORCLIM can not be applied directly to simulate these forests because it requires climatic input data of monthly resolution (cf. Appendix III). However, if the annual cycle of the monthly variables shows a reasonably constant pattern over the whole climatological space, then it is possible to provide the climatic input data required by forest gap models such as FORCLIM.

The climatological data from the 12 sites presented in Appendix III were analysed for their annual cycles (Fig. 5.2). The monthly mean temperature can be predicted well from the annual mean temperature because the temperature amplitude, i.e. the difference between the temperature of the warmest and the coldest month, does not vary much among the climate stations. The monthly precipitation sum can be expressed adequately as a fraction of the annual precipitation sum. The standard deviations of the two variables are more difficult to predict, with better results for temperature than for precipitation. Specifically, the two sites on the southern slope of the Alps (Airolo and Locarno) had to be excluded from the analysis of the standard deviation of precipitation because they exhibit a pattern strongly different from the one at the stations on the northern slope of the Alps.

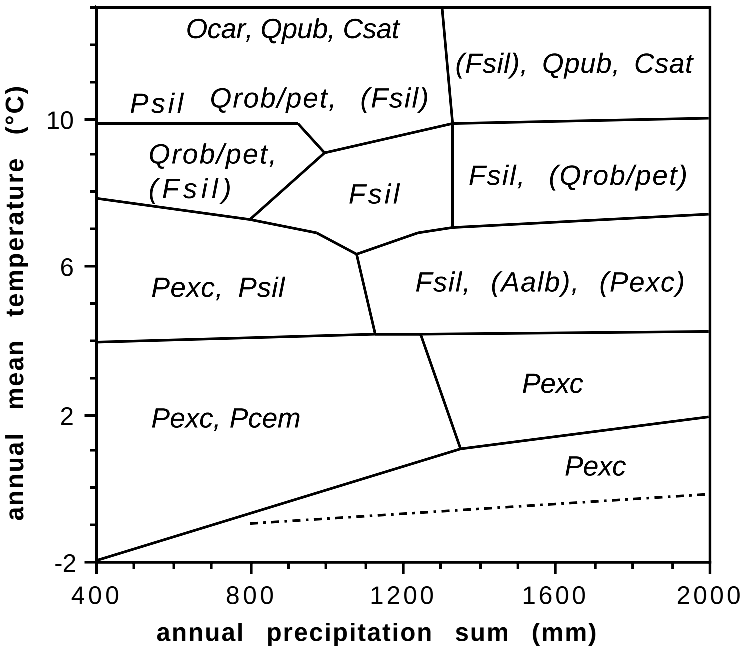


Fig. 5.1: Dominating tree species in a space spanned by the annual precipitation sum and the annual mean temperature according to Rehder (1965) and Ellenberg (1986). Key to species: Aalb – *Abies alba*; Csat – *Castanea sativa*; Fsil – *Fagus silvatica*; Ocar – *Ostrya carpinifolia*; Pcem – *Pinus cembra*; Pexc – *Picea excelsa*; Psil – *Pinus silvestris*; Qpet – *Quercus petraea*; Qpub – *Quercus pubescens*; Qrob – *Quercus robur*. The dash-spotted line close to the bottom of the graph indicates the approximate location of the alpine timberline.

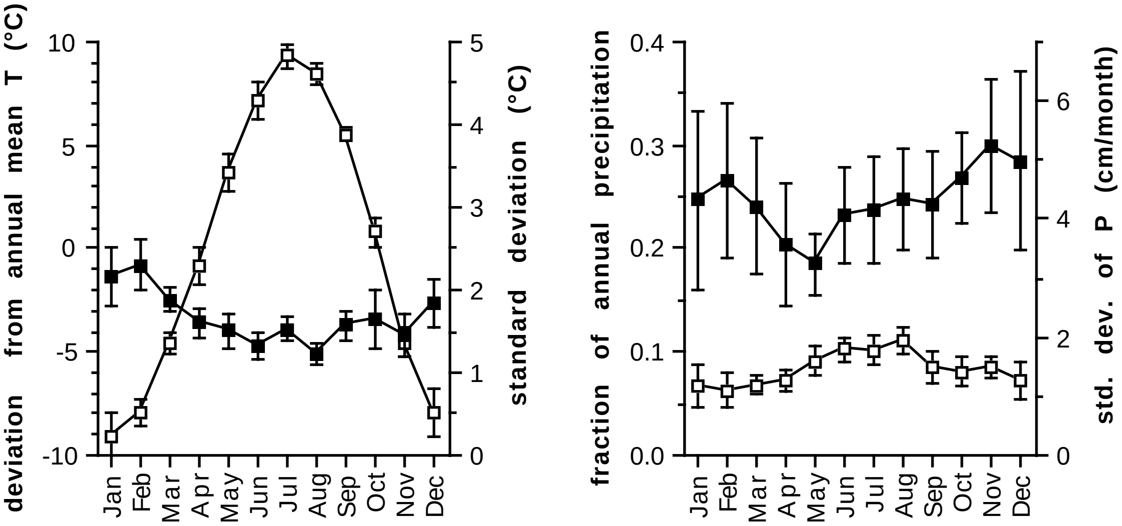


Fig. 5.2: Analysis of the annual cycle of the long-term climatic parameters at the 12 study sites (Appendix III). Left: Average deviation of monthly mean temperatures from the annual mean temperature (open squares); average standard deviation of the monthly mean temperatures (black squares). Right: Average fraction of the annual precipitation sum falling in every month (open squares); average standard deviation of the monthly precipitation sums at 10 sites on the northern slope of the Alps (black squares, excluding Airolo and Locarno). The error bars in both graphs denote one standard deviation.

There is a confounding factor inherent in the derivation of the monthly temperature data from the annual mean: The temperature amplitude increases slightly in drier climates, and this is the reason why the alpine timberline in Fig. 5.1 is found at lower annual mean temperatures as precipitation decreases. Linear regressions of the annual temperature amplitude against the annual precipitation sum from various subsets and the whole set of the 12 climate stations (Appendix III) generally yielded insignificant correlation coefficients, but the intercept was always close to 20 °C, and the slope varied between -0.002 and -0.0009. In spite of the insignificance of the regressions, the following approximation for the effect of the annual precipitation sum (P_l) on temperature amplitude (A_l) was used to reconstruct the annual cycle of monthly mean temperatures:

$$A_l \approx 20 - 0.0014 \cdot P_l \qquad (5.1)$$

Based on these considerations, the long-term mean monthly temperature ($T_{m,l}$) is calculated from the annual mean temperature (T_l) and the annual precipitation sum (P_l) according to Eq. 5.2:

$$T_{m,l} = T_l + \Delta T_m \cdot \frac{(1180 - P_l) \cdot 0.0007 + |\Delta T_m|}{|\Delta T_m|} \qquad (5.2)$$

where ΔT_m is the average deviation of the monthly mean temperature from the annual mean temperature (Fig. 5.2), and the equation is scaled so that at the average precipitation sum of all sites ($P_l^* = 1180$ mm/yr) their average temperature amplitude is reached ($A_l^* = \Delta T_{Jul} - \Delta T_{Jan} = 18.4$ °C, Fig. 5.2). The monthly precipitation sum and the standard deviations of temperature and precipitation are calculated from the data presented in Fig. 5.2.

Simulation studies were conducted with the FORECE model and two FORCLIM variants, FORCLIM-E/P and -E/P/S. The annual mean temperature was varied from -2 to 13 °C, and one simulation experiment was performed every 0.5 °C. The annual precipitation sum was varied from 400 to 2000 mm/yr, with one experiment every 100 mm/yr, yielding a total of $31 \cdot 17 = 527$ simulation experiments. For each of these points in the (T,P) space, the equilibrium species composition was estimated using $n = 200$ points and an interval (Δt) of 150 years, discarding the first 1000 years (cf. section 4.4).

The field capacity parameter (kFC) was assumed to be 30 cm throughout the (T,P) space and in all models. For the model variant FORCLIM-E/P, available nitrogen was assumed to be 100 kg/ha throughout the (T,P) space. For both FORCLIM variants the cross-correlation coefficients were assumed to be -0.6 in summer (April–Sept.), and 0 in winter (Oct.–March). For FORECE, the additional site parameters were taken from Tab. 2.2 (Bern), and the 200 samples with $\Delta t = 150$ years were extracted from the default output file. The simulation studies with the FORCLIM models were executed on Macintosh computers; because simulation studies with FORECE require much more computing time, they had to be performed on a Sun SS630 workstation and still took more than three weeks.

Data processing for creating three-dimensional plots was done with the software Microsoft EXCEL V4.0, and unsmoothed contour plots were drawn using MATHEMATICA V2.03 on an Apple Macintosh computer model Quadra 700.

5.3.2 Results & discussion

First, let us examine the pattern of total aboveground biomass simuated by the three models (Fig. 5.3): The most striking feature is that FORECE simulates the highest biomass close to the alpine treeline, whereas both FORCLIM variants predict a steady increase with increasing temperature and precipitation. It may be argued that the assumption in FORECE that the SOILQ parameter is constant throughout the (T,P) space is unreal-

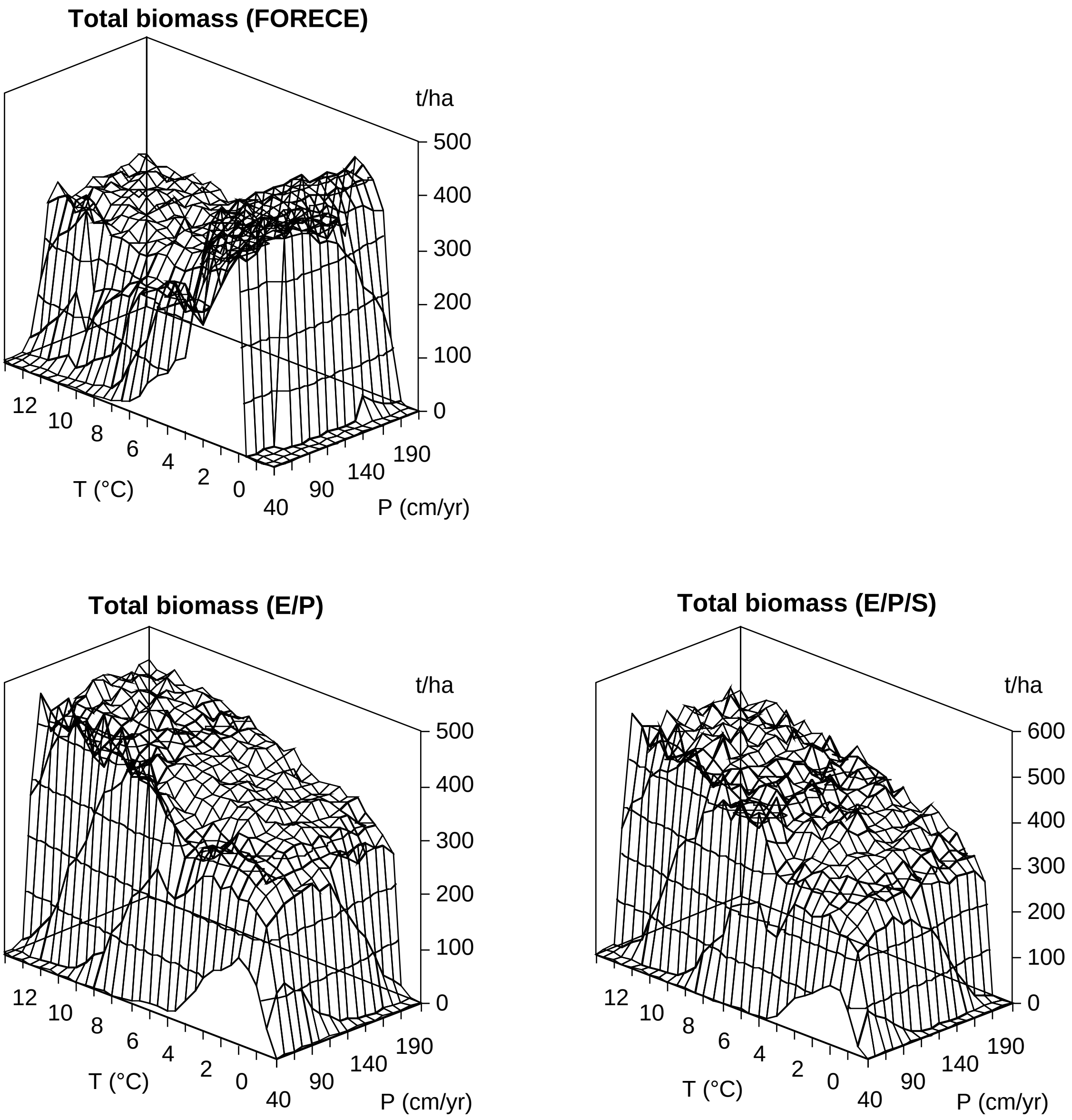


Fig. 5.3: Total aboveground biomass as simulated by the three models Forece, ForClim-E/P and ForClim-E/P/S in a space spanned by the annual precipitation sum (P) and the annual mean temperature (T).

istic. However, it should be noted that nitrogen availability has been introduced in ForClim as a substitute of SOILQ, and that the assumption of a constant supply of nitrogen (100 kg/ha) in ForClim-E/P is equally unrealistic; yet this model does not produce the anomaly evident from Forece (Fig 5.3).

The major difference of aboveground biomass between the two ForClim variants is that in ForClim-E/P/S nitrogen availability rises above 100 kg/ha at higher temperatures, and total biomass increases above the level reached by ForClim-E/P (Fig. 5.3, cf. Fig. 5.8).

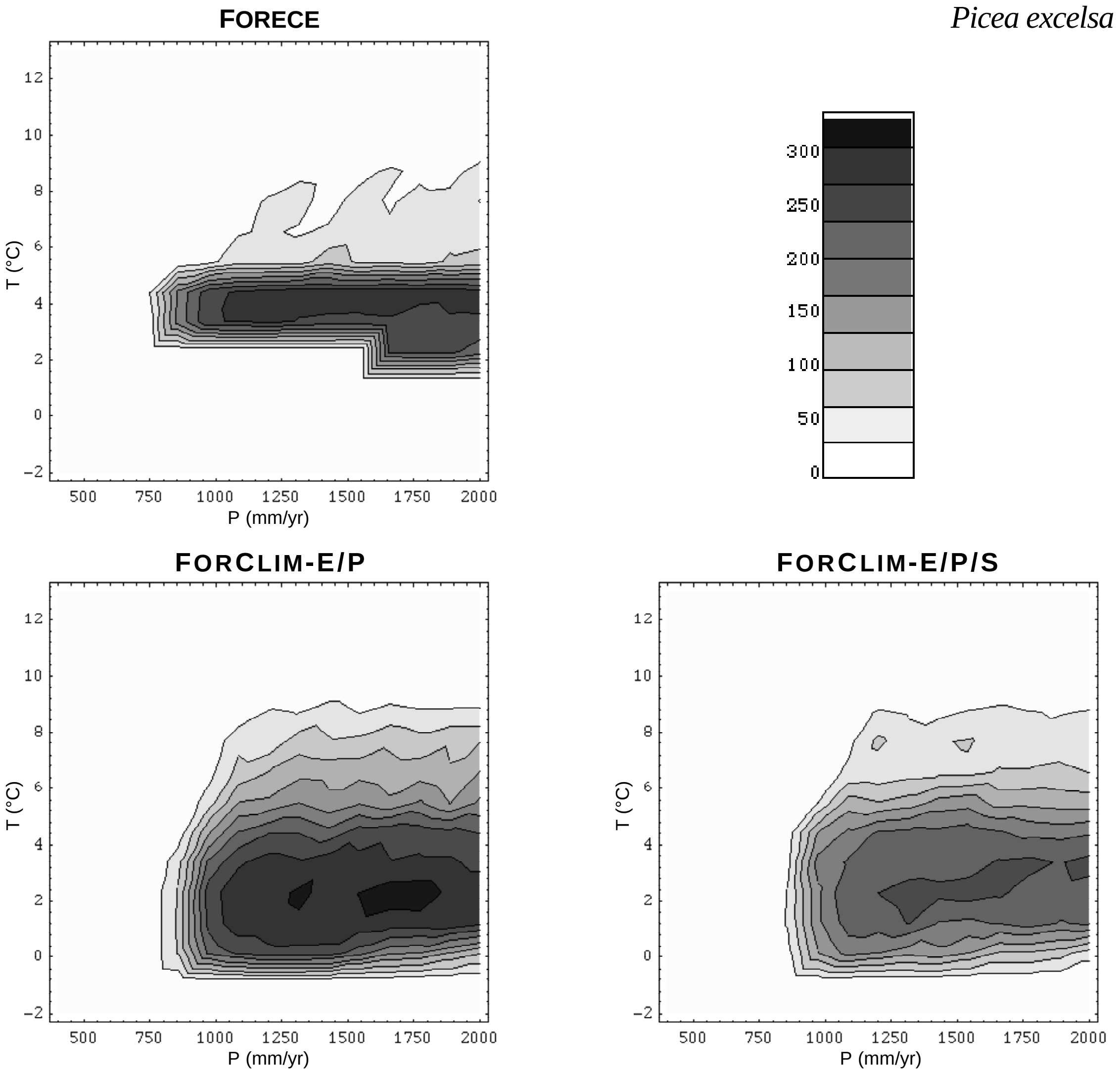


Fig. 5.4: Contour plot of *Picea excelsa* biomass [t/ha] as simulated by FORECE (top), FORCLIM-E/P (bottom left), and FORCLIM-E/P/S (bottom right).

Comparing the distribution of several dominating tree species from Fig. 5.1 with the simulated biomass distributions, it becomes evident that extremely steep gradients are characteristic of FORECE: In this model, *P. excelsa* is excluded from the area where $T_l < 2$ °C although it should approach the upper timberline in moist areas (Fig. 5.4). There is a similarly steep gradient of its biomass when approaching 5 °C. In both FORCLIM variants, the species grows up to the alpine timberline (Fig. 5.4) and decreases more smoothly towards higher temperatures, conforming to the phytosociological expectations (Fig. 5.1). However, both FORECE and FORCLIM run into difficulties in the area centered around 6 °C and 700 mm, where *P. excelsa* should dominate; both models exclude this species due to the occurrence of strong droughts, which may be unrealistic. It should be noted that FORECE predicts the occurrence of *P. excelsa* somewhat further into

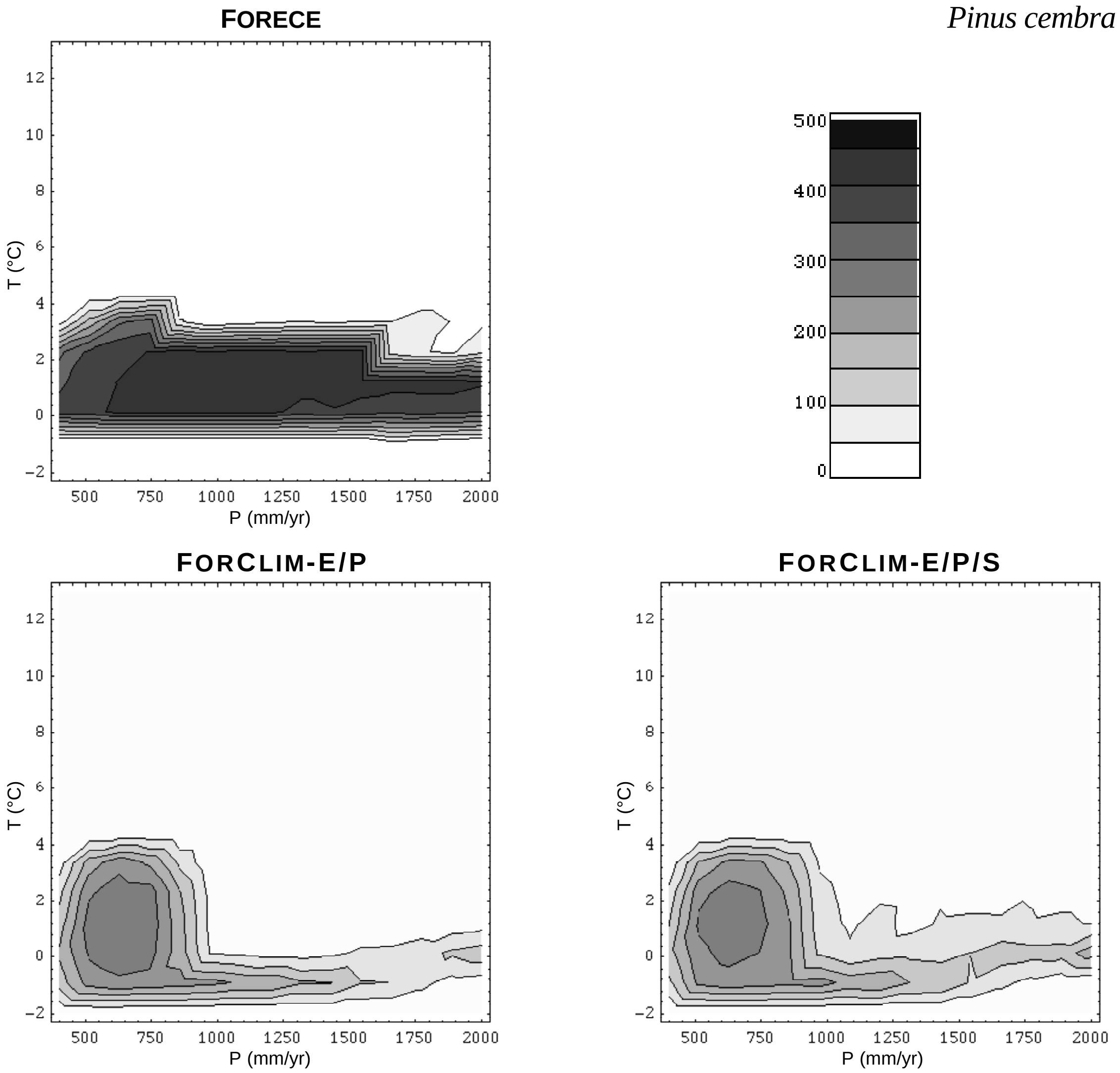


Fig. 5.5: Contour plot of *Pinus cembra* biomass [t/ha] as simulated by FORECE (top), FORCLIM-E/P (bottom left), and FORCLIM-E/P/S (bottom right).

this area; however, neither model corresponds well to the scheme in Fig. 5.1. The major difference between FORCLIM-E/P and FORCLIM-E/P/S is that the biomass of *P. excelsa* is reduced to some extent when soil nitrogen availability is treated explicitly (Fig. 5.4), because this species is not tolerant of the low nitrogen availability simulated during certain phases of the gap dynamics cycle (cf. section 4.3).

The FORECE model suggests that *P. cembra* dominates under all precipitation regimes when T_l is less than 2 °C (Fig. 5.5), although *P. excelsa* should approach the alpine timberline in moist regions (Fig. 5.1). With both FORCLIM variants *P. cembra* is abundant in the dry (continental) subalpine zone, and it is codominant close to the alpine timberline in the other areas (Fig. 5.5), a pattern also supported e.g. by Renner (1982).

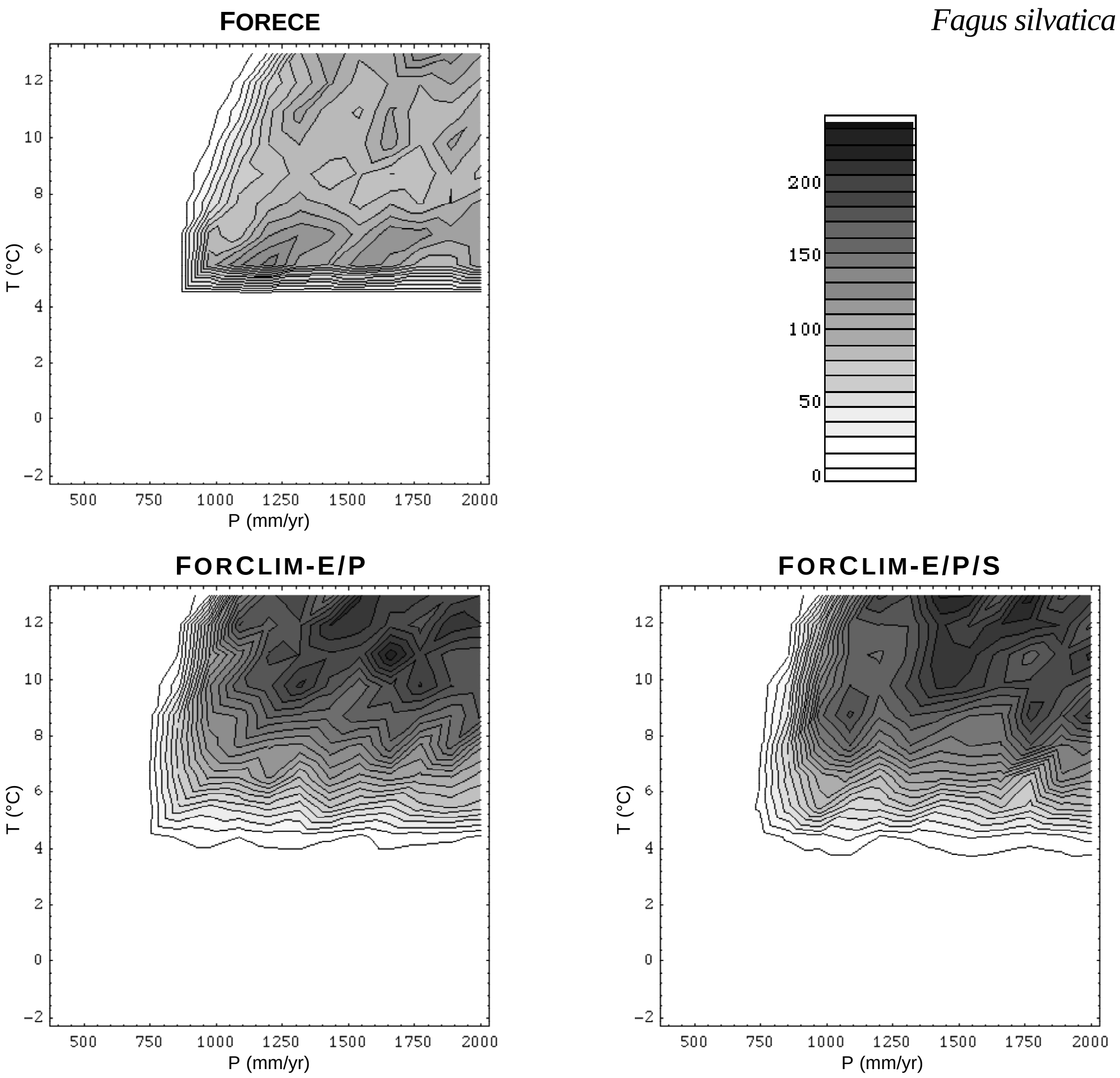


Fig. 5.6: Contour plot of *Fagus silvatica* biomass [t/ha] as simulated by FORECE (top), FORCLIM-E/P (bottom left), and FORCLIM-E/P/S (bottom right).

Similar steep gradients as observed with *P. excelsa* and *P. cembra* occur with *F. silvatica* in the FORECE model (Fig. 5.6): There is an abrupt decline at $T_l \approx 5$ °C, which is located in the middle of the upper montane beech-silver fir zone (Fig. 5.1). Again, both variants of FORCLIM produce smoother and more realistic gradients; specifically, the species extends down to $T_l \approx 4$ °C, where the transition between montane and subalpine forests should occur (Fig. 5.1). Moreover, in FORCLIM *F. silvatica* extends down to a precipitation of about 800 mm, which is plausible as well (Fig. 5.6).

Neither FORECE nor FORCLIM are capable of simulating the transition from beech forests to insubrian and mediterranean forests dominated by oak *(Quercus spp.)* and chestnut *(C. sativa)*, which should occur at $T_l \approx 10$ °C (Fig. 5.6). In both models, *Fagus silvatica*

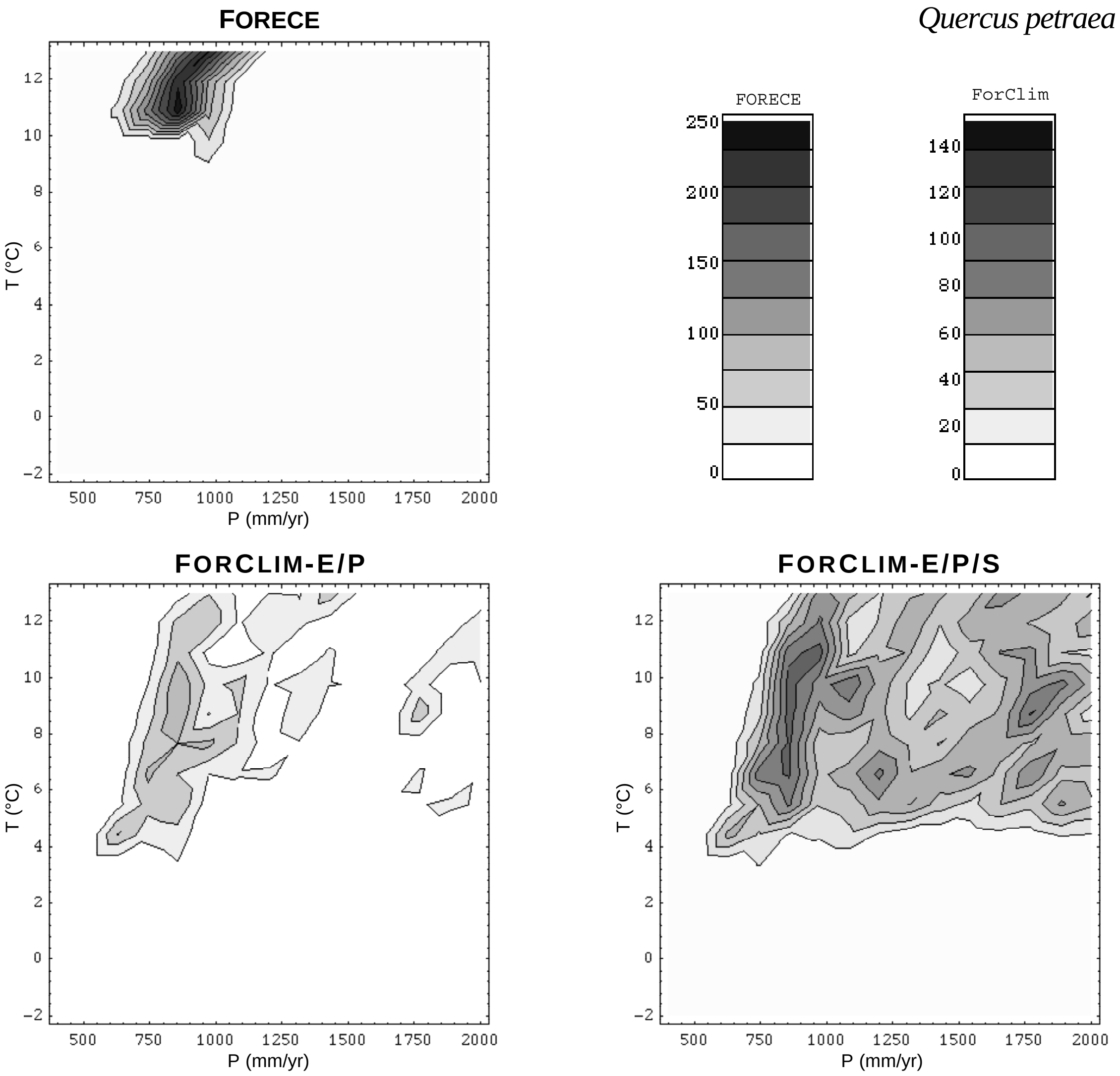


Fig. 5.7: Contour plot of *Quercus petraea* biomass [t/ha] as simulated by FORECE (top), FORCLIM-E/P (bottom left), and FORCLIM-E/P/S (bottom right).

remains the most abundant species. In FORCLIM, *Quercus spp.* (Fig. 5.7) is present as well, but it does not attain the abundance hypothesized by Rehder and Ellenberg.

The FORCLIM-S submodel is especially important for simulating *Quercus spp.* (cf. Fig. 5.7 with *Q. petraea* as an example). While FORECE fails to simulate the presence of oak as long as *F. silvatica* is present, the FORCLIM-E/P model generally predicts the occurrence of *Q. petraea* in the right places (Fig. 5.1), but the species extends too far into the area around T_l = 5 °C and P_l = 700 mm (Fig. 5.7). The E/P/S model may exaggerate the importance of *Q. petraea* at temperatures below 10 °C, where oaks attain more than 10% of the total aboveground biomass. Moreover, in FORCLIM-E/P/S *Q. petraea* may extend too far towards low temperatures (down to $T_l \approx 5$ °C).

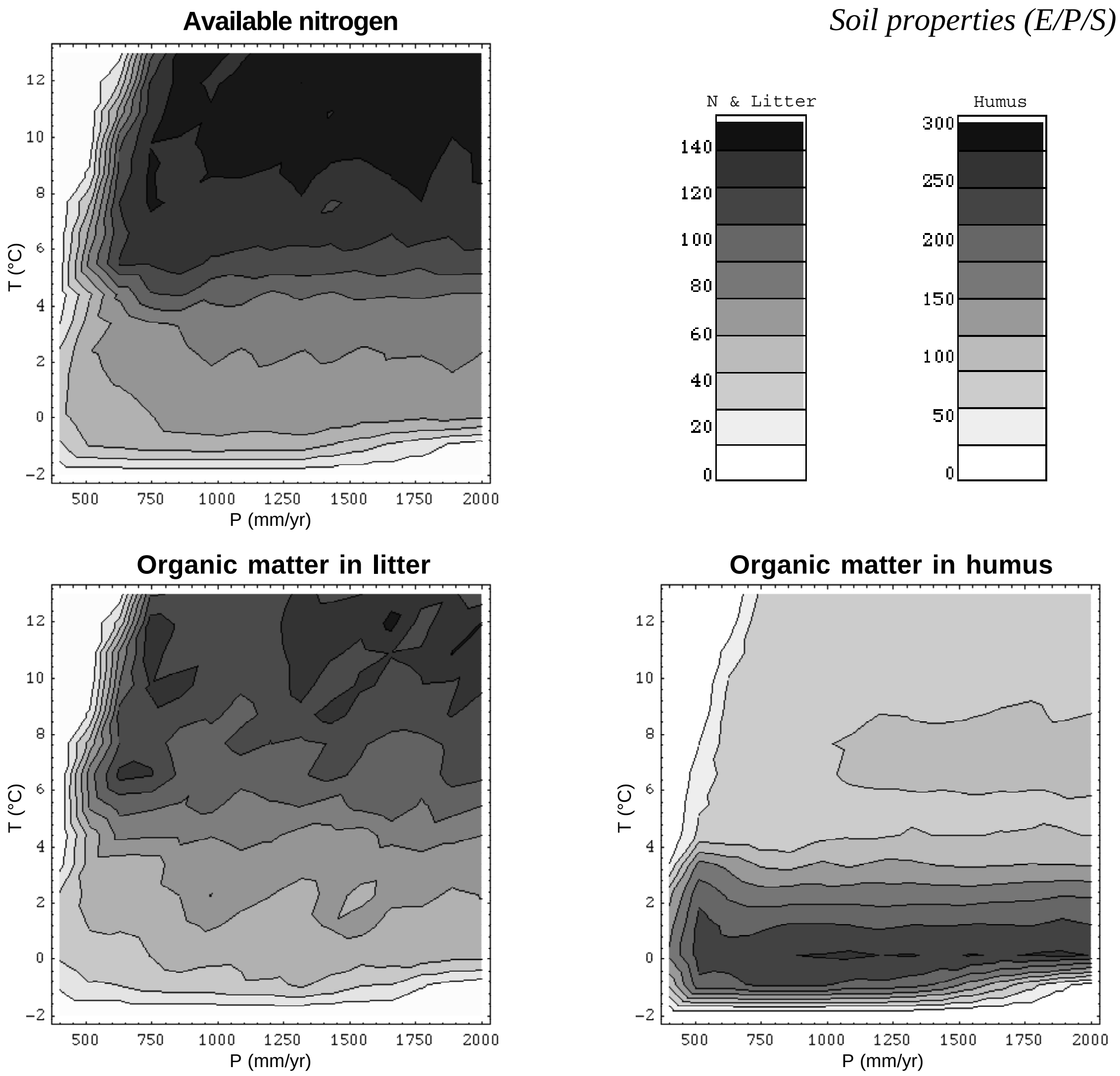


Fig. 5.8: Contour plot of available nitrogen (kg/ha, top), organic matter in litter (t/ha, bottom left), and organic matter in humus (t/ha, bottom right) as simulated by FORCLIM-E/P/S.

The belowground properties simulated by FORCLIM-E/P/S (Fig. 5.8) can not be compared to anything simulated by the other two models. The E/P/S model produces a gradient of nitrogen availability that ranges from 50 kg/ha close to the timberlines to around 140 kg/ha in warm and humid regions. The amount of “litter” simulated by the model reflects a gradient of net primary productivity, whereas the accumulation of “humus” is indicative of the nitrogen mineralization rates. All three gradients appear to be realistic. The total amount of soil organic matter (i.e. the sum of “litter” and “humus”) increases from 200 t/ha in warm climates to around 250 t/ha in the subalpine region. Also with this index, FORCLIM produces a plausible gradient, although one might expect it to be steeper (e.g. Richard et al. 1978).

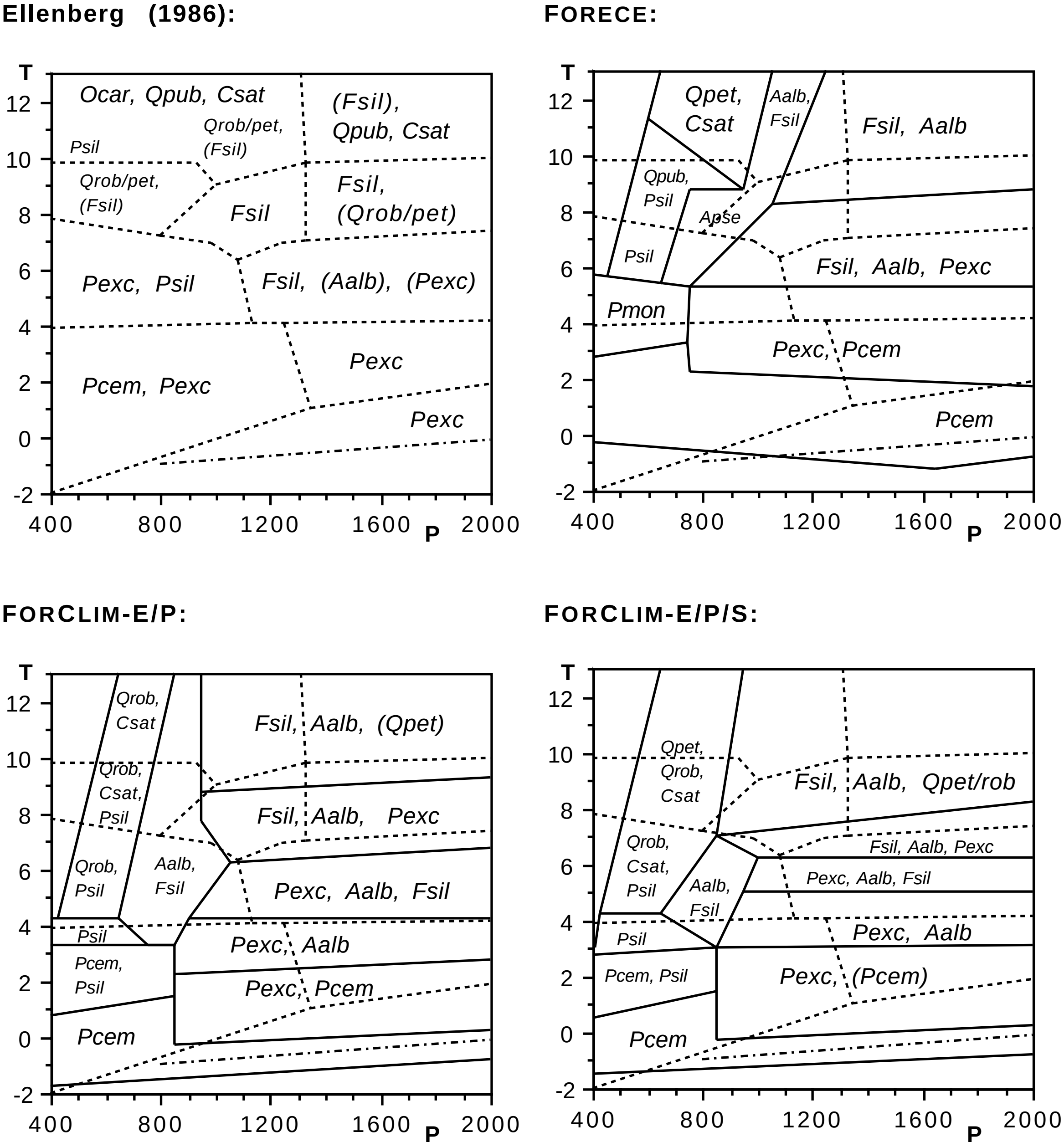


Fig. 5.9: Dominating tree species according to Ellenberg (1986) and the three forest models. The key to species is the same as in Fig. 5.1; additional species are Apse – *Acer pseudoplatanus*; Pmon – *Pinus montana*. For the forest models, the timberline was assumed to occur when total aboveground biomass drops below 20 t/ha.

Finally, the simulation results will be examined in a scheme similar to the one by Rehder (1965) and Ellenberg (1986). The regions were outlined according to the pattern of the three most important tree species (Fig. 5.9). The following points of interest will be discussed in turn: (1) the location of the timberlines; (2) the temperature gradient under moist conditions ($P_l > 1000$ mm) from the alpine timberline to $T_l \approx 10$ °C; (3) the subalpine dry zone ($T_l < 4$ °C, $P_l < 900$ mm/year); (4) the warm, dry zone above 4 °C and below 900 mm/year; (5) the transition from beech forests to insubrian and mediterranean forests dominated by oak *(Quercus spp.)* and chestnut *(Castanea sativa)*.

Location of the timberlines: All three models agree that the dry timberline extends from the point (13 °C, 600 mm/year) down to about (5 °C, 400 mm/year) (Fig. 5.9). Unfortunately, Rehder (1965) and Ellenberg (1986) did not include the location of this timberline in their hypothesis. However, the location of the alpine timberline can be compared to the simulation results: For P_l < 1600 mm/year, the FORECE model produces a timberline that contradicts the expectations formulated by Rehder and Ellenberg, whereas both FORCLIM models conform to their hypothesis. The fact that the alpine timberline simulated by FORCLIM extends ≈0.5 °C too far into the alpine zone is partly due to its definition: 20 t/ha of aboveground biomass simply may not be a forest any more.

Temperature gradient under moist conditions: All three models simulate the transition from the subalpine coniferous to mixed deciduous forests at lower elevations; however, FORECE and FORCLIM diverge to a large extent concerning the distribution of single species:

The strong dominance of *Pinus cembra* along the alpine timberline in the FORECE model (Fig. 5.9) has been discussed already (Fig. 5.5), as well as the abrupt decline of *Fagus silvatica* in the middle of the upper montane beech-silver fir zone (Fig. 5.6). FORECE simulates oak exclusively in the warm-dry zones approaching the dry timberline, although the species should be generally present when the annual mean temperature is higher than about 8 °C (cf. Fig. 5.7). Thus, while the general pattern simulated by FORECE may be correct, the model contains several thresholds that are unrealistic and occur in the wrong places.

The FORCLIM-E/P model produces a plausible gradient of species composition from the alpine timberline up to about 10 °C: A small belt of *P. cembra* close to the timberline is followed by the subalpine spruce zone, by the montane spruce-silver fir-beech zone, and ends with the beech forests typical of the Swiss Plateau, corresponding to a large extent to the hypothesis by Rehder (1965) and Ellenberg (1986). A characteristic difference to the FORECE model is that the gradients are smoother, which is reflected in more subtle differences between the zones; for example, the FORCLIM-E/P model simulates a small spruce-silver fir zone between the subalpine spruce zone and the montane beech-silver fir-spruce zone, a level of detail that is not present in the Rehder-Ellenberg scheme, but which appears to be realistic.

The pattern of the dominating species simulated by FORCLIM-E/P/S corresponds by and large to the one simulated by FORCLIM-E/P (Fig. 5.9). The major difference is the increased importance of *Quercus spp.* at temperatures above 8 °C (cf. also Fig. 5.7).

Subalpine dry zone: All three models agree that this zone is dominated by *Pinus cembra* (Fig. 5.9). FORECE predicts a sharp decline of this species and its replacement by *P. montana* when temperature increases. Both FORCLIM variants diverge slightly by predicting a gradual replacement of *P. cembra* by *P. silvestris*. However, the major pattern is portrayed well by all models.

Transition to the warm, dry zone: First, it should be noted that the pattern hypothesized by Rehder and Ellenberg in this subcontinental transition zone is rather fuzzy (Fig. 5.1). For example, the boundaries of the regions where *F. silvatica*, *Q. pubescens*, and *C. sativa* should be present still or become dominant are not outlined clearly, which makes it difficult to evaluate the simulation results.

Both FORECE and FORCLIM encounter major difficulties in this area (Fig. 5.9). The FORECE model simulates the occurrence of strong droughts, which lead to the decline of *Picea excelsa* and *F. silvatica* at low and high temperatures, respectively. These species give way to transition forests that are dominated by *Acer pseudoplatanus* and – at higher temperatures – by *Abies alba*, which is striking and probably represents an anomaly. When drought increases further, oak-chestnut and oak-pine stands are simulated.

Also FORCLIM-E/P shows unexpected behaviour in this area: While it does not simulate the dominance of *A. pseudoplatanus*, the transition forests are dominated entirely by *A. alba* and are replaced by oak-chestnut and oak-pine stands as well. Hence, similar to FORECE we have to conclude that the behaviour of FORCLIM-E/P is unrealistic in this area.

FORCLIM-E/P/S produces a direct transition from beech to oak forests above $T_l = 7$ °C; *A. alba* comes to dominance only in the area centered around 6 °C and 700 mm/year. Although these results appear to be more plausible than the ones obtained from FORCLIM-E/P, it is difficult to evaluate them because the pattern in the Rehder–Ellenberg scheme is not precise enough to allow for a falsification of the simulation results.

Hence, it appears that all three models do not simulate convincing species compositions along drought gradients. Several hypotheses can be brought forward that could explain this phenomenon: (1) Most simply, the parameters denoting the drought tolerance of the tree species may have been estimated erroneously; (2) the soil water balance submodel is not capable of tracking soil moisture content under warm-dry conditions, especially where soils are sandy; (3) the feedbacks between vegetation properties (e.g. LAI) and soil water balance (e.g. evapotranspiration) that have been neglected in the model formulation may become important under these conditions; (4) neither the “dry days” approach (FORECE) nor the evapotranspiration deficit approach (FORCLIM) are appropriate indices for expressing drought stress as experienced by trees; (5) the indices are appropriate, but the relationship between the index and the annual growth increment is wrong. Further research is required to address these issues.

Transition to insubrian and mediterranean forests: None of the three models is capable of simulating the transition from beech forests to insubrian and mediterranean oak-chestnut forests (Fig. 5.9): When the precipitation sum is above 1000 mm/yr, the models do not simulate any drought. However, the large precipitation sum in these areas (e.g. Ticino, Switzerland) does not mean that there is no drought: Often there are extreme precipitation events where a large fraction of the monthly precipitation falls within a few days. The monthly averages used in all three models do not capture the properties of such distributions, and this may allow beech to dominate although it should be outcompeted due to summer drought. Moreover, the moderate standard deviations of precipitation used in the present analysis are not characteristic of these areas (cf. the omission of Locarno for the derivation of climatic input data); this may also prevent the occurrence of dry months with concomitant drought. Finally, it should also be taken into account that under mediterranean conditions other species become abundant that were not included in the species pool for European conditions, such as *Quercus ilex*. Also for this reason, the present model approaches the limits of applicability in this area.

5.3.3 Conclusion

From the analysis of the steady-state species compositions of FORECE, FORCLIM-E/P and FORCLIM-E/P/S in a space spanned by the annual mean temperature and the annual precipitation sum, we may conclude that the two FORCLIM model variants produce steady state species compositions that conform well to field-based empirical expectations in large parts of this (T,P) space (e.g. Ellenberg & Klötzli 1972, Ellenberg 1986; Fig. 5.1). On the other hand, the FORECE model contains several unrealistic thresholds (Fig. 5.4, 5.5, 5.6).

The FORECE model fails to simulate the occurrence of oak *(Quercus spp.)* except under warm-dry conditions close to the dry timberline. In the FORCLIM-E/P model, oak is a codominant species at higher temperatures, which conforms better to the expectations by Rehder (1965) and Ellenberg (1986). In the FORCLIM-E/P/S model, the soil submodel (FORCLIM-S) produces periods with low nitrogen concentrations, and oak gets a competitive advantage, thus increasing its abundance (Fig. 5.7). According to the FORCLIM model, oak requires this heterogeneity of nutrient availability to be competitive; this constitutes an interesting hypothesis that requires further testing.

The problems encountered with all three models along drought gradients deserve to be studied in more detail: Simulation experiments performed with the FORECE, FORSKA, and FORCLIM models in the warm, dry area extending from Germany through Poland into Byelorussia suggest that each model fails in different ways, also affecting the behaviour of species such as *Tilia spp.* and *Carpinus betulus* (M. Lindner & P. Lasch, pers. comm.). They found vast differences between the models e.g. concerning the amount of simulated evapotranspiration and drought stress. Probably several of the hypotheses listed above are involved in causing the failure of forest gap models in this area.

Excluding the areas where both FORECE and FORCLIM fail to produce plausible results, we may conclude that FORCLIM simulates more plausible species compositions and more realistic gradients, whereas FORECE contains many threshold effects. Especially the latter renders the application of FORECE for impact studies of climatic change questionable. On the other hand, FORCLIM may be considered to be a valid tool for simulating forest dynamics for a large part of the range of temperature and precipitation explored in this experiment.

5.4 Behaviour of FORCLIM in eastern North America

In a well-known application of the forest gap model FORENA, Solomon (1986) studied forest dynamics at 21 locations along a latitudinal gradient in eastern North America, extending from the Canadian tundra to the temperate-subtropical forests of southern Georgia. The application of FORCLIM to perform simulation experiments along this same gradient appears to be interesting, but is faced with two problems: First, the near-natural forests of Central Europe and eastern North America have no species in common; thus it is necessary to change the species pool and to derive the FORCLIM species parameters for the 72 species used e.g. by Solomon (1986). Second, the monthly climatic data and the field capacity parameters at the 21 locations are needed.

5.4.1 Tree species and climatic data of eastern North America

The derivation of the FORCLIM parameters for the 72 eastern North American species was based on those of FORENA (Solomon 1986) and LINKAGES (Pastor & Post 1985). Four of the 14 FORCLIM parameters per species were adopted directly from the FORENA data, seven of them had to be recalculated based on the FORENA parameters, and three could be derived using the species descriptors published by Pastor & Post (1985) (Tab. 5.5). A detailed description of the transformation rules and a summary of all the FORCLIM species parameters are listed in Appendix VI.

The climatic data for all 21 sites/regions in eastern North America that were used by Solomon (1986) were provided by Allen M. Solomon (pers. comm.). The following subset of this climatic data was used for simulating forest succession along a climate gradient in eastern North America (cf. Solomon 1986, p. 570):

- Tundra/woodland-northern boreal forest: Churchill, Manitoba; Shefferville, Quebec; Armstrong, Ontario
- Southern boreal forest: West Upper Division, Michigan
- Northern deciduous forest: Central Lower Division, Michigan
- Western deciduous forest: West Central Division, Ohio; West Ozarks Division, Missouri; South Central Division, Arkansas
- Eastern deciduous forest: Cumberland Plateau Division, Tennessee; South Central Division, Georgia.

These 10 locations cover a latitudinal gradient from 58 °N to 31 °N, with annual mean temperatures ranging from -7.3 °C (Churchill) to 19.6 °C (Georgia), and annual precipitation sums from 396 mm/year (Churchill) to 1378 mm/year (Tennessee). The climatic data of the locations are listed in Appendix VII.

Tab. 5.5: Derivation of FORCLIM parameters for the tree species of eastern North America from the data used in the models FORENA (Solomon 1986) and LINKAGES (Pastor & Post 1985).

Parameter(s)	Transformation rule	Reference
sType	cf. Appendix VI	Pastor & Post (1985)
kDm, kHm, kAm, kDrT	none	Solomon (1986)
kG	recalculated from equation developed in Appendix II	Solomon (1986)
kDDMin, kDDMax	recalculated according to correction formula developed in chapter 3	Solomon (1986)
kWiT	cf. Appendix VI	Solomon (1986)
kNTol	assigned from LINKAGES parameters	Pastor & Post (1985)
kBrow	"FALSE" = 1, "TRUE" = 3	Solomon (1986)
kL_y, kL_a	"1" = 3, "2" = 7	Solomon (1986)
kLQ	cf. Appendix VI	Pastor & Post (1985)

5.4.2 Simulation experiments

At each of the 10 locations, 200 patches were simulated during 1200 years (cf. section 2.2.2). It should be noted that this is a much larger sample size and a longer time span than the one used by Solomon (1986), who simulated only 10 patches over 400 years with the current climate.

Both the FORCLIM-E/P and the FORCLIM-E/P/S models were run along the transect in order to investigate the importance of explicitly modelling soil organic matter dynamics and nutrient availability. At all locations a mesic silt loam with a field capacity (kFC) of 30 cm was simulated. For the model variant FORCLIM-E/P, nitrogen availability at all locations was assumed to be 100 kg/ha. No disturbances such as windthrow or fire were simulated. The steady-state species composition of the simulated forests was estimated by averaging the output from the years 1000–1200 of each patch.

5.4.3 Results & discussion

TUNDRA-WOODLAND TRANSITION AND NORTHERN BOREAL FOREST

Fig. 5.10 summarizes the steady-state species compositions along the northern part of the gradient. Only few and stunted trees grow at Churchill and Shefferville, correspond-

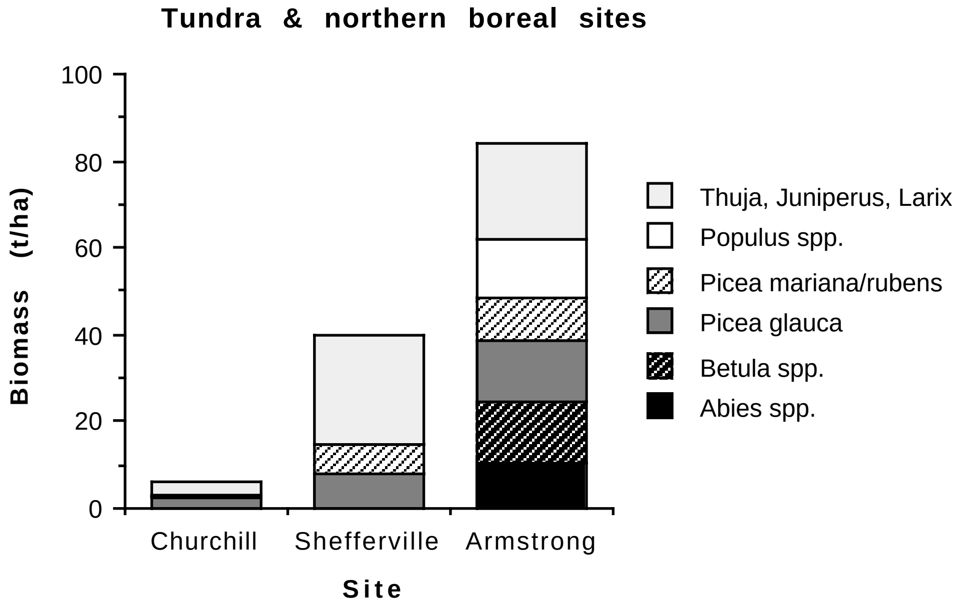


Fig. 5.10: Steady-state species composition at tundra and northern boreal sites in eastern North America as estimated by the FORCLIM-E/P model.

ing to the tundra-forest transition zone typical of this area (Rowe 1972). While the occurrence of *Picea glauca* is plausible, the large fraction of *Larix laricina* appears to be unrealistic (Rowe 1972). In eastern North America, *L. laricina* is characteristic of cold-air drainage situations and low peatlands, which are not simulated here. Although it may also grow in closed upland forests in the northern half of its range, the large abundance simulated by FORCLIM represents an anomaly. However, the physiognomic characteristics of the open woodland are reflected correctly in the simulation results.

Typical species for real forests at boreal sites like Armstrong (Fig. 5.10) are *Picea glauca, P. mariana,* and *Betula papyrifera* (Rowe 1972). These species are correctly simulated as dominants, but other species attain anomalous abundance: Again, *L. laricina* should be of marginal importance or should even be absent from the simulation. Maybe the description of its natural history is inappropriate in FORCLIM: In reality, its establishment from seeds is strongly limited by light availability; this was accounted for in FORENA by preventing its establishment when LAI is above 0.05 $m^2 \cdot m^{-2}$, a factor that was not included in FORCLIM because the important European tree species appear to be more shade tolerant. Moreover, *L. laricina* grows more slowly than evergreen conifers because of the cost of developing new needles each year; thus, in reality it is outcompeted on uplands unless winter is cold enough to kill evergreen needles. However, competition is low in the simulated low-biomass forests (Fig. 5.10), which means that *L. laricina* establishes and grows well.

The large abundance of *Populus spp.* at Armstrong would be realistic only under a strong disturbance regime; however, the simulation experiment is for undisturbed forests. *Pinus banksiana* is not important at this site because its degree-day requirements are not met in the model, which may be due to erroneous parameter estimation (Rowe 1972, Hare & Thomas 1979). In reality, both *Populus spp.* and *P. banksiana* need abiotic disturbances (especially fire, but also windthrow) to provide them with full sunlight. Thus the occurrence of *Populus spp.* represents a model anomaly, and *P. banksiana* appears to be absent for the wrong reasons. In FORENA, *Populus spp.* is absent as well because its establishment is prevented by the LAI requirement mentioned above.

Generally speaking, the characteristics of the transition zone from tundra to boreal forests, such as low tree species diversity, small tree stature and low total biomass, are simulated plausibly by the FORCLIM model (Fig. 5.10).

SOUTHERN BOREAL FOREST

The simulation results for Western Upper Michigan, the transition zone between boreal and deciduous forests, appear to be quite realistic (Rowe 1972, Frelich & Lorimer 1991; Fig. 5.11) and exhibit several features not present in the FORENA simulation results (Solomon 1986): The sugar maple *(Acer saccharum)* – eastern hemlock *(Tsuga canadensis)* forest simulated by FORCLIM is typical of rich, undisturbed sites (Rowe 1972, Küchler 1975). In this area, *T. canadensis* is a dominant species although it approaches its western boundary. The forest simulated by FORENA (Solomon 1986) was dominated by *Thuja occidentalis*, which is of low importance in the FORCLIM simulation chiefly because leaf area is calculated more accurately. In FORCLIM, the *T. occidentalis* trees generally are suppressed and do not come to dominance. Moreover, in reality *T. occidentalis* is competitive on calcareous soils only, a differentiation modelled neither in FORENA nor in FORCLIM.

As soils become coarser, lower in organic matter and poorer in moisture capacity, pines take over, first *Pinus strobus*, then *P. resinosa*, and finally in pure stands, *P. banksiana*. With disturbance such as fire or windthrow, *Populus tremuloides*, which occurred in the FORCLIM simulation peaking at about 10 t/ha in the year 100, and *Betula papyrifera* dominate for periods of 50-100 years; the occurrence of these species during the first 400 years of the simulation thus appear to be realistic. Three species may be simulated with too high biomass: *Picea rubens*, which is not present in the Michigan area, *Fagus*

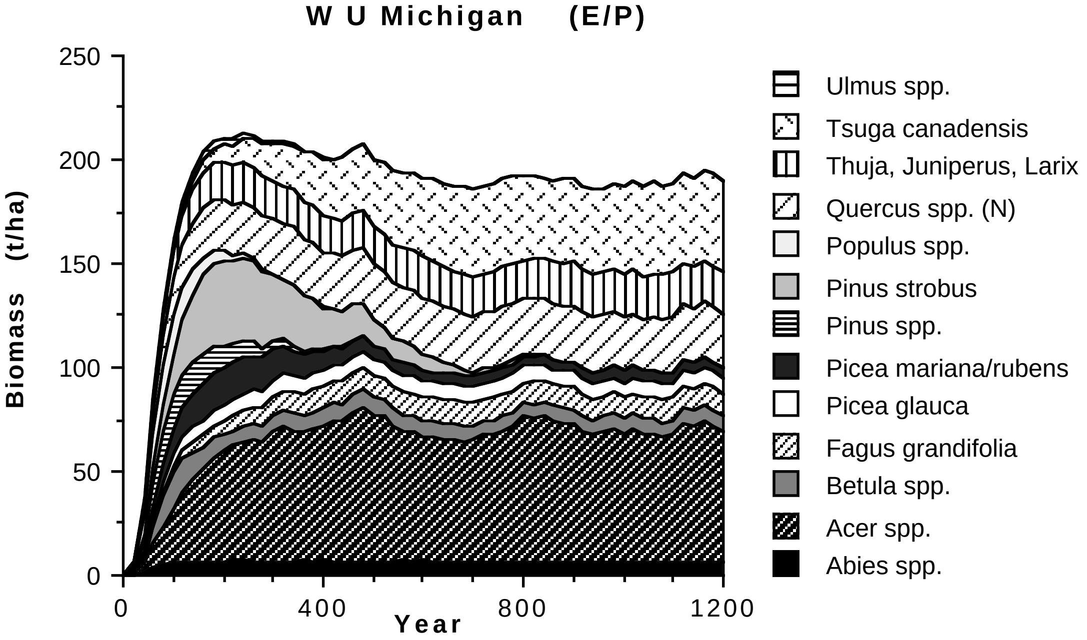


Fig. 5.11: Simulation results from FORCLIM for Western Upper Division, Michigan.

grandifolia, which in reality is subject to considerable drought stress here, and *Quercus macrocarpa* (making up most of the northern oaks in Fig. 5.11), a very fire resistant and relatively shade intolerant species which is more typical of the oak savanna towards the prairie-forest border of Minnesota and Wisconsin.

The increase of both species diversity and total above-ground biomass simulated by FORCLIM appears to be realistic (DeAngelis et al. 1981), and the species composition simulated by this model agrees more with the descriptions of near-natural forests of the area (Rowe 1972, Küchler 1975, Frelich & Lorimer 1991) than the FORENA simulations (Solomon 1986).

NORTHERN AND SOUTHWESTERN DECIDUOUS FOREST

Fig. 5.12 gives an overview of the steady-state species composition along a gradient from the northern to the southwestern deciduous forests; the climate is characterized by strongly increasing temperature and precipitation, but at the same time also increasing drought stress. The forest simulated at Central Lower Michigan (Fig. 5.12) is in the transition zone from the sugar maple-eastern hemlock forests typical of locations in the north (Fig. 5.11) to the oak-hickory forests characteristic of locations further south (Fig. 5.12 & 5.13). Comparing these results to the ones from Western Upper Michigan

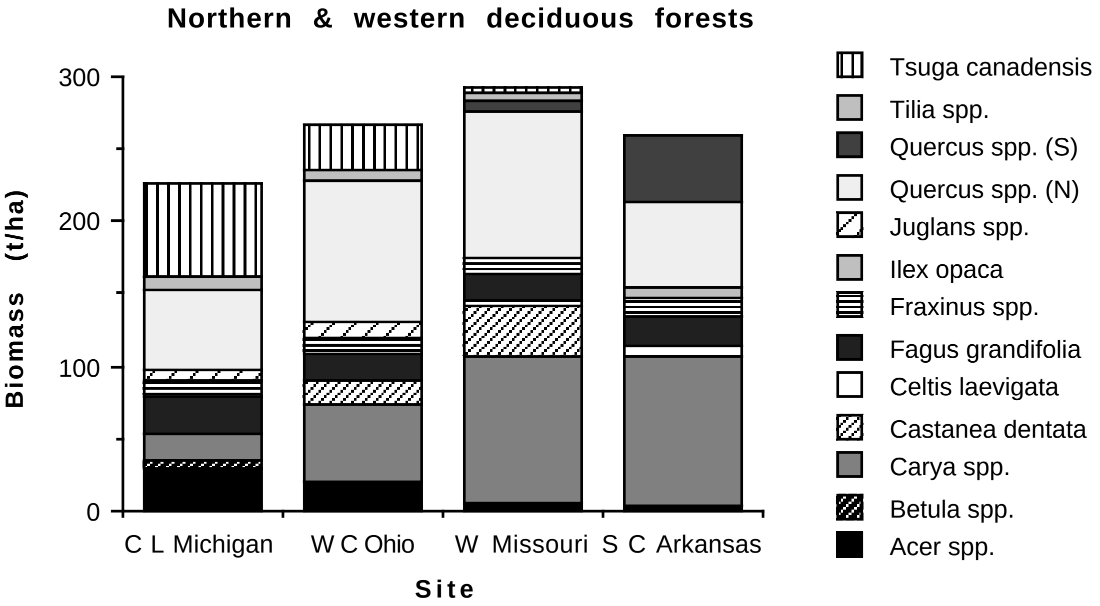


Fig. 5.12: Species composition of northern and western deciduous forests in eastern North America as estimated by the FORCLIM-E/P model.

(Fig. 5.11), major differences are (1) the disappearance of *Thuja*, *Picea*, and *Abies* species; (2) a strong decrease of *Acer saccharum;* (3) an increase in the biomass of *Fagus grandifolia* and northern oaks; (4) the appearance of southern genera, such as *Carya*, *Fraxinus*, *Juglans*, *Juniperus*, and *Tilia*. The FORCLIM model succeeds well simulating these transition forests (Küchler 1975).

The forest simulated for West Central Division, Ohio, is dominated by northern oaks and hickory species (Fig. 5.12). Chestnut *(Castanea dentata)* attains some importance, whereas the abundance of hemlock decreases with decreasing latitude; in fact, it should be less abundant here than simulated by FORCLIM, if not absent entirely. FORENA and FORCLIM agree to a large extent on the composition of near-natural forests of this area (Solomon 1986).

The Western Missouri area is characterized by open, almost woodland structured forests, a feature that is due to moisture stress, which is not simulated with the generous assumption of 30 cm field capacity (Fig. 5.12). Thus, total biomass increases compared to the Ohio area, which is not realistic. Possibly for the same reason FORCLIM simulates *Fagus grandifolia*, which is absent from this area. Moreover, FORCLIM produces small amounts of *Tsuga canadensis* although the species should be absent at these latitudes and longitudes. However, the dominance of oak, hickory, and chestnut, including the exact species of the former two genera, agrees well with descriptions of the near-natural forests of the area. The overall performance of FORCLIM thus is fairly good.

Major differences between the two models become evident with the Arkansas climate (Fig. 5.12): While the FORENA simulation is dominated by southern oaks, FORCLIM produces stands dominated by *Carya spp.* and northern oaks. However, the most important oak species simulated by FORCLIM are also prominent on the landscape: *Q. alba* and *Q. velutina* (Küchler 1975). *Carya spp.* is a warmth and drought-adapted genus, as are many of the oak species, which makes the FORCLIM simulation results quite realistic. The decrease of the total aboveground biomass as compared to Missouri (Fig. 5.12) is due to drought stress; yet the real forests of the area are less dense, and biomass should be lower (DeAngelis et al. 1981). If the field capacity in the FORCLIM model is reduced to 10-15 cm, total aboveground biomass decreases below 200 t/ha, which may be more plausible.

SOUTHEASTERN DECIDUOUS FORESTS

The simulation results from Georgia, the southernmost site along the transect, are given in Fig. 5.13. Southern oaks and *Carya spp.* dominate this forest. However, there is a large discrepancy between real and simulated forests both in FORCLIM and in FORENA: On the landscape, southern pines *(Pinus spp.* in Fig. 5.13) dominate the forests, which is due to the occurrence of extrinsic disturbances such as fire and the droughtiness of the sandy soils prevailing in that area. However, on the clay soils of the piedmont, for which the simulation results are more representative, oaks and hickories dominate. Thus, as a statement about the potential natural forest vegetation in the absence of disturbance, the FORCLIM model is rather successful.

Similar simulation results are obtained for Cumberland Plateau, Tennessee (not shown). Although the annual precipitation sum is high, the area is subject to considerable drought because of the sandy soils, leading to low-biomass forests. However, at Cumberland Plateau FORCLIM produces the largest amount of aboveground biomass along the transect. The FORENA model also misrepresents the effects of drought at this site. It is clear that the assumption of 30 cm water at field capacity does not represent sandy soils; unfortunately, the large amount of aboveground biomass simulated by FORCLIM is by and large independent of the value of the field capacity parameter that is used in the simulations. These anomalies may constitute a serious problem for both models.

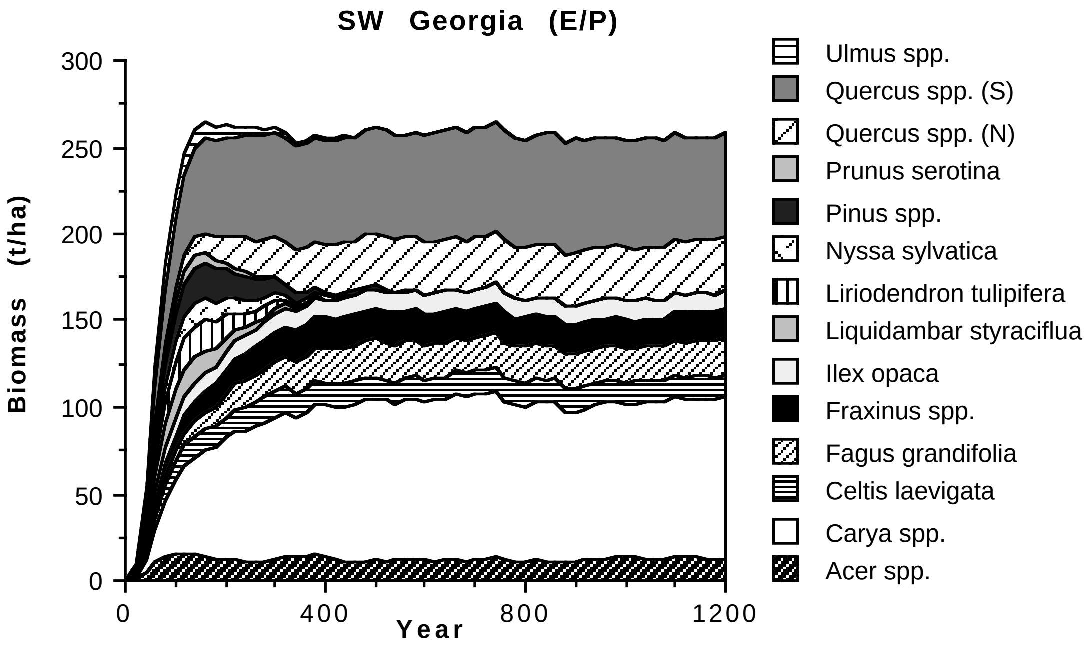


Fig. 5.13: Simulation results from FORCLIM for Southwest Division, Georgia.

The results presented above were based on the FORCLIM-E/P model; the simulations conducted with FORCLIM-E/P/S revealed only small differences concerning the steady-state species composition of the simulated forests, although the simulated transient behaviour differed to some extent, especially for the southern locations. There the abundance of species such as *Liquidambar styraciflua*, *Liriodendron tulipifera*, and *Nyssa sylvatica* is reduced if nitrogen availability is modelled explicitly, which is due to their intolerance of the low nitrogen availability during early succession (cf. section 4.3). On the other hand, the biomass of *Pinus spp.* increased considerably under these conditions.

5.4.4 Conclusion

The application of the FORCLIM model along a latitudinal gradient in eastern North America and the comparison of the results with those obtained by Solomon (1986) and with descriptions of near-natural forests of the area (Rowe 1972, Küchler 1975) reveals several interesting features:

First, FORCLIM successfully simulates the general pattern observed in the landscape, i.e. the transition from tundra to the boreal forest down to northern deciduous forests. However, the model misrepresents the increased influence of drought on forest structure when approaching the southwestern edge of the simulated geographical range. The increase of total biomass simulated by FORCLIM, approaching 300 t/ha under mesic conditions in the south, appears to be more realistic than the low-biomass forests simulated by FORENA (DeAngelis et al. 1981).

Second, FORCLIM produces plausible species compositions in eastern North America. It performs best in the central part of the climate gradient explored in this study, where the simulation results are more realistic than those obtained from FORENA. In the northern part, an anomalous behaviour of some light-demanding species becomes evident, whereas in the southwestern part of the gradient, FORCLIM reveals a larger deficiency than FORENA to lose drought-intolerant species and to have total aboveground biomass constrained by drought. In part this may be due to the generous assumption of 30 cm water at field capacity in the present simulations. Soil moisture appears to be more important throughout most of the deciduous forests of eastern North America than it is in the forests of the European Alps. However, simulation results conducted with lower values of the field capacity parameter suggest that the FORCLIM model is likely to encounter similar problems along drought gradients as were revealed for European forests (cf. section 5.3).

Third, it should be noted that several of the FORCLIM parameters have a more differentiated scale than their FORENA counterparts, such as those denoting the tolerance to browsing (kBrow) and shading (kL_y, kL_a). The simple assignments made in this study (Tab. 5.5) could be improved considerably by using more precise descriptions of the natural history of these tree species. The relative tolerance of the species was documented e.g. by Baker (1949); data sources like this should allow one to define the tolerance of the species with a differentiation appropriate for the FORCLIM model (cf. chapter 3). Maybe such improvements could help to solve some of the problems mentioned above.

Finally, we may conclude that FORCLIM behaves fairly well with the set of species of eastern North America and under climatic conditions characterized by much higher annual temperature amplitudes than in Europe. The introduction of factors that are important for providing a realistic picture of forest dynamics as observed in the landscape, such as sandy soils and disturbance regimes (e.g. windthrow and fire) could be used to improve the results obtained so far. Yet at some sites the present FORCLIM simulation results are more plausible than those produced by the FORENA model (Solomon 1986). This study suggests that FORCLIM has the potential to yield realistic results also when it is applied with a set of species and under climatic conditions for which it has not been developed.

6. Model applications

Climatic change is a common phenomenon that may occur not only in the future: Climate has been changing continuously in the past both on long and short timescales (Barnola et al. 1987, Briffa et al. 1990, 1992). Thus, a look at past climatic variations on a similar timescale as the anticipated future climatic change, i.e. for the last few centuries, will allow to analyse the ecological effects of such variations, e.g. to determine how well buffered forest ecosystems are (section 6.1). Subsequently, the possible ecological implications of future climatic changes will be explored (section 6.2).

6.1 Effects of historical climate anomalies on forest dynamics

6.1.1 Input data and simulation experiments

In a unique effort, Pfister (1988) developed a system of monthly thermic and hydric indices to characterize the temperature and precipitation regime of every month between 1525 and 1979 AD in Switzerland. The indices were based on a wealth of historical data sources, ranging from temperature measurements at a few sites and written records of extreme events (e.g. lake glaciations) to agricultural yield data and tree-rings. The temperature indices refer to the site Basel, while the precipitation indices are an average of the sites Bern, Cottens/Begnins, Rickenbach, Basel, Geneva, and Zurich (Pfister 1988).

Based on these indices and the regression equations developed by Pfister (1988), the monthly temperature and precipitation data of a virtual site “CLIMINDEX” were reconstructed for the present study (Tab. 6.1). This site is representative of a large fraction of the Swiss Plateau, the area of Switzerland most densely populated throughout history.

The FORCLIM-E/P model was selected for this study because it is more efficient than the full E/P/S model but produces very similar results at low-elevation sites (chapter 4). The following simulation experiment was designed based on the climatic data by Pfister (1988): First, the model was allowed to reach its steady-state under current climatic conditions by running it for 1000 years (525-1525 AD) and 200 patches starting from bare ground and assuming a constant climate, i.e. by sampling weather data stochastically from the long-term distributions in Tab. 6.1. Then the years 1525 through 1979 were simulated using the reconstructed series of weather data from Pfister (1988) to calculate the bioclimatic variables in ForClim-E deterministically. The temperature and precipitation of months with missing values (Pfister 1988) were assumed not to deviate from the long-term statistics (Tab. 6.1). The latitude of the ClimIndex "site" is 47.5 °N (Swiss Plateau), field capacity was set to 30 cm, and nitrogen availability to 100 kg/ha.

Tab. 6.1: Climatic data reconstructed from the thermic and hydric indices of the period 1901-1960 for the virtual site "ClimIndex" (Pfister 1988). Symbols: $\mu(T)$ – monthly mean temperature [°C]; $\sigma(T)$ – standard deviation of T; $\mu(P)$ – monthly precipitation sum [cm/month]; $\sigma(P)$ – standard deviation of P; r – cross-correlation coefficient of T and P. The long-term mean annual temperature of the ClimIndex site is 9.2 °C, and the annual precipitation sum is 1187 mm.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
$\mu(T)$	-0.2	1.3	5.2	8.8	13.5	16.5	18.3	17.5	14.4	9.2	4.3	1.3
$\sigma(T)$	2.6	2.1	1.9	1.7	1.7	1.3	1.5	1.3	1.5	1.5	1.5	2.3
$\mu(P)$	10.23	9.83	9.75	9.82	9.85	9.60	9.66	9.93	9.47	10.55	9.97	10.05
$\sigma(P)$	4.93	6.09	4.66	3.41	3.06	4.01	3.33	2.82	2.89	5.46	5.97	3.58
r	0.33	0.27	-0.04	-0.22	-0.38	-0.46	-0.62	-0.49	-0.32	-0.17	0.22	0.4

6.1.2 Results & discussion

The simulation results from the first phase of the experiment (Fig. 6.2) are similar to those obtained when running ForClim with the climate of the site Bern (cf. chapter 4). The simulated forest is characterized by a strong dominance of beech *(Fagus silvatica)* accompanied by silver fir *(Abies alba)* and oak *(Quercus spp.)*. Due to the comparably high temperature, spruce *(Picea excelsa)* is outcompeted by those species. These results appear to be plausible (Ellenberg & Klötzli 1972).

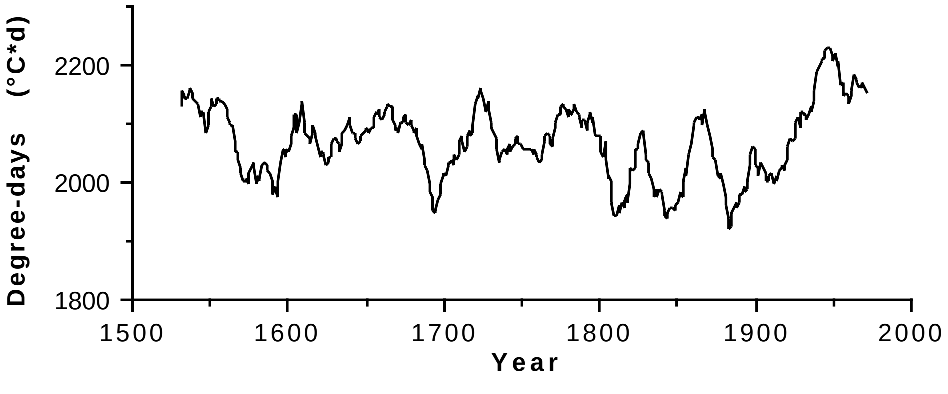


Fig. 6.1: Simulated annual sum of degree-days (1525-1979 AD) based on the monthly temperature indices from Pfister (1988). The graph shows moving averages over 15 years.

The simulated winter temperature during the period from 1525 to 1979 was always above -5 °C; thus its ecological significance in the FORCLIM model is negligible (chapter 3). Similarly, the simulated drought stress is mostly below 10%, with a few exceptions where stronger drought occurred, the strongest being almost 30% in the “mediterranean” year 1540 (cf. Pfister 1988). Hence, the variable that could have the largest effect on simulated forest dynamics is the annual sum of degree-days (Fig. 6.1). Most of the periods outlined by Pfister (1988) as mid-term climatic variations are evident from Fig. 6.1, such as the warm period from 1530-1564, the maximum of the Little Ice Age from 1688-1701, the rapid warming from 1702-1730, and the cool phase from 1812-1860. These variations had strong effects e.g. on agricultural yield (Pfister 1988) – did they also have effects on the characteristics of near-natural forests, such as species composition and total aboveground biomass?

The simulated forest dynamics from 1525-1979 (Fig. 6.3) do not show any relationship to the climatic variations visible in Fig. 6.1. The variability of the simulated aboveground biomass is due to the stochastic formulation of tree establishment and mortality in FORCLIM (cf. Tab. 3.6), not to the changing abiotic environment. Thus, we may conclude that the forest simulated by FORCLIM-E/P at the CLIMINDEX site is well buffered against climatic variations of the duration and magnitude that occurred during the last 450 years, corroborating the findings by Davis & Botkin (1985). From an evolutionary point of view, these results are plausible as well: Trees typically have lifespans of several centuries; given the fact that climatic variations like the ones reconstructed by Pfister (1988) occur on the timescale of decades, trees must be capable of surviving such anomalies, otherwise they could not grow to adult size and would not be able to reproduce.

Hence, the inertia to climatic variations of the simulated species composition probably is characteristic of real forests of the Swiss Plateau as well. However, these findings can not be generalized to other areas. For example, under conditions of strong environmental stress, such as close to the alpine or the dry timberlines, it is conceivable that climatic variations on the timescale of decades might lead to breakdown phenomena – at least in forest models. However, further studies would be required to address this issue.

Finally, it should also be noted that this experiment could not have been performed using the FORECE model by Kienast (1987). In an earlier study, we have shown that the “dry days” approach incorporated in FORECE and other forest gap models leads to unrealistic forest breakdown events when the same realization of weather is used to drive successional dynamics on all the patches that are simulated (Fischlin et al. 1994).

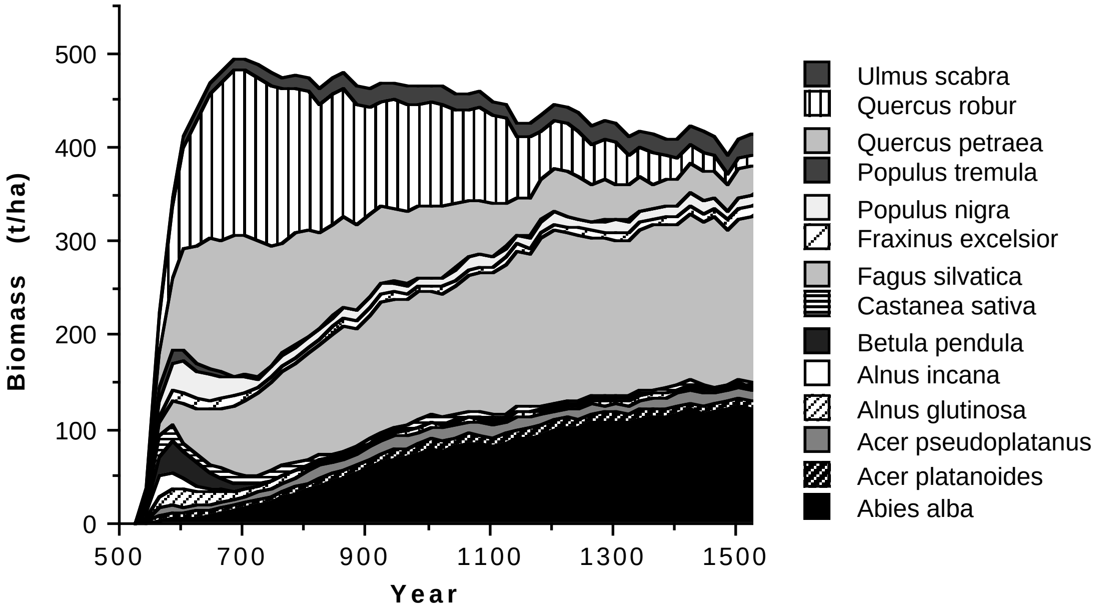


Fig. 6.2: Simulation results at the site "CLIMINDEX" for the years 525-1525 AD when sampling the weather stochastically from the long-term statistics (Tab. 6.1). The simulation starts with a bare plot in the year 525.

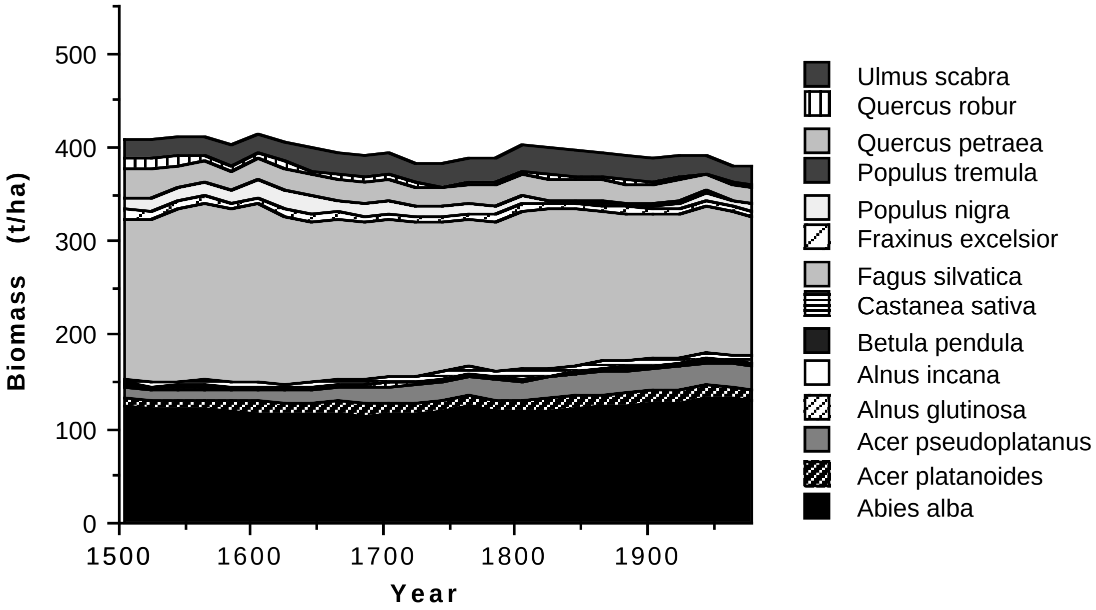


Fig. 6.3: Simulation results at the site "CLIMINDEX" for the years 1525 to 1979 AD when using the reconstructed weather data from Pfister (1988) to drive the FORCLIM-E model. The initial state of the forest is taken from the results presented in Fig. 6.2.

6.2 Possible effects of future climatic change on forest ecosystems in the European Alps

Any assessment of the possible effects of future climatic change on forest ecosystems is faced with a twofold problem: First, there is a considerable uncertainty inherent in the predictions of future climate, both on the global and even more pronounced on the regional scale (Houghton et al. 1990, 1992, Wigely & Raper 1992). Second, every forest model incorporates different and highly simplified parametrizations of ecological processes; these certainly contain errors both on the quantitative and maybe even on the conceptual level (Solomon 1986, Shugart & Prentice 1992). Thus, it appears to be more promising to analyse the behaviour of several ecological models under several scenarios of climatic change instead of focusing on just one model and one scenario. This approach also emphasizes that such studies are tests of the sensitivity of forests ecosystems to climatic changes, and not predictions of their future structure and functioning.

In this section, scenarios of climatic change will be used that refer to the year 2100, and it will be assumed that the climatic parameters reached by then can be used to define a new, constant climate. It is undisputed that this assumption is unrealistic because there is no evidence that climatic change would come to a halt by the end of the next century (Houghton et al. 1990, 1992). Again, it should be noted that the simulation results obtained like this do not constitute predictions of the future state of forests in the European Alps, but simple sensitivity tests.

First, let us assume that there was one forest model that we could favour over all the others. How does this model behave when it is exposed to several climate scenarios? How sensitive are the projections obtained from the forest model to the differences between these climate scenarios?

Second, given that there was no uncertainty in the prediction of future climate, i.e. that one climate scenario could be identified unequivocally as the “best estimate”, how does the behaviour of several forest models compare under this climate scenario? Are the projections on future forest ecosystem structure sensitive to the assumptions incorporated in the various forest models?

Third, even if we could favour one climate scenario over the others, there is some uncertainty inherent in this scenario. How sensitive are the projections obtained from a forest model to these uncertainties?

Finally, most climate scenarios give us an indication about what the change in a given weather variable will be by a certain point in the future. However, in most scenarios it is not known how this change will be realized. Most impact studies so far have assumed that climate changes linearly (Solomon 1986, Pastor & Post 1988, Kienast 1991); other authors have studied the response of forest models to an instantaneous climatic change, i.e. its step response (Fischlin et al. 1994, Bugmann & Fischlin 1994). Thus, there arises the question how sensitive the behaviour of forest gap models is to the assumptions on the nature of transient climatic change.

6.2.1 Material & methods

Forest models

Five forest gap models are used in this study: The first model, FORECE (Kienast 1987), is a conventional gap model that was analyzed in detail in chapter 2. The second model, FORCLIM 1.1 (Bugmann & Fischlin 1994), is a simplified descendant of FORECE and comprises only the most fundamental ecological processes (cf. section 2.3.1); the formulation of climatic factors in FORCLIM 1.1 is done in the same way as in FORECE. The third model, FORCLIM 1.3 (Bugmann & Fischlin 1994), was developed from FORCLIM 1.1 by altering the mathematical formulations of the climatic factors (cf. section 2.3.2 and Fischlin et al. 1994). The fourth model, FORCLIM-E/P, is one variant of the model developed in chapter 3; it differs from FORCLIM 1.3 concerning the formulation of ecological factors and of climatic influences. The last model is FORCLIM-E/P/S, which incorporates also belowground carbon and nitrogen turnover (chapter 3).

Study sites and steady state climate scenarios

Six sites were selected along a climatological and at the same time altitudinal gradient, ranging from above the current alpine timberline to central alpine valleys close to the dry timberline. In a previous study of possible impacts of climatic change on forests, Kienast (1991) presented simulation results from the sites St. Gotthard, Airolo, and Sion along with results from 15 other sites. To allow for a comparison of the results from the Kienast (1991) study with the ones obtained here, these three sites will be used as well. Gyalistras et al. (1994) developed a methodology to relate large-scale temperature and pressure anomalies to local weather anomalies by means of principal component analysis and canonical correlation analysis (“Downscaling”). Based on the results obtained by this technique for the sites Bever, Davos, and Bern, Bugmann & Fischlin (1994) performed simulation studies with the FORECE, FORCLIM 1.1, and FORCLIM 1.3 models. Thus, these three sites are included in the present study as well. Moreover, a slight modification was applied to the climatic data from the site St. Gotthard: Under current climatic conditions (SMA 1901-1970), FORCLIM simulates the existence of forests at an elevation of 2090 m, which appears to be realistic (e.g. Renner 1982). To obtain a site above timberline, i.e. at an elevation about 100 m higher than the climate station St. Gotthard, its temperature was lowered by 0.7 °C throughout the year, resulting in the site Gotthard II, where FORCLIM simulates no forest under current climate.

Tab. 6.2: Scenarios of climatic change for the year 2100 according to various sources. All changes are relative to current climate. The "IPCC" scenario is based on the "Business–As–Usual" scenario A of fossil fuel emissions. The "Kienast" scenario is based on steady-state $2xCO_2$ GCM runs. The "Regionalized" scenarios are based on the downscaled trends from an uncorrected 100-year (1986-2085) transient run of the ECHAM GCM for the IPCC "Business–As–Usual" scenario A (Cubasch et al. 1992). **Bold face denotes the scenarios used in the present study**. Precipitation changes are given as percentages or as centimeters per month (cm/mo). The standard deviations of T and P were assumed not to change.

Scenario	T_{Summer}	P_{Summer}	T_{Winter}	P_{Winter}	Ref.
IPCC, 2030 (global)	+1.5 °C	+ a few %	+1.5 °C	+ a few %	1
IPCC, 2030 (C. Europe)	+2.5 °C	-15%	+1.5 °C	–	1
IPCC, 2100 (global)	+3.7 °C	–	+3.7 °C	–	1
IPCC, 2100 (C. Europe)	+4.7 °C	–	+3.7 °C	–	1
Kienast	+3.0 °C	+10%	+3.5 °C	+10%	2
Regionalized, Bern	+2.64 °C	+3.98 cm/mo	+3.76 °C	+3.13 cm/mo	3
Regionalized, Davos	+3.28 °C	+0.91 cm/mo	+3.00 °C	+2.14 cm/mo	3
Regionalized, Bever	+4.16 °C	+3.82 cm/mo	+1.48 °C	+2.54 cm/mo	3

[1] Houghton et al. (1990), Fischlin et al. (1994)
[2] Mitchell (1983), Mitchell & Lupton (1984), Wigley & Jones (1988), Kienast (1991)
[3] Gyalistras et al. (1994), Bugmann & Fischlin (1994)

The scenarios of future climatic change stem from three sources (Tab. 6.2). First, a scenario was developed based on the report of the Intergovernmental Panel on Climate Change (IPCC, Houghton et al. 1990). This scenario was extrapolated from the difference between the regional scenario for central and southern Europe and the global average scenario for the year 2030 (Tab. 6.2). Second, a scenario similar to the one used by Kienast (1991) was adapted; the only difference is that Kienast (1991) applied the changes projected for the winter months to the climatic parameters of December through February, whereas in the present study these changes are used to modify the climatic parameters of the six "winter" months October through March in accordance with IPCC practice. Third, the regionalized scenarios of climatic change (Gyalistras et al. 1994) for the sites Bever, Davos, and Bern were taken from Bugmann & Fischlin (1994).

Uncertainty inherent in climate scenarios

Some of the uncertainty inherent in the regionalized scenarios of climatic change can be quantified explicitly (Gyalistras et al. 1994), whereas this would be more difficult for the IPCC scenario (Fischlin et al. 1994); for the Kienast scenario, it is hardly feasible. Thus, the regionalized scenarios of climatic change at the sites Bever, Davos, and Bern were selected to study the uncertainty inherent in a given climate scenario (Tab. 6.3).

Tab. 6.3: Uncertainty inherent in the regionalized scenarios of climatic change (Tab. 6.2), expressed as twice the standard deviation ($2 \cdot \sigma$) of the downscaling models (Gyalistras et al. 1994); these uncertainties were also used in the gap model study by Bugmann & Fischlin (1994).

Site	T_{Summer}	P_{Summer}	T_{Winter}	P_{Winter}
Bern	±1.21 °C	±3.96 cm/mo	±1.33 °C	±1.72 cm/mo
Davos	±0.74 °C	±1.95 cm/mo	±1.26 °C	±3.18 cm/mo
Bever	±1.59 °C	±2.39 cm/mo	±0.94 °C	±1.20 cm/mo

Transient climatic changes

It is a common practice in systems theory to explore the response of a system to a step change in the input data (Fig. 6.4). On the other hand, most of the previous impact assessments using forest gap models have adopted a linear change of climatic parameters over time (e.g. Solomon 1986, Pastor & Post 1988, Kienast 1991). In reality, climatic change will follow neither of these assumptions, and a more gradual, e.g. sigmoid change would be more likely to occur. Thus, these three types of climatic changes were used in the present study (Fig. 6.4).

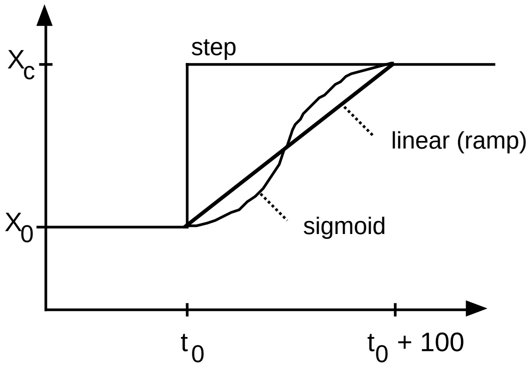


Fig. 6.4: Three types of transient climatic change that are explored in this study. X_0: Long-term mean value of a climatic variable (e.g., average of July temperature) under current climatic conditions; X_c: Long-term mean value of the variable under the climatic change scenario. The time axis is in years; t_0 is the time when the climate starts to change.

Simulation experiments

To explore the behaviour of one forest model under various climate scenarios, the FORCLIM-E/P model was selected. At the sites Bever, Davos, and Bern, all three climate scenarios were used. At the other sites, only the Kienast scenario and the IPCC scenario were available. The steady-state species compositions were estimated under current and under the future climate using $n = 200$ points and $\Delta t = 150$ years (cf. section 4.4).

The behaviour of the five forest models was compared using the regionalized climate scenarios (Tab. 6.2). They bear the advantage of providing a picture of possible future climate that is consistent with global climate change as projected by General Circulation Models (GCMs) and with measurements of the variations of temperature and precipitation at the respective locations. The equilibrium species composition of the various models was estimated either as outlined above or by averaging the output from transient simulations over 500 years (Bugmann & Fischlin 1994).

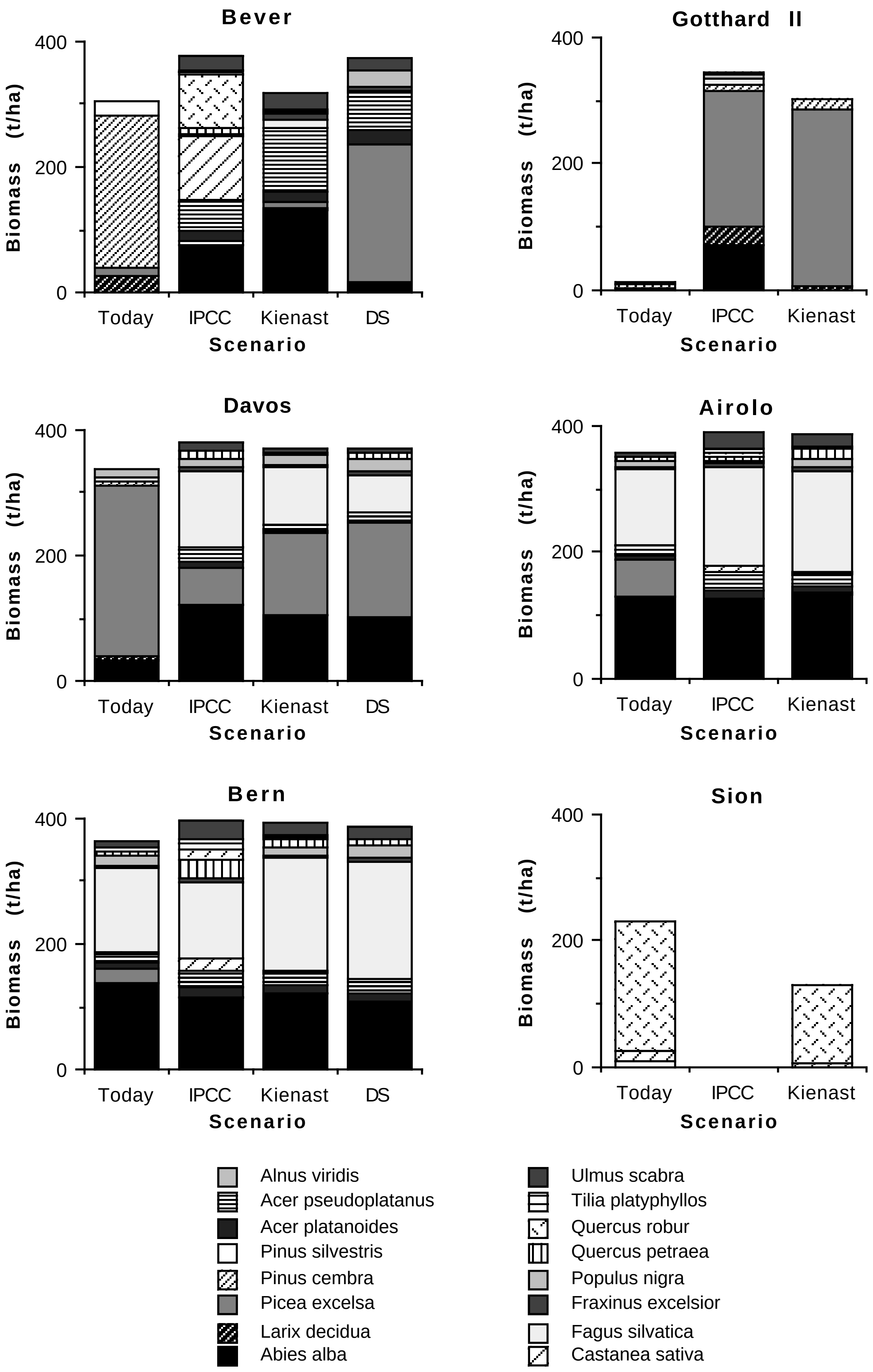
The ecological effects of the uncertainty inherent in the regionalized scenarios were explored with the FORCLIM-E/P model. The steady-state species compositions were estimated using $n = 200$ points and $\Delta t = 150$ years (cf. section 4.4).

Finally, to analyse the effects of various assumptions on transient climatic change, the regionalized scenarios and the FORCLIM-E/P model were used, and 200 patches were simulated. During the first 800 years the models were allowed to reach the steady-state species composition under current climate; then the transient climatic change was applied, and after the year 900 the future climate was assumed to be constant again.

6.2.2 Results & discussion

The behaviour of FORCLIM-E/P under various scenarios of climatic change

The simulation studies with FORCLIM-E/P reveal that there is no uniform response of the model across the sites (Fig. 6.5). However, all the steady states at a given site are significantly different from each other ($\alpha = 5\%$, cf. section 4.4) except for the comparison between the IPCC and Kienast scenario at the site Airolo, where the percentage similarity coefficient (PS, cf. Eq. 2.3) is 0.91, and the comparison between the Kienast and the regionalized scenario at the site Bern (PS = 0.93). The effects of the various scenarios on the simulated steady-state species composition will be discussed for each site in turn:


Bever
Gotthard II
Davos
Airolo
Bern
Sion
Biomass (t/ha)
0
200
400
Today
IPCC
Kienast
DS
Scenario
Alnus viridis
Acer pseudoplatanus
Acer platanoides
Pinus silvestris
Pinus cembra
Picea excelsa
Larix decidua
Abies alba
Ulmus scabra
Tilia platyphyllos
Quercus robur
Quercus petraea
Populus nigra
Fraxinus excelsior
Fagus silvatica
Castanea sativa

At the site Bever (Fig. 6.5), there is hardly any agreement among the simulated forests under climatic change. The projections under the various climate scenarios range from spruce-maple *(Picea excelsa – Acer spp.)* forests under the regionalized scenario, which resemble those typical of today's montane belt (Ellenberg & Klötzli 1972), to species compositions as surprising as silver fir-chestnut-oak *(Abies alba – Castanea sativa – Quercus spp.)* forests under the IPCC scenario. However, there is one pattern that is common to all scenarios of future climate: All these steady-state species compositions differ radically from the species composition simulated under current climatic conditions, which is also typical of the actual vegetation at Bever. Thus, sites like Bever are likely to undergo drastic changes, but it appears to be impossible to give an indication of what the exact changes will be, even if we optimistically assume that the forest model does not contain any uncertainties.

At the site St. Gotthard (Fig. 6.5), both scenarios agree (1) that the timberline will rise and this area would become afforested, and (2) that spruce *(P. excelsa)* would come to dominate these forests. However, the two scenarios produce slightly diverging results concerning the abundance of species such as silver fir *(A. alba)* and larch *(Larix decidua)*. Comparing these findings to the results published by Kienast (1991), who used the FORECE model, a large discrepancy becomes evident: In the Kienast study, *Pinus cembra* was abundant after the first 100 years of climatic change, which most probably represents an anomaly (cf. section 5.3). Moreover, the forests simulated in that study had very low biomass (around 100 t/ha) irrespective of the magnitude of climatic change, whereas FORCLIM simulates an aboveground biomass of almost 300 t/ha (Fig. 6.5). The low biomass obtained from FORECE probably is an artifact of the aboveground carrying capacity that was not adjusted, thus producing inconsistent results under climatic change (cf. section 2.3.2).

At the site Davos (Fig. 6.5), all three climate scenarios induce a shift from the subalpine spruce *(P. excelsa)* forests prevailing today to forests where silver fir *(A. alba)*, spruce, and beech *(Fagus silvatica)* are abundant. Thus, the model predicts an invasion of species that are typical of today's montane belt (Ellenberg & Klötzli 1972). Again, there are some differences among the various scenarios concerning the abundance of single species.

Fig. 6.5 (facing page): Steady-state species composition simulated by the FORCLIM-E/P model under various climate scenarios at six locations along a climate gradient in the European Alps. The scenarios of future climate are described in more detail in Tab. 6.2.
Symbols: Today – Current climate; IPCC – IPCC scenario of climatic change; Kienast – Climate scenario as used by Kienast (1991) for the year 2100; DS – Regionalized climate scenario obtained by the downscaling methodology (Gyalistras et al. 1994).

At the site Airolo (Fig. 6.5), spruce *(P. excelsa)*, which is characteristic of montane mixed forests, is replaced by silver fir *(A. alba)*, beech *(F. silvatica)*, and other deciduous species under both climate scenarios. Comparing these results to the ones by Kienast (1991) is difficult because of the large sensitivity to species parameters in the FORECE model (cf. section 5.1), and further studies with the FORECE model would be required to allow for a meaningful comparison.

At the site Bern (Fig. 6.5), only slight changes occur as compared to current climatic conditions. The major features of the current forests, especially the dominance of beech *(F. silvatica)* and silver fir *(A. alba)*, remain characteristic also of future forests; under all scenarios, similar forest compositions are obtained.

At Sion, major differences become evident concerning the physiognomy of the site under climatic change: While the IPCC scenario leads to steppification, a scrawny, low-biomass forest continues to exist under the Kienast scenario. Using FORECE, Kienast (1991) found that steppification may occur within 50 years after the onset of climatic change. Moreover, simulation results from FORCLIM-E/P/S under the regionalized scenario (A. Fischlin, pers. comm.) also project that forests would cease to grow at Sion. Hence, according to these simulation studies there is a considerable risk that sites close to the dry timberline may be confronted with forest dieback phenomena and steppification under climatic change.

The behaviour of five forest models under the regionalized scenarios

The simulation results from the five forest models at the sites Bever, Davos, and Bern are shown in Fig. 6.6. At the site Bever, the models produce strongly differing species composition under this scenario of climatic change. While the percentage similarity coefficient (PS, Eq. 2.3) between FORCLIM-E/P and E/P/S is 0.75, and PS = 0.85 between FORCLIM 1.1 and 1.3, there is little resemblance between these two groups and the FORECE species composition (PS < 0.4). At the site Davos, there are also considerable differences among the models, but they are more gradual than at Bever. The forest composition at the low-elevation site Bern exhibits the smallest differences among the five models (Fig. 6.6).

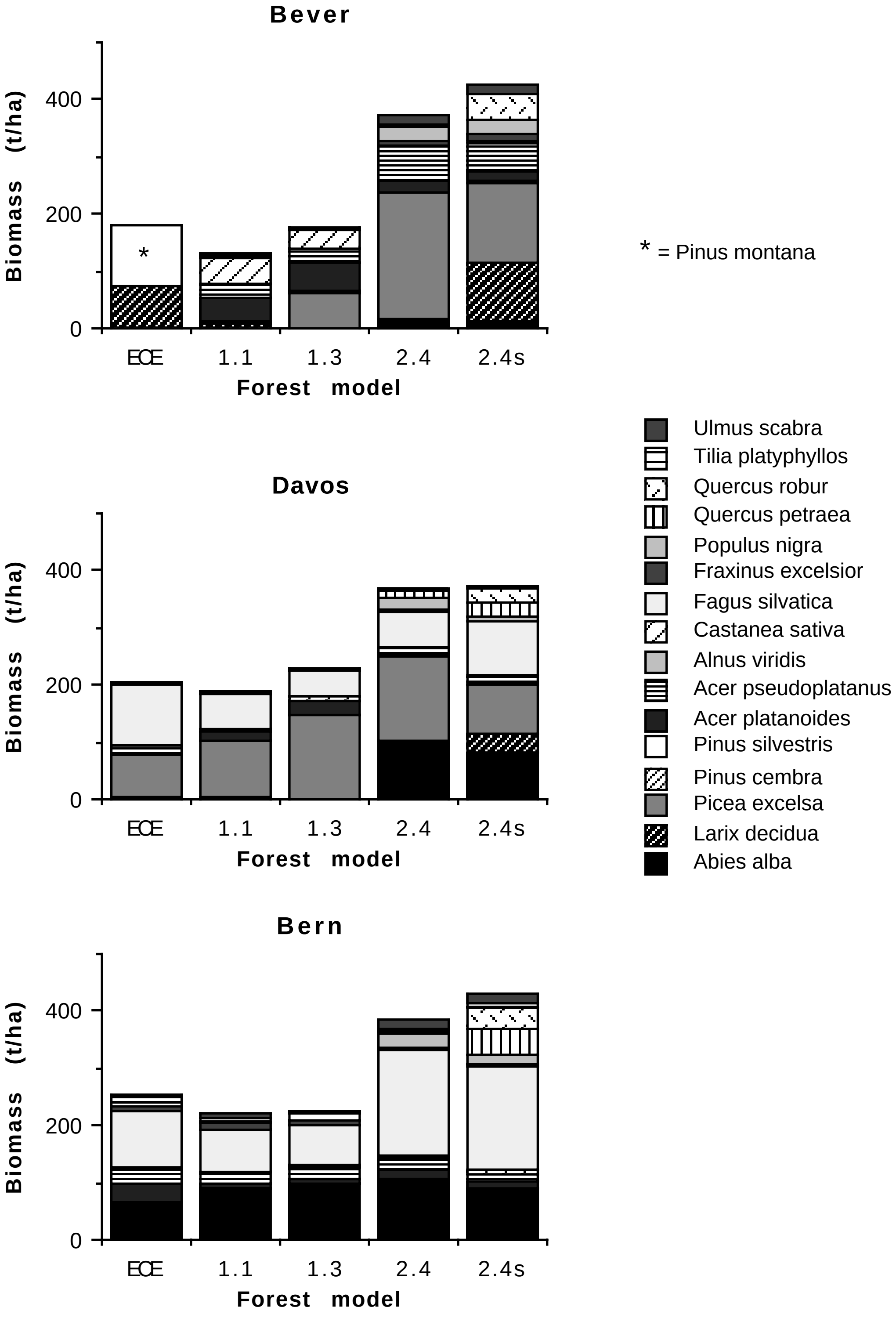


Fig. 6.6: Steady-state species compositions as simulated by various forest gap models under the same scenario of climatic change obtained by the downscaling methodology (Gyalistras et al. 1994, cf. Tab. 6.2).
Symbols: ECE – FORECE model (Kienast 1987); 1.1 – FORCLIM version 1.1 (Bugmann & Fischlin 1994); 1.3 – FORCLIM version 1.3 (Bugmann & Fischlin 1994); 2.4 – FORCLIM-E/P, version 2.4 (this study); 2.4s – FORCLIM-E/P/S, version 2.4 (this study).

However, albeit species compositions differ less the lower the elevation is, there is a large disagreement on total aboveground biomass between FORCLIM-E/P(/S) and the other three models at all three sites both under current climate (results not shown) and under the scenarios of climatic change (Fig. 6.6). At Bern, the difference of total aboveground biomass leads to low PS coefficients although the simulated species composition is rather similar among the forest models (e.g. between FORCLIM 1.3 and FORCLIM-E/P PS = 0.57, between FORCLIM-E/P and FORCLIM-E/P/S PS = 0.82). Thus, we may conclude that the models are sensitive to the formulation of ecological factors especially when simulating subalpine forests (cf. Fischlin et al. 1994).

Sensitivity of FORCLIM to the uncertainty inherent in the regionalized scenarios

For the sites Bern and Davos, where the different climate scenarios did not lead to large differences in the simulated forest community, there is also little sensitivity to the uncer-

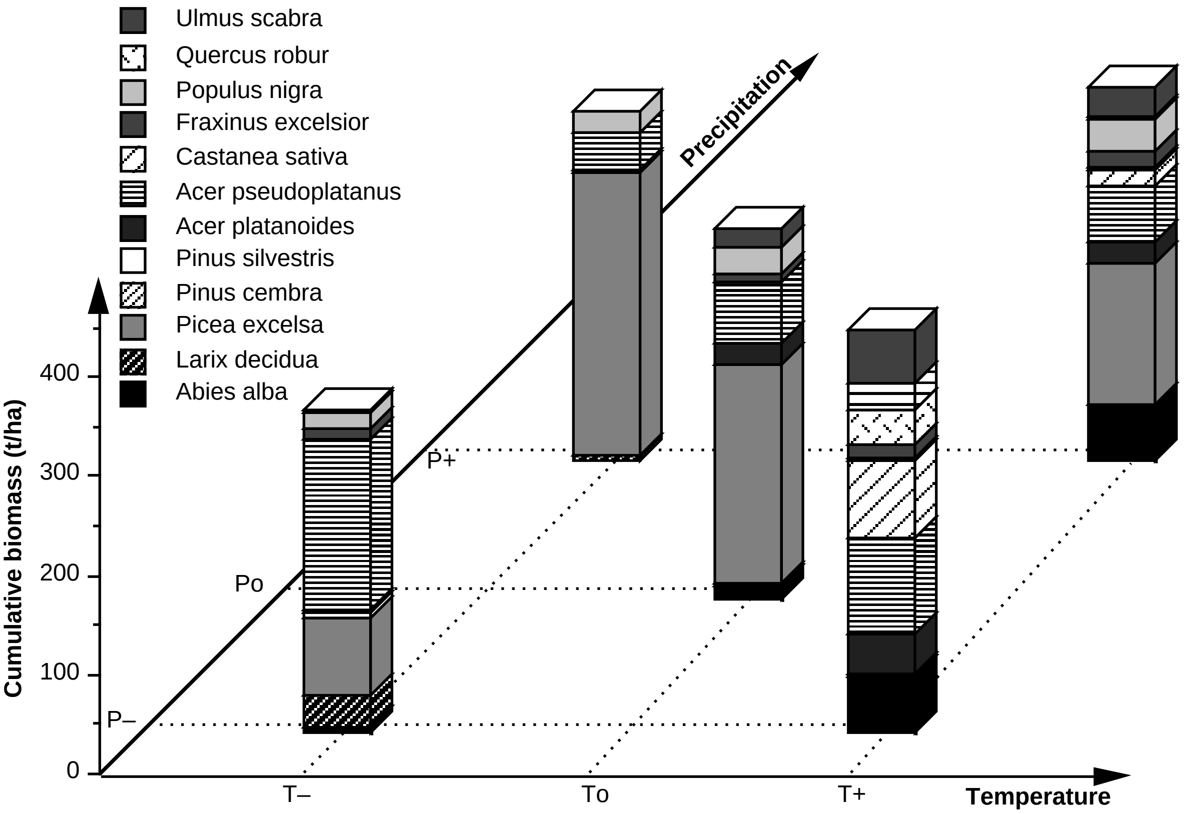


Fig. 6.7: Effect of the uncertainty inherent in the regionalized climate scenario (Tab. 6.3) at the site Bever on the steady-state species composition as simulated by the forest model FORCLIM-E/P.
Symbols: T_0, P_0: Best estimate change of temperature and precipitation (Tab. 6.2). T±, P±: lower and upper end of uncertainty range for temperature and precipitation, respectively ($X\pm = X_0 \pm 2\cdot\sigma_X$, where $X \in \{T,P\}$; cf. Tab. 6.3).

tainty inherent in one climate scenario: At Davos, the smallest PS between the species composition simulated under the "best estimate" regionalized scenario (Tab. 6.2) and those simulated under the scenarios corresponding to the lower and upper end of the uncertainty range (Tab. 6.3) is 0.73, and the average PS is 0.82. At Bern, the smallest PS is 0.84, while the average PS amounts to 0.89. At the site Bever, however, accounting for the uncertainty inherent in the downscaling scenario produces a wide array of forest compositions (Fig. 6.7): The lowest PS is 0.25, and the average PS amounts to 0.51 only. Thus, some of the simulated forests have hardly anything in common (Fig. 6.7).

Moreover, the simulated total aboveground biomass (Fig. 6.7) varies from 338 t/ha (T-P-) to 419 t/ha (T+P-); thus there is also a large uncertainty concerning the aboveground carbon storage of these potential future forests. These results also corroborate the findings by Fischlin et al. (1994), which were based on the IPCC scenario for the year 2030.

Sensitivity of FORCLIM to assumptions on the course of transient climatic change

The transient simulation results based on scenarios of step, ramp, and sigmoid climatic change reveal that there are no large differences at any site. At the site Bever, the largest differences between the three scenarios of transient climatic change occur (Fig. 6.8). This is because at Bever the difference between the steady-state species compositions under current and regionalized scenarios of climatic change is larger than at the other sites (Fig. 6.5).

The evaluation of the percentage similarity (PS) coefficients from the simulation years 700 through 1300 suggests that there is a short period (from the years 820-860) where the disagreement between the step and the ramp scenario is large ($PS_{840} = 0.33$); this is due to the fact that in the step scenario the breakdown of the community takes place immediately after the year 800, whereas in the ramp scenario it starts a few decades later and proceeds more gradually. The fast breakdown of the community in the step scenario increases light availability markedly, which enables the establishment and enhanced growth of light-demanding species like *Larix decidua* and *Quercus robur;* however, these species do not become dominant and are outcompeted during the following centuries.

On the other hand, there is hardly any difference between the species composition simulated with the ramp and the sigmoid scenario (PS = 0.84 in the year 860, in all other years PS > 0.93). Thus, for a climatic change of the anticipated magnitude taking place during the relatively short time of one century, assumptions about how the climate

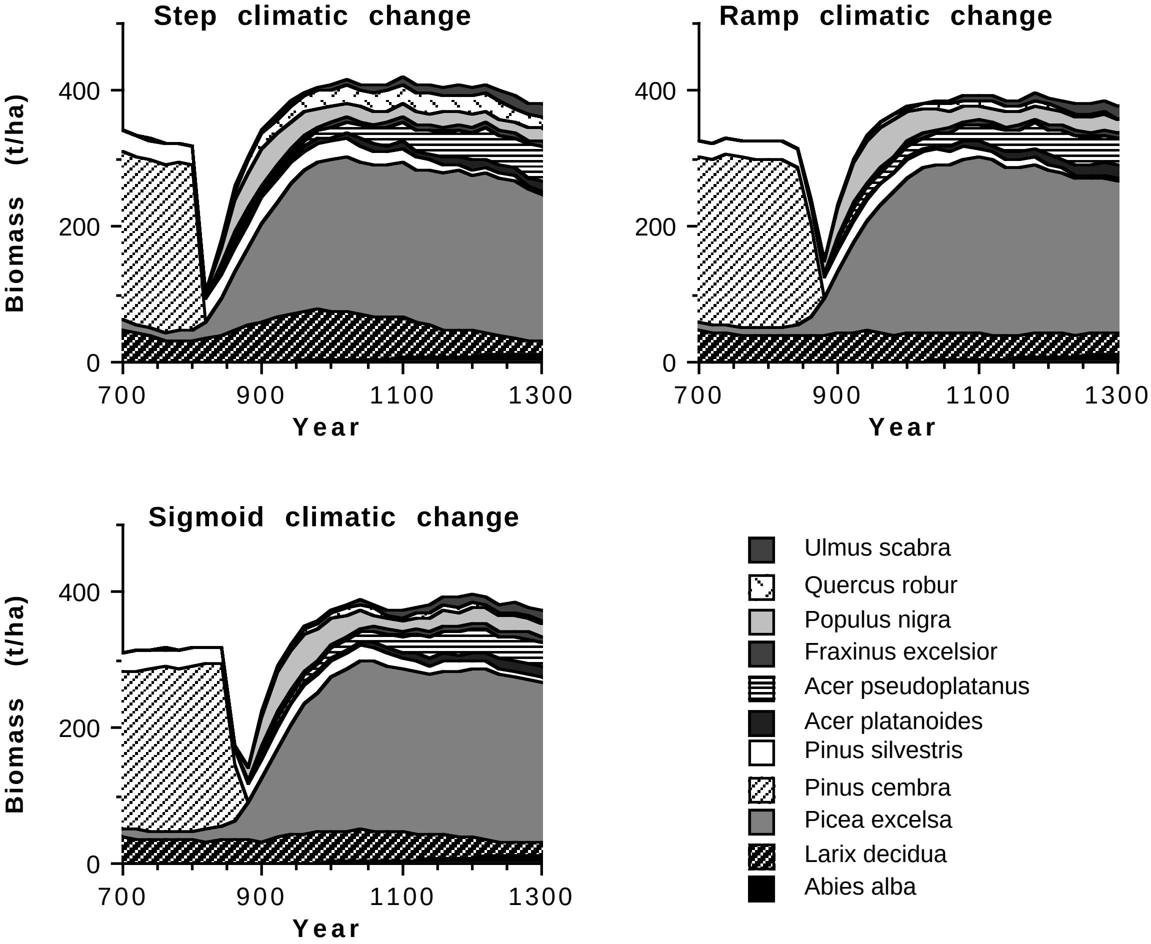


Fig. 6.8: Effect of various assumptions about the nature of transient climatic change between the simulation years 800 and 900 on the transient behaviour of FORCLIM-E/P at the site Bever (cf. Fig. 6.7).

changes are not important because such a climatic change proceeds very fast compared to successional dynamics. Only the assumptions about the level of a hypothesized future *constant* climate are crucial (cf. Fig. 6.8).

6.2.3 Conclusion

Several conclusions can be drawn from the simulation studies with various forest models under various climate scenarios developed to represent a hypothetical constant climate at the end of the 21st century:

First, the species composition simulated by FORCLIM-E/P under various scenarios of climatic change at sites close to the alpine and the dry timberline differs markedly from the one simulated under current climatic conditions. This pattern is independent of the climate scenario chosen. However, the exact species composition simulated by FORCLIM-E/P at these sites and under climatic change depends strongly on the scenario used. On the other hand, sites at mid altitudes show smaller and more uniform changes of their species composition across the various climate scenarios.

Second, similar effects are visible when evaluating the response of various forest models to one specific scenario of climatic change: The species composition simulated close to the alpine timberline varies considerably depending on the forest model used, i.e. on the number of factors incorporated in a model and their formulation. It is surmised that the same is valid also for sites close to the dry timberline, but this was not investigated in the present study. Sites at mid altitudes appear to be less sensitive to the choice of the forest model.

Third, the uncertainty inherent in the regionalized scenario of climatic change leads to a wide array of possible future forest compositions. Thus, even if one climate scenario could be identified as the “best estimate”, its uncertainty would preclude precise statements about future forest composition and aboveground carbon storage, especially at subalpine sites.

Finally, the comparison of step, linear (ramp), and sigmoid climatic changes during 100 years show that the choice of the transient scenario is not important because the change of the abiotic conditions proceeds fast compared to the successional dynamics. However, if climatic change continues for several centuries, i.e. when the time scale of climatic change approaches the time scale of forest succession (Bugmann & Fischlin 1994), the differences between the various scenarios of transient climatic change certainly would be more pronounced; as mentioned in the introduction to this section, there is no evidence that climatic change would come to a halt by the end of the next century. Moreover, these findings may not hold for changes of the variance of climatic parameters, which have not been investigated here.

7. Discussion

7.1 Analysis of existing forest gap models

Forest gap models, although conceptually simple, have grown to complex ecological models with a huge parameter space. The analysis of the FORECE model (Kienast 1987) showed that the level of complexity reached in these stochastic models calls for a careful evaluation of the model formalism and the statistical properties of the underlying stochastic process (cf. Bugmann & Fischlin 1992). Like this, inconsistencies in the implementation of many forest gap models were detected (e.g. Pastor & Post 1985, Solomon 1986, Kienast 1987, Leemans & Prentice 1989), and an inappropriate design of some experiments performed with these models was revealed (cf. Bugmann & Fischlin 1992).

These issues appear to be related to the sheer impossibility of publishing all the equations of the mathematical model in detail, which is indispensable because other researchers using the model must understand its assumptions and limitations, but which is not usually possible given the page limitations of scientific journals. In order to become familiar with a forest gap model, it is often necessary to extract its conceptual elements from the simulation model, i.e. the computer code, which is a tedious and inefficient way of scientific communication. Like this it is easily possible that artifacts are introduced when adding new features, or that the model is run under conditions where it produces inconsistent results. Hence, the analysis of existing forest gap models provided a safer basis for model simplifications, refinements, extensions, and the design of simulation experiments.

The analysis of the sensitivity of FORECE to structural simplifications allowed to quantify the importance of the various factors included in the model. By conjecturing that the sensitivity of FORECE is representative of the sensitivity of real forests, a quantitative hypothesis could be derived on the most important ecological factors governing the long-term successional properties of forest ecosystems in the European Alps. According to this hypothesis, four major factors determine tree growth, three factors determine sapling establishment, and two factors determine tree mortality. Hence, such an analysis may contribute not only to our understanding of the internal workings of a complex forest model, but also to our understanding of the ecology of forest ecosystems.

Finally, the analysis of the formulation of climate-dependent factors in forest gap models revealed that many conventional models implicitly assume a constant climate, and that model behaviour is sensitive to relaxing these assumptions (cf. Bugmann & Fischlin 1994, Fischlin et al. 1994). Other researchers came to similar findings using a different approach, i.e. by combining conventional forest gap models with detailed biophysical or physiological submodels for calculating the influence of climatic parameters (Martin 1990, 1992, Bonan & van Cleve 1992, Friend et al. 1993). However, the fact that a model is sensitive to the formulation of a factor is a necessary, but not a sufficient condition to show that a detailed submodel is required to calculate that factor. The present study suggests that at least in some instances simple yet realistic parametrizations of abiotic factors can be developed, and that they improve the reliability of a model considerably. Thus, the call for detailed biophysical or physiological submodels forming part of forest gap models appears not conclusive yet (cf. Bonan 1993).

7.2 Structure and behaviour of FORCLIM

The construction of FORCLIM as a forest gap model composed of three submodels (E – abiotic environment, P – plant population dynamics, and S – soil organic matter turnover) provided the flexibility to evaluate the behaviour of each submodel and any desirable combination of the submodels. This constitutes a distinct advantage over conventional forest gap models, where the complete model is the single scope of simulation studies. These analyses revealed that FORCLIM-P on its own does not provide realistic species compositions under conditions of strong environmental stress, e.g. when approaching the alpine and the dry timberline, suggesting that FORCLIM-E is of paramount importance for simulating forest dynamics under these conditions. The forest gap model FORSKA-2 (Prentice et al. 1993) does not incorporate the effects of a stochastic environment, although the model was designed for boreal and broadleaf forests of Scandinavia, where precipitation sums often are small and drought stress is large. Thus it would be interesting to investigate if the above findings are restricted to forests in the European Alps, or whether they apply also to other areas.

The influence of FORCLIM-P on the amount of litter and humus simulated by FORCLIM-S is small. This may partly be due to the fact that the quality of a large fraction of the litter produced by FORCLIM-P does not vary with the species producing it, i.e. twig, wood, and root litter, which constitute up to 90% of the total litter production. Thus, a more detailed modelling of litter production would be desirable; unfortunately, the data base for

European conditions is scarce. On the other hand, the influence of FORCLIM-S on the dynamics of FORCLIM-P appears to be stronger, although it is still less important than the coupling between FORCLIM-E and FORCLIM-P. Based on these considerations, the fact that most forest gap models developed to date ignore the turnover of soil organic matter but include a stochastic weather generator gets an empirical, quantitative underpinning.

FORCLIM-S is the first submodel for belowground carbon and nitrogen turnover used in a gap model for central European conditions, and the simulation studies with it were encouraging. However, this submodel should be scrutinized carefully, several of its equations should be reformulated on a more mechanistic basis, and it should be validated extensively. Model improvements should deal primarily with adding a "slow" compartment (Parton et al. 1987, Verberne et al. 1990), and with a reformulation of the mineralization rate of the humus. Moreover, there is a serious problem of mapping the compartments in FORCLIM-S ("litter", i.e. material that immobilizes nitrogen, and "humus", i.e. material that releases nitrogen) to field measurements typically distinguishing "forest floor" and "mineral soil" primarily on a morphological basis (e.g. Vogt et al. 1986).

In FORCLIM-E, the sensitivity of the drought stress index (Cramer & Prentice 1988, Prentice & Helmisaari 1991) to small changes of actual evapotranspiration raises the question whether it is robust enough to be used for parametrizing the ecological effects of drought on tree growth. It is suggested that further research should address this issue.

Two aspects that have made forest gap models especially elegant could be maintained in FORCLIM: The simple representation of crown geometry, i.e. that all the leaves are concentrated at the top of the bole, and the lack of spatial interactions among forest patches. While the former assumption might have to be changed if boreal forests were to be simulated (Leemans 1992), the latter would have to be relaxed if migration phenomena were to be considered, e.g. for validation studies using pollen proxy data (Lotter & Kienast 1992), or if the spatial dynamics of landscapes were to be simulated (Urban et al. 1991).

7.3 Parameter sensitivity

The analysis of the parameter sensitivity of FORCLIM-E/P/S revealed that the model is comparably robust to the values of its species parameters when they are varied within their range of plausibility. Thus the simulated species composition is not an artifact of arbitrarily chosen parameters, which increases our confidence that the simulation results obtained from FORCLIM represent reliable hypotheses on the forests under study.

The parameter describing the tolerance to low nitrogen availability (kNTol) proved to be most important for determining the simulated species composition. This sensitivity calls for a careful scrutinization of the simple formulation used for modelling the effects of nitrogen availability on tree growth in FORCLIM (Pastor & Post 1985). With an improved formulation of this growth factor the coupling between FORCLIM-S and FORCLIM-P may become more important, which in turn would underline the significance of improved modelling of soil carbon and nitrogen turnover (e.g. Perruchoud 1994).

The simulated species composition is also sensitive to the scaling constant in the tree growth equation (kG). Since tree growth is directly linked to competitive ability, this sensitivity appears to be quite realistic. The parameter determines tree growth during the early stage of tree life, where competition is especially strong due to extensive shading. The other parameters of the growth equation (kHm, kDm) have a stronger influence on older trees only. Competition for light is a major factor both in real and in model forests, and FORCLIM therefore is correct in producing a high sensitivity to the species parameters describing the tolerance of low light availability (kL_y, kL_a).

Thus we may conclude that the equation determining the maximum diameter increment is among the most sensitive parts of FORCLIM. These findings suggest that the basic assumptions such as the carbon balance of trees and the various allometric relationships used in the current growth equation should be scrutinized carefully. For example, the parabolic relationship between tree height and diameter may be questionable because it requires that diameter growth always comes to a halt when height growth ceases, which certainly is unrealistic and makes it difficult to estimate the parameters of the current growth equation (cf. Appendix II).

Finally, the sensitivity analysis revealed that the precision of the biomass estimates obtained from FORCLIM is low, i.e. the abundance of a given species varies considerably depending on the values of the parameters used to characterize its natural history. It is interesting to view this finding within the framework proposed by Levins (1966): FORCLIM appears to be realistic (it produces plausible species compositions) and general (it is applicable under a wide range of climatological and ecological conditions), but the species composition simulated by FORCLIM is not precise.

7.4 Model validation

The three models FORECE, FORCLIM-E/P and FORCLIM-E/P/S all produced plausible species composition when applied at sites along a climatological gradient in the European Alps (cf. Kienast & Kuhn 1989a,b). Based on these results alone, it would not be possible to favour one of the models over the others, although the formulation of FORCLIM is mathematically more rigorous, it depends to a larger extent on causal relationships, and it is simpler. Only the systematic simulation studies performed in a climatological parameter space spanned by the annual mean temperature and the annual precipitation sum revealed that FORECE contains several unrealistic thresholds and that it produces unrealistic species compositions in a larger fraction of this (T,P) space than FORCLIM.

There are two areas in the (T,P) space where both FORECE and FORCLIM encounter major difficulties: (1) The warm-dry zone in central Alpine valleys as well as outside the Alps, such as in large areas of Germany and France, where the models fail to simulate realistic species compositions along drought gradients; (2) The insubrian and mediterranean zones, where the models fail to simulate the occurrence of drought. These shortcomings may be especially important for sites on the Swiss Plateau, where climatic change could lead to such conditions (cf. Gyalistras et al. 1994). Hence further research on soil water balance and the ecological effects of drought should be conducted.

The study in the (T,P) space was confronted with a serious methodological problem: The hypothesis on the dominating species in this space (Rehder 1965, Ellenberg 1986) lacks an exact quantification. Thus, the comparison of the simulated species compositions with phytosociological data was possible on a qualitative basis only, and many aspects of the simulation results had to be ignored although they could give important indications on deficiencies of FORECE and FORCLIM. The comparisons of model output with phytosociological data performed along an altitudinal and a latitudinal gradient in the European Alps and in eastern North America, respectively, were faced with similar problems: There is a mismatch between the qualitative nature of phytosociological descriptions of near-natural forests (e.g. Ellenberg & Klötzli 1972, Küchler 1975) and the quantitative data obtained from forest gap models.

The simulation results obtained along a latitudinal gradient in eastern North America, which differs from European conditions both climatologically (i.e. larger continentality) and ecologically (i.e. different species), are encouraging for two reasons: First, the performance of the unmodified FORCLIM model was realistic at many locations. Second, comparably small improvements, such as adding an additional light tolerance class for saplings, could strongly increase the realism of the results obtained so far. However, similar to the findings from the (T,P) space, FORCLIM encounters major difficulties along drought gradients, i.e. in the southeastern U.S.; yet other models like FORENA (Solomon 1986) and LINKAGES (W.M. Post, pers. comm.) are faced with the same problem. Hence it appears that current forest gap models generally are not apt for simulating forest dynamics along drought gradients.

Both the simulation study in the (T,P) space and along a latitudinal gradient in eastern North America suggest that the simplification of a complex model like FORECE does not have to hamper the realism with which it is capable of simulating forest succession. On the contrary, the improvements introduced when developing the FORCLIM model appear to have increased its realism. Moreover, the parameter space of the model could be reduced drastically, from more than 1300 (FORECE) to 540 parameters (FORCLIM). However, additional validation studies should be conducted to analyse further deficiencies of FORCLIM, e.g. using proxy data like pollen records or spatial data obtained by remote sensing techniques.

7.5 Possible effects of climatic change on forests in the Alps

The investigation of the behaviour of the FORCLIM-E/P model under three different climate scenarios suggests that forests close to the current alpine (Bever, Davos) or dry timberline (Sion) are especially sensitive to the climatic changes expressed in the various scenarios. Given that the sensitivity of FORCLIM is representative of real forests, there are two important implications of these findings: First, the forests currently growing at these sites may be affected drastically by the expected changes of temperature and precipitation. Second, given that one wanted to predict the potential future forest composition at specific locations, the forecasts of future climate would have to be more precise than this appears to be currently possible (e.g. Santer et al. 1990, Giorgi & Mearns 1991).

On the other hand, near-natural forests at mid altitudes, e.g. at the sites Airolo and Bern, appear to be least sensitive to climatic change (cf. Bugmann & Fischlin 1994). They show small and uniform changes of their species composition across different climate scenarios. If this small sensitivity is real, this implies that mid altitude forests are likely to undergo minor changes only. However, the sensitivity tests performed in this study have a time horizon of 100 years only, although climatic change is likely to continue after the year 2100 (Houghton et al. 1990, 1992). Hence these results do not mean that future climatic change will not affect these forests drastically, but that they are buffered better against climatic change than forests that are subject to environmental stress already under current climate (Bugmann & Fischlin 1994).

The comparison of the behaviour of five forest gap models under one scenario of climatic change shows that the models disagree most sharply at sites close to the alpine timberline. Thus, under these conditions the models are sensitive to climatic parameters as well as to the formulation of ecological factors. Although there is less divergence at the other sites and it is felt that FORCLIM-E/P and FORCLIM-E/P/S are the most trustworthy of all the five models studied, it is daunting to see the differences the five models produce. Moreover, there is no clue that future versions of FORCLIM will be robust in their projections. For example, ongoing research (Perruchoud 1994) is aimed at providing an improved version of FORCLIM-S, which again may lead to projections about future forests differing strongly from the present ones. Thus, there is a serious problem concerning the number of factors to be included in forest ecosystem models and their exact formulation (cf. Bonan 1993).

Even if the best scenario of climatic change could be unequivocally identified, there would remain some uncertainty in it. The investigation of the propagation of the uncertainties inherent in a state-of-the-art scenario obtained from large-scale GCM data (Gyalistras et al. 1994) showed that, again mainly at sites close to the timberline, a bewildering array of possible future forest compositions is obtained. Thus also such a climate scenario does not currently match the precision requirements of forest ecosystem models, corroborating the findings by Fischlin et al. (1994), which were based on a different climate scenario.

FORCLIM was developed to include reliable formulations of the influence of temperature and precipitation on ecological processes. Thus it may be hypothesized that the model is trustworthy enough to assess the possible impact of climatic change on forest ecosystems in the European Alps. However, as discussed above little confidence can be placed in its projections both for climatological and ecological reasons. Yet, even if we are not able to give precise information on the potential future species composition at a given location, this does not mean that no statements could be made at all: The strength of the application of forest gap models in impact assessments of climatic change lies in determining the sensitivity of the simulated species composition to changes of climatic parameters. In this sense and under the assumption of a constant climate corresponding to the climate at the end of the 21st century, we may conjecture that mid altitudes in the European Alps are likely to undergo minor changes only, whereas subalpine areas and those close to the dry timberline are likely to undergo drastic changes of species composition, including forest dieback phenomena.

These results suggest that the prediction of the species composition of near-natural forests under a changed climate is quite difficult. Hence it would be even more difficult to predict the transient dynamics of forest ecosystems in response to a transient climatic change (Schneider & Thompson 1981). The comparison of step, ramp, and sigmoid climatic changes during 100 years show that the choice of the transient scenario is not of paramount importance at this temporal scale because the anticipated climatic change proceeds much faster than the successional dynamics. Hence, the step and ramp scenarios used in previous studies (e.g. Solomon 1986, Pastor & Post 1988, Kienast 1991, Fischlin et al. 1994, Bugmann & Fischlin 1994) constitute a sufficient approximation of more detailed scenarios of transient climatic change on the timescale of 100 years.

7.6 Tools for modelling and simulation

The RAMSES software for modelling and simulation (Fischlin et al. 1990, Fischlin 1991) proved to be very helpful for becoming familiar with forest gap models in the first, explorative phase of the project. The flexibility it offers for interactively changing parameters, monitoring any desired variable, and adding or removing single submodels without having to change the code was especially useful in that phase. Throughout the thesis, working interactively with the user interface of ModelWorks (Fischlin et al. 1990) was important. Moreover, the ModelWorks experiment mechanism made it possible to program large simulation experiments as well and to run them in a batch-oriented mode on up to four remote simulation servers at a time. This turned out to be indispensable and became ever more important towards the end of this study, especially for performing the analyses presented in chapter 5.

The access to the high-level programming language Modula-2 (Wirth 1985) allowed to split the implementation of FORCLIM into several modules with well-defined interfaces. This made it easy to change single features of FORCLIM without the risk of producing side effects on other features. Moreover, the Dialog Machine (Fischlin 1986, Fischlin & Ulrich 1987) and Modula-2 made it possible to program a number of additional features, which provided even more flexibility from both the modeller's and the user's perspective.

8. Conclusions

Exploring the mechanisms of forest dynamics with forest gap models

The complexity of forest ecosystems together with the large temporal and spatial scales involved in successional processes render experimental approaches to study forest succession extremely difficult (chapter 1; Shugart 1984). Forest gap models (Botkin et al. 1972a,b) have been used successfully to synthesize the existing knowledge on successional dynamics of forests. However, the complexity of these models in turn bears problems, e.g. because their properties are ill-known. The analyses performed in chapter 2 together with the re-implementation of FORECE within RAMSES yielded several systems theoretical, statistical and ecological insights into the structure and functioning of the FORECE gap model (Kienast 1987), which provided a safer basis for improving and interpreting the model.

Forest gap models are capable of depicting the successional characteristics of many forest ecosystems in a realistic way (Shugart 1984). The analyses performed in the present study and the subsequent changes to the model, such as the update of state variables and the structural simplification, did still lead to realistic model behaviour for a wide range of sites in the European Alps (chapter 4 & section 5.3) and even in eastern North America (section 5.4). Moreover, the factors that turned out to be most important in the model conform to ecological expectations, e.g. light availability. On the other hand, the factors that contributed little to the simulated dynamics in FORECE and thus could be omitted are those that are also considered to be less important in ecology (Shugart 1984, Ellenberg 1986), or their use in a forest gap model is debatable for principal reasons, e.g. indicator concepts.

These results support the hypothesis that forest gap models are powerful tools for exploring the dynamics of forest ecosystems on scales that are not directly observable, and that the models can be used successfully to interface the ecological knowledge from various disciplines (cf. Levin 1992).

Ecological factors determining forest dynamics in the European Alps

The analysis of the sensitivity of FORECE to structural simplifications (chapter 2) made it possible to derive a hypothesis on the most important factors determining the successional dynamics. According to this hypothesis, forest succession in the European Alps can be portrayed realistically using the following factors: Tree growth is governed by the availability of light, nitrogen, water, and sufficient summer warmth. Major factors influencing sapling establishment are winter minimum temperature, browsing, and again light availability. Tree mortality can be portrayed with two simple functions related to maximum longevity and the occurrence of stress. The point here is not that these factors would not have been identified before (Waring & Schlesinger 1985, Kimmins 1987, Lyr et al. 1992); rather, it is notable how few ecological factors are sufficient to synthesize a realistic picture of successional processes.

The systematic simulation studies performed in chapter 5 suggest that the simplification of a complex model like FORECE does not have to hamper its realism. On the contrary, the simplification and the improvements introduced when developing FORCLIM have increased its capability to simulate realistic forest dynamics especially along climate gradients. Moreover, it was possible to simplify some of the remaining equations, such as the formulation of maximum tree growth. Some of these simplified equations even turned out to be biologically more sound. Finally, the parameter space of the model could be reduced drastically, from more than 1300 parameters in FORECE to 540 in FORCLIM.

Applicability of FORCLIM to study the impact of climatic change on mountainous forests

The theoretical analysis conducted in chapter 2 and the simulation experiments in section 5.3 showed that the FORECE model has not been built and is not apt for impact studies of climatic change. Since most forest gap models share many common features, the same may be surmised for many of these models (Shugart 1984). On the other hand, the validation experiments performed with FORCLIM revealed that this model yields plausible results when it is applied along climate gradients in central Europe (section 5.3) and under the climatic conditions of eastern North America, for which it has not been developed (section 5.4). Moreover, the simulated species composition appears to be reasonably robust to changes of the species parameters (section 5.1). Thus it may be conjectured that FORCLIM yields realistic results also when applied to study the impact of climatic change on forest ecosystems in these areas.

Several problems remain when attempting to use FORCLIM to study the impact of climatic change on near-natural forests: First, such applications basically deal with extrapolations in time and beyond current ecological conditions. The fact that FORCLIM – although developed for European conditions – provides plausible descriptions of forest dynamics also in eastern North America may provide a clue that such extrapolations may be legitimate. However, it would be highly desirable to conduct validation experiments under conditions of climatic change, e.g. in the early Holocene (cf. Solomon et al. 1980, 1981, Solomon & Tharp 1985, Solomon & Bartlein 1993). Although few suitable palaeoecological records are available and it is difficult to derive independent climatic data to drive FORCLIM, such experiments would be important to increase our confidence that the model is appropriate for studying some possible impacts of climatic change on forests.

Second, some factors that are important in mountainous terrain are not considered in FORCLIM, such as soil erosion and landslides, which may occur after forest dieback phenomena and may render large areas inappropriate for forest growth. Moreover, air pollution in conjunction with climatic change may lead to unexpected synergistic effects, such as an increased sensitivity of forests to climatic change (e.g. Schulze et al. 1989), and herbivores could also modify the response of forests to climatic change (e.g. Fajer et al. 1989). Finally, in FORCLIM it is assumed that seeds of every species are always available. In reality, migration of trees is slow (e.g. Fenner 1985, Roberts 1989, Leck et al. 1989), and the growth of new species at a given site often would start later than predicted by FORCLIM because of delayed immigration. Thus, the changes of community composition projected by FORCLIM often are too fast and may overestimate the recovery rates especially after forest dieback phenomena.

In spite of these restrictions, which have to be taken into account especially when interpreting the results obtained from FORCLIM, it is concluded that this model yields realistic results when applied along climate gradients and thus can be considered to be appropriate for assessing the impact of climatic change on the species composition of near-natural forests in large parts of central Europe and eastern North America.

Implications for impact assessments of climatic change

The study of forest dynamics for the last 500 years at a site representative of the Swiss Plateau, using reconstructed monthly temperature and precipitation data to drive the model, showed that these historical climate variations have no impact on the simulated species composition of near-natural forests (section 6.1). However, future climatic change is likely to affect the species compositon of these forests (section 6.2). Hence not only the magnitude and rate of future climatic change (Wigely & Raper 1992), but also the biotic responses to these changes are beyond the limits of natural variability and deserve to be studied in detail.

The simulation experiments conducted with several forest gap models under several scenarios of climatic change for the year 2100 (chapter 6) reveal a common pattern: The effects of the anticipated climatic change on forest ecosystems differ strongly depending on the geographical location considered. Specifically, forests that are subject to considerable environmental stress under current conditions, such as close to the alpine and the dry timberline, are likely to undergo major changes, whereas sites at mid altitudes appear to be buffered rather well to these climatic changes. However, forests at mid altitudes may be affected as well if climatic change should exceed that projected for the year 2100, which is quite probable (Houghton et al. 1990, 1992, Wigely & Raper 1992).

At some sites, the forests simulated by one model under various scenarios of climatic change have little in common except that they are different from current forests. It is not possible to identify unequivocally which of these scenarios describes the future climate best and to ignore the others. Hence we have to conclude that the precision of the forecasts of future climatic change falls short relative to the sensitivity of the forest models, and it is therefore not possible to predict the potential natural vegetation at a given time and a given place in the future. Moreover, there are marked differences between the projections obtained from various forest models under the same scenario of climatic change. Hence there is also a considerable uncertainty concerning the number of ecological factors to be included in forest gap models and, even more pronunced, their specific formulation.

However, these restrictions do not mean that no statements can be made at all. The strength of the application of forest gap models for impact assessments is that they provide us with statements on the sensitivity of the current potential natural vegetation to climatic change. The present study shows that many forest ecosystems in the European Alps are sensitive to climatic parameters. Already under the climatic change anticipated for the year 2100 dieback phenomena could occur in some forests, possibly with irreversible consequences for the structure and functioning of these ecosystems. These findings strongly suggest that it is important to implement abatement policies to fight the increase of greenhouse gas concentrations in the atmosphere on the global as well as the national scale.

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Appendix

I. Scientific and common names of European tree species

The scientific names of the European tree species (Tab. A-1) follow Hess et al. (1980). The common names are from Phillips (1978).

Tab. A-1: Scientific and common names of the 30 European tree species used in the FORCLIM model.

Scientific name	Common name
Abies alba Miller	European Silver Fir, Common Silver Fir
Larix decidua Miller	European Larch, Common Larch
Picea excelsa (Lam.) Link	Norway Spruce
Pinus cembra L.	Swiss Stone Pine, Arolla Pine
Pinus montana Miller	–
Pinus silvestris L.	Scots Pine
Taxus baccata L.	English Yew, Common Yew
Acer campestre L.	Field Maple, Hedge Maple
Acer platanoides L.	Norway Maple
Acer pseudoplatanus L.	Sycamore, Sycamore Maple
Alnus glutinosa (L.) Gaertn.	Black Alder, Common Alder
Alnus incana (L.) Moench	Grey Alder, European Alder
Alnus viridis (Chaix) DC.	–
Betula pendula Roth	Silver Birch, European White Birch
Carpinus betulus L.	European Hornbeam, Common Hornbeam
Castanea sativa Mill.	Sweet Chestnut, Spanish Chestnut
Corylus avellana L.	Hazel, Cobnut
Fagus silvatica L.	European Beech, Common Beech
Fraxinus excelsior L.	European Ash, Common Ash
Populus nigra L.	Black Poplar
Populus tremula L.	European Aspen, Aspen
Quercus petraea (Mattuschka) Lieblein	Sessile Oak, Durmast Oak
Quercus pubescens Willd.	Downy Oak
Quercus robur L.	Pedunculate Oak, English Oak
Salix alba L.	White Willow
Sorbus aria (L.) Crantz	Whitebeam
Sorbus aucuparia L.	Rowan, (European) Mountain Ash
Tilia cordata Miller	Small-leaved Lime
Tilia platyphyllos Scop.	Large-leaved Lime
Ulmus scabra Miller	Scotch Elm, Wych Elm

II. Derivation of parameters for European tree species

sType parameter

The sType parameter serves two purposes:

First, it separates evergreen (coniferous) from deciduous species; the two types differ in the specific leaf area (the foliage area per unit foliage weight, parameter kC_2), and the dry to wet weight ratio of foliage (parameter kC_1). Values for these parameters were derived based on a large data set covering 8 species *(Abies alba, Picea excelsa, Pinus silvestris, Pinus cembra, Pinus montana, Larix decidua, Fagus silvatica, Quercus spp.)* in Burger (1945-1953). The data by Mitscherlich (1970, p. 28) was also evaluated, but it was concluded that the Burger data provided a more reliable basis for estimating these parameters.

Second, it describes the relationship between diameter at breast height (D) and foliage weight of the species. These relationships were derived based on Burger (1945-1953) as well. Because of the scarcity of data on other species, five relationships were defined from the Burger data, and the remaining species were assigned to one of these classes based on their capability to cast shade as described by Ellenberg (1986, p. 82) and on the values of the parameters A1 and A2 used in the FORECE model (Kienast 1987).

Specific leaf area and dry to wet weight ratio

Regression analyses of foliage area vs. foliage weight showed large correlation coefficients, whereas the intercepts were not significantly different from zero ($\alpha = 5\%$) for all species except for Quercus spp., where the intercept differs from zero at $\alpha = 0.002$ (Tab. A-2). The slope for evergreen (coniferous) species varies between 5.1 and 6.6 [$m^2 \cdot kg^{-1}$]; thus a value of $kC_2 = 6\ m^2 \cdot kg^{-1}$ was used. For deciduous species, the range of the slope is 10.1 to 14.9 [$m^2 \cdot kg^{-1}$]; a value of $kC_2 = 12\ m^2 \cdot kg^{-1}$ was used.

Tab. A-2: Regression analysis of foliage area (gFolA) vs. foliage wet weight (L) according to the equation $gFolA = i + kC_2 \cdot L$, dry to wet weight ratio of foliage (kC_1), and sample size (n) from Burger (1945-1953).

Species	i	kC_2	r^2	kC_1	n
Pinus silvestris	0.24	5.50	0.983	0.386	210
P. montana	2.29	5.95	0.989	0.489	18
P. cembra	-2.59	6.64	0.994	0.408	4
Picea excelsa	-0.51	5.27	0.979	0.478	56
Abies alba	-1.47	5.09	0.987	0.465	52
Fagus silvatica	9.78	14.89	0.948	0.363	91
Larix decidua	6.67	10.05	0.984	0.366	99
Quercus spp.	17.41	10.07	0.983	0.362	51

The dry to wet weight ratio for deciduous trees shows small variability between the species (Tab. A-2); a value of 0.35 was used. For evergreen species, variability is larger and the average dry to wet weight ratio is 0.445; thus a value of 0.45 was used.

Derivation of a relationship between foliage weight and DBH

The analysis of the species-specific data in Burger (1945-53) indicated that several species have similar relationships between foliage wet weight (L) and diameter at breast height (D). Thus, these species were grouped. Tab. A-3 gives the regression formulae obtained for four species/species groups, plus an additional species group having low foliage weight (e.g. *Betula, Salix),* for which kA_1 was set arbitrarily 20% lower, i.e. to

80% of the foliage weight obtained for group 2 (Tab. A-3). The relationships between foliage weight and diameter as well as a comparison of the new parametrization with the one used by Kienast (1987) are plotted in Fig. A-1.

Tab. A-3: Regressions of foliage wet weight (L) vs. diameter at breast height (D) for several species groups as derived from the data in Burger (1945-53), where $L = kA_1 \cdot D^{kA_2}$. Linear regressions were calculated based on the transformation $Ln(L) = Ln(kA_1) + kA_2 \cdot Ln(D)$. n denotes sample size.

Species	kA_1	kA_2	r^2	group no.	n
Abies alba, Picea excelsa, Pinus cembra, P. montana	0.23	1.56	0.93	5	130
P. silvestris	0.17	1.40	0.76	4	210
Fagus silvatica, Quercus spp.	0.06	1.70	0.93	3	144
Larix decidua	0.10	1.43	0.87	2	99
Betula sp., Salix sp. (no data)	0.08	1.43	–	1	–

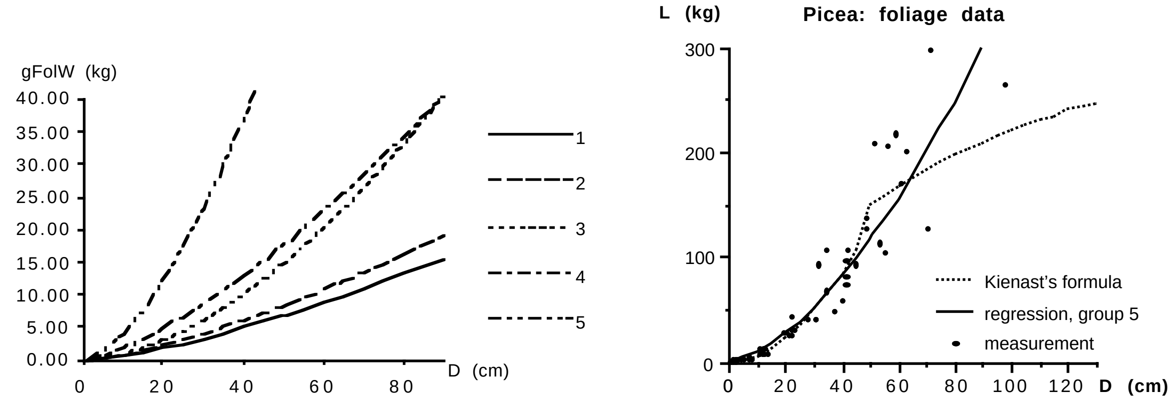

Fig. A-1: Left: Relationship between foliage dry weight (gFolW) and diameter at breast height (D) of the species groups defined in Tab. A-3. Right: Measured foliage fresh weight of *Picea excelsa* (dots), the FORECE parametrization (Kienast 1987) and the parametrization for group 5 derived from the original Burger data (Tab. A-3).

Grouping of the species

To assign every species to one of the five groups defined above (Tab. A-3), the ranking of the species with respect to their capability of casting shade from Ellenberg (1986) and the values of the parameters A1 and A2 used by Kienast (1987) were consulted (Tab. A-4). These data sources allowed to rank the 30 tree species with respect to the sType parameter.

kDm, kHm & kAm parameters

Probably the best way to determine these three parameters would be based on diameter, height, and age distributions of trees in old-growth forests that are not subject to strong environmental stress. A theoretical distribution could be fitted to such data, e.g. an exponential distribution in the case of maximum age (cf. Eq. 3.29f. in section 3.3.1), and the parameters could be estimated from these distributions. However, data from old-growth European forests is scarce (e.g. Leibundgut 1993). Moreover, it would be difficult to obtain these data for many tree species, let alone for all the 30 species used under European conditions in FORCLIM. Therefore, a simpler and necessarily less accurate approach had to be adopted to derive an estimate of these parameters.

Tab. A-4: Tree species, Ellenberg's (1986) ranking of their capability to cast shade as pure stands (1 = low, 5 = high), the parameters kA$_1$ and kA$_2$ as used in FORECE (Kienast 1987) and the sType parameters derived from these sources and the regressions in Tab. A-3. For species in bold face, the data is from Burger (1945-53).

Species name	Ellenberg	FORECE kA$_1$	FORECE kA$_2$	sType
Abies alba	5	0.08	1.96	**C5**
Larix decidua	1	0.04	1.64	**D2**
Picea excelsa	4	0.08	1.90	**C5**
Pinus cembra	4	0.08	1.90	**C5**
Pinus montana	1	0.08	1.90	**C5**
Pinus silvestris	1	0.10	1.58	**C4**
Taxus baccata	5	0.08	1.96	C5
Acer campestre	3	0.05	1.75	D2
Acer platanoides	4	0.05	1.75	D3
Acer pseudoplatanus	4	0.05	1.75	D3
Alnus glutinosa	3	0.05	1.75	D2
Alnus incana	3	0.05	1.75	D2
Alnus viridis	–	0.05	1.75	D2
Betula pendula	1	0.05	1.58	D1
Carpinus betulus	5	0.05	1.80	D3
Castanea sativa	3	0.05	1.80	D3
Corylus avellana	–	0.05	1.80	D3
Fagus silvatica	5	0.05	1.79	**D3**
Fraxinus excelsior	3	0.06	1.70	D2
Populus nigra	2	0.05	1.70	D2
Populus tremula	2	0.05	1.70	D2
Quercus petraea	3	0.04	1.78	**D3**
Quercus pubescens	2	0.04	1.78	**D3**
Quercus robur	2	0.04	1.78	**D3**
Salix alba	2	0.05	1.70	D1
Sorbus aria	4	0.05	1.70	D2
Sorbus aucuparia	2	0.05	1.70	D1
Tilia cordata	4	0.05	1.75	D3
Tilia platyphyllos	4	0.05	1.75	D3
Ulmus scabra	4	0.05	1.75	D3

To this end, a large data base was compiled for deriving the three parameters from the silvics descriptions in Amann (1954), Fenaroli & Gambi (1976), Brosse (1977), Polunin (1977), Phillips (1978), Bernatzky (1978), Krüssmann (1979), Mitchell (1979), Hess et al. (1980), Edlin & Nimmo (1983), Marcet & Gohl (1985), Godet (1986), Leibundgut (1991), and Prentice & Helmisaari (1991). From every reference, the maximum diameter, height and age were recorded for every species listed.

The following rationale, which undoubtedly is *ad hoc*, was used to derive species parameters from this data base: The arithmetic mean of all values does not reflect true maximum dimensions since some authors probably were not aware of very large specimen. On the other hand, using the maximum of all the values would introduce a strong bias towards exaggerated large dimensions. Thus, it was decided to calculate the species parameters as the *average of the mean and the maximum values* found (Tab. A-5 – A-7).

Maximum tree diameter (Tab. A-5) is covered rather well in the literature; for most species, at least 3 values could be compiled. For some species that not usually dominate forests (i.e. *Pinus montana, Corylus avellana, Quercus pubescens)* only one value could be found. No parameter for *Alnus viridis* could be derived at all; since this species is a bush rather than a tree (cf. Tab. A-6), its kDm is small and thus was estimated as 20 cm.

Maximum tree height (Tab. A-6) is covered well in the literature (seven or more values for all species except *Pinus montana* and *Alnus viridis).*

The same species as for maximum diameter and height have a low coverage concerning maximum age (Tab. A-7): *Pinus montana* and *Alnus viridis*. It is known that the latter species is not very long-lived, thus its maximum age was arbitrarily set to 100 years. A similar procedure had to be adapted when estimating kAm for *Quercus pubescens:* Oaks can grow quite old, but *Q. pubescens* does not attain the high age of the other two native oak species (860 and 1060 years); thus, its maximum age was set to 500 years.

Tab. A-5: Values for maximum tree diameter (cm) from the literature. n – sample size (number of values found in the literature); Min, Mean, Max – minimum, average and maximum value. kDm used in FORCLIM is the arithmetic mean of the average and the maximum values, rounded to the nearest 5 cm.

	n	Min	Mean	Max	(Mean+Max)/2	kDm
Abies alba	7	150	183	250	216	215
Larix decidua	7	100	168	200	184	185
Picea excelsa	6	100	166	250	208	210
Pinus cembra	5	105	161	200	181	180
Pinus montana	1	50	50	50	50	50
Pinus silvestris	6	100	125	190	157	155
Taxus baccata	5	50	260	450	355	355
Acer campestre	4	40	69	95	82	80
Acer platanoides	3	100	147	190	168	170
Acer pseudoplatanus	5	200	205	223	214	215
Alnus glutinosa	5	50	81	180	130	130
Alnus incana	2	40	120	200	160	160
Alnus viridis	0	–	–	–	–	20
Betula pendula	6	60	82	150	116	115
Carpinus betulus	6	50	90	127	108	110
Castanea sativa	6	100	301	410	356	355
Corylus avellana	1	70	70	70	70	70
Fagus silvatica	7	150	193	260	226	225
Fraxinus excelsior	6	100	162	220	191	190
Populus nigra	4	127	182	200	191	190
Populus tremula	3	60	103	150	127	125
Quercus petraea	3	250	267	300	283	285
Quercus pubescens	1	89	89	89	89	90
Quercus robur	6	200	256	382	319	320
Salix alba	3	100	100	100	100	100
Sorbus aria	3	40	47	60	54	55
Sorbus aucuparia	6	30	52	80	66	65
Tilia cordata	3	100	187	270	228	230
Tilia platyphyllos	3	185	312	500	406	405
Ulmus scabra	6	100	167	223	195	195

Tab. A-6: Values for maximum tree height (m) from the literature. n – sample size (number of values found in the literature); Min, Mean, Max – minimum, average and maximum value. kHm used in FORCLIM is the arithmetic mean of the average and the maximum values, rounded to the nearest meter.

Species	n	Min	Mean	Max	(Mean+Max)/2	kHm
Abies alba	12	45	54	65	59.5	60
Larix decidua	12	35	47	57	52.1	52
Picea excelsa	13	36	54	63	58.3	58
Pinus cembra	11	20	24	27	25.7	26
Pinus montana	3	15	20	25	22.5	23
Pinus silvestris	12	35	42	48	45.2	45
Taxus baccata	10	15	20	25	22.4	22
Acer campestre	11	9	19	26	22.5	23
Acer platanoides	11	20	28	35	31.5	32
Acer pseudoplatanus	12	30	34	40	37.1	37
Alnus glutinosa	13	19	27	35	31.0	31
Alnus incana	8	10	20	25	22.4	22
Alnus viridis	4	2.5	3.4	5.0	4.2	4
Betula pendula	13	18	27	31	29.0	29
Carpinus betulus	12	19	25	30	27.3	27
Castanea sativa	11	20	31	35	33.0	33
Corylus avellana	8	5	8	12	9.9	10
Fagus silvatica	13	30	39	50	44.7	45
Fraxinus excelsior	13	30	39	45	42.0	42
Populus nigra	11	30	33	40	36.4	36
Populus tremula	11	15	26	35	30.3	30
Quercus petraea	9	30	41	50	45.3	45
Quercus pubescens	7	16	21	30	25.4	25
Quercus robur	11	30	43	60	51.6	52
Salix alba	10	20	25	30	27.3	27
Sorbus aria	10	12	18	25	21.7	22
Sorbus aucuparia	13	15	17	20	18.7	19
Tilia cordata	12	22	29	32	30.5	30
Tilia platyphyllos	11	30	38	41	39.4	39
Ulmus scabra	11	30	39	48	43.3	43

Tab. A-7: Values for maximum tree age (years) from the literature. n – sample size (number of values found in the literature); Min, Mean, Max – minimum, average and maximum value. kAm used in FORCLIM is the arithmetic mean of the average and the maximum values, rounded to the nearest 10 years.

Species	n	Min	Mean	Max	(Mean+Max)/2	kAm
Abies alba	6	300	600	800	700	700
Larix decidua	6	300	700	1000	850	850
Picea excelsa	8	200	650	1200	925	930
Pinus cembra	6	600	900	1200	1050	1050
Pinus montana	1	300	300	300	300	300
Pinus silvestris	7	400	614	900	757	760
Taxus baccata	7	1000	1714	2500	2107	2110
Acer campestre	4	100	143	200	171	170
Acer platanoides	7	150	264	500	382	380
Acer pseudoplatanus	7	350	493	600	546	550
Alnus glutinosa	6	100	182	300	241	240
Alnus incana	5	50	95	200	148	150
Alnus viridis	0	–	–	–	–	100
Betula pendula	7	100	149	300	224	220
Carpinus betulus	5	150	180	250	215	220
Castanea sativa	6	600	1017	2000	1508	1510
Corylus avellana	3	50	67	80	73	70
Fagus silvatica	7	300	357	500	429	430
Fraxinus excelsior	5	250	300	400	350	350
Populus nigra	4	200	250	300	275	280
Populus tremula	5	100	126	160	143	140
Quercus petraea	4	500	725	1000	863	860
Quercus pubescens	0	–	–	–	–	500
Quercus robur	9	500	922	1200	1061	1060
Salix alba	4	100	143	200	171	170
Sorbus aria	3	100	167	200	183	180
Sorbus aucuparia	6	90	105	120	113	110
Tilia cordata	7	500	871	1000	936	940
Tilia platyphyllos	7	500	914	1000	957	960
Ulmus scabra	4	400	450	500	475	480

kG parameter

Based on yield table data (Anonymous 1983, Schober 1987), identification procedures (Press et al. 1986) were used in an attempt to determine the kG parameters of 10 species: *Quercus petraea, Q. robur, Fagus silvatica, Alnus glutinosa, Fraxinus excelsior, Betula pendula, Picea excelsa, Abies alba, Pinus silvestris*, and *Larix decidua.* However, for the other 20 species no yield table data could be found, and there was no convincing relationship between the kG parameters used by Kienast (1987) and those obtained from the identification algorithms; moreover, yield table data do not reflect the maximum growth of single trees, but rather the average growth of tree populations. To determine kG, Kienast (1987) used a qualitative approach based on descriptions of tree growth rates (Mitscherlich 1970), the FORET gap model (Shugart & West 1977) and yield tables (Anonymous 1983); the method was designed to yield a correct ranking of the species with respect to their kG parameters, but the absolute values of kG may not be reliable (Kienast, personal communication). Competitive success is based mainly on the relative ranking with respect to a certain parameter; thus the procedure taken by Kienast appears to be appropriate for deriving kG.

Botkin et al. (1972a, p. 872) noted that kG is related to the maximum diameter increment δD_{max}. The relationship between kG and δD_{max} was determined both for Botkin's and for Moore's (1989) growth equation by means of simulation studies. Then the FORECE values of kG (Kienast 1987) were recalculated via δD_{max} to fit Moore's (1989) growth equation based on the following formula, whose derivation will be published elsewhere:

$$kG_{ForClim} = kG_{Forece} \cdot \frac{0.1765}{0.1465} \cdot \frac{kH_m + 538.27}{kH_m + 72.01} \qquad \text{(A1)}$$

where kHm is in [cm]. The resulting kG parameters are given in section 3.4, Tab. 3.11.

kDDMin & kDDMax parameters

The derivation of the degree-day parameters was based on the work by Kienast (1987), who used the data compiled by Meusel et al. (1965, 1978), Rudloff (1981), and Müller (1982). Previous analyses (Fischlin et al. 1994) showed that the degree-day calculation used in conventional forest gap models is subject to a site-specific bias. Therefore, a general correction formula for the annual sum of degree-days was developed (cf. section 3.3.3), and the degree-day parameters in Kienast (1987) were recalculated with this correction formula (Fig. A-2). The resulting kDDMin and kDDMax parameters are listed in section 3.4, Tab. 3.11.

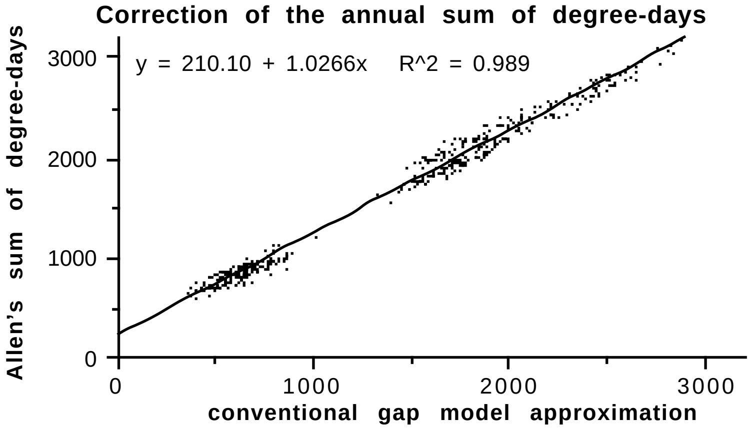

Fig. A-2: Regression of the annual sum of degree-days according to Allen's (1976) method vs. the conventional gap model approximation (e.g. Kienast 1987). Data from 6 sites in the European Alps (Basel, Bern, Davos, Bever, Locarno, Sion; *n* = 418).

kWiT parameter

Tab. A-8: Values of kWiT given by Kienast (1987) and Prentice & Helmisaari (1991). N – no susceptibility to low winter temperatures. No entry (blank) denotes that Prentice & Helmisaari (1991) did not include this species in their compilation.

Species	Kienast (1987)	Prentice & Helmisaari (1991)	kWiT
Abies alba	-5		-6
Larix decidua	-10		-11
Picea excelsa	-7	N	N
Pinus cembra	-10		-11
Pinus montana	N		N
Pinus silvestris	N	N	N
Taxus baccata	N	-4	-5
Acer campestre	N		N
Acer platanoides	N	-16	-17
Acer pseudoplatanus	N		N
Alnus glutinosa	N	-15	-16
Alnus incana	N	N	N
Alnus viridis	N		N
Betula pendula	N	N	N
Carpinus betulus	N	-8	-9
Castanea sativa	N		N
Corylus avellana	N	-15	-16
Fagus silvatica	-4	-3	-4
Fraxinus excelsior	N	-16	-17
Populus nigra	N		N
Populus tremula	N	N	N
Quercus petraea	-3	-4	-5
Quercus pubescens	N		N
Quercus robur	-3	-16	-17
Salix alba	N		N
Sorbus aria	N		N
Sorbus aucuparia	N	N	N
Tilia cordata	N	-18	-19
Tilia platyphyllos	N		N
Ulmus scabra	N	-15	-16

The minimum winter temperature parameter was adapted from the values given in Kienast (1987) and Prentice & Helmisaari (1991); these authors assume that the coldest month always is January. A comparison of the current mean January temperature with the minimum of the current mean December, January, and February temperatures conducted at the 12 sites used in the present study revealed that the latter minimum temperature is at average 1.27 °C lower than the current mean January temperature; thus the kWiT parameters obtained from Kienast (1987) and Prentice & Helmisaari (1991) were lowered by 1 °C. In cases where both authors give parameters, the Prentice & Helmisaari (1991) values were adopted with higher priority (Tab. A-8; cf. discussion in Prentice & Helmisaari 1991).

kNTol & kDrT parameters

Nitrogen (kNTol) and drought (kDrt) tolerance values of all tree species were compiled from Landolt (1977), Ellenberg (1986), Prentice & Helmisaari (1991) and Jahn (1991). The kNTol parameters (Tab. A-9) were derived from these sources by averaging and rounding to the nearest integer number.

Tab. A-9: Nitrogen tolerance values of the tree species according to Ellenberg (1986; 1 = tolerant, 9 = intolerant, x = indifferent), Landolt (1977; 1 = tolerant, 5 = intolerant), Prentice & Helmisaari (1991) and Jahn (1991). For the latter two references, 1 = tolerant, 3 = intolerant. The Ellenberg and Landolt data were converted to the range [1…3] by assuming that “indifferent” species are tolerant of low nitrogen concentrations.

Species	Ellenberg (1986)	Landolt (1977)	*Prentice & Helmisaari (1991)*	*Jahn (1991)*	*Ellenberg (1986), classes*	*Landolt (1977), classes*	kNTol
Abies alba	x	3		2	1	2	2
Larix decidua	3	2		2	1	1	1
Picea excelsa	x	3	2	1	1	2	2
Pinus cembra		2				1	1
Pinus montana	3	2		2	1	1	1
Pinus silvestris	x	2	1	1	1	1	1
Taxus baccata	x	2	1	3	1	1	2
Acer campestre	6	3		3	2	2	2
Acer platanoides	x	3	3	2	1	2	2
Acer pseudoplatanus	7	3		2	3	2	2
Alnus glutinosa	x	4	1	2	1	3	2
Alnus incana	x	4	1	3	1	3	2
Alnus viridis	x	4		2	1	3	2
Betula pendula	x	2	2	1	1	1	1
Carpinus betulus	x	3	2	2	1	2	2
Castanea sativa	x	2		1	1	1	1
Corylus avellana	x	3	2		1	2	2
Fagus silvatica	x	3	1	1	1	2	1
Fraxinus excelsior	7	4	3	3	3	3	3
Populus nigra	7	4			3	3	3
Populus tremula	x	3	1		1	2	1
Quercus petraea	x	2	2	2	1	1	1
Quercus pubescens	x	2		3	1	1	2
Quercus robur	x	3	1	1	1	2	1
Salix alba	7	4			3	3	3
Sorbus aria	3	2		3	1	1	2
Sorbus aucuparia	x	2	1	1	1	1	1
Tilia cordata	5	2	3	2	2	1	2
Tilia platyphyllos	7	3		2	3	2	2
Ulmus scabra	7	4	3	3	3	3	3

The problem of deriving reliable drought tolerance data for tree species (Tab. A-10) was discussed in detail by Prentice & Helmisaari (1991); the data compiled for the FORCLIM model (Tab. A-10) show that there are large discrepancies in the drought tolerance assigned by various authors (e.g. *Betula pendula*, *Fagus silvatica*). Thus, rather than averaging the various assignments, it was decided to use mainly the values given by Ellenberg (1986) because his data appear to be most accurate:

- Landolt (1977) assigned a low drought tolerance to *Pinus montana*, which is quite frequent in the dry Swiss National Park, but a high tolerance to *Alnus spp.*, which is judged to be drought-intolerant by all other authors.

- Prentice & Helmisaari (1991) judged *Fagus silvatica* to be very tolerant, which means that *Fagus* would dominate the forests also in dry central alpine valleys, where it is absent in reality. On the other hand, their value of 0 for alder most probably is exaggerated, implying that alder can grow only at sites with soil moisture permanently at or above field capacity.

- The values by Jahn (1991) are not differentiated enough (only three tolerance classes).

Finally, the drought tolerance classes [1..5] obtained like this (kDrT', Tab. A-10) were converted linearly to evapotranspiration deficits (corresponding to uDrStr) by assuming that a tolerance class of 5 corresponds to 30% evapotranspiration deficit (cf. Prentice & Helmisaari 1991), i.e. kDrT = 0.3 (Tab. A-10).

Tab. A-10: Drought tolerance of tree species according to Landolt (1977, 1 = tolerant, 5 = intolerant, x = indifferent), Prentice & Helmisaari (1991, 0 = intolerant, 0.36 = tolerant), Jahn (1991, 1 = tolerant, 3 = intolerant), and Ellenberg (1986, 1 = intolerant, 5 = tolerant). All data were converted to the scale [1…5] where 1 = intolerant and 5 = tolerant (columns with headers in italics).

Species	Landolt (1977)	Prentice & Helmisaari (1991)	Jahn (1991)	*Ellenberg (1986)*	*Landolt (1977) classes*	*Prentice & H. classes*	*Jahn (1991) classes*	kDrT'	kDrT
Abies alba	4		2	**3**	2		3	3	0.18
Larix decidua	3		2	**2**	3		3	2	0.12
Picea excelsa	3	0.12	2	**1**	3	3	3	1	0.06
Pinus cembra	3			**5**	3			5	0.30
Pinus montana	2		1	**5**	4		5	5	0.30
Pinus silvestris	x	0.24	1	**5**	5	4	5	5	0.30
Taxus baccata	2	0.06	2	**4**	4	2	3	4	0.24
Acer campestre	3		1	**4**	3		5	4	0.24
Acer platanoides	3	0.24	1	**3**	3	4	5	3	0.18
Acer pseudoplatanus	3		3	**3**	3		1	3	0.18
Alnus glutinosa	5	0		**1**	1	1		1	0.06
Alnus incana	4	0		**1**	2	1		1	0.06
Alnus viridis	4		2		2		3	2	0.12
Betula pendula	x	0.24	1	**2**	5	4	5	2	0.12
Carpinus betulus	3	0.24	2	**3**	3	4	3	3	0.18
Castanea sativa	3		1	**4**	3		5	4	0.24
Corylus avellana	3	0.24			3	4		4	0.24
Fagus silvatica	3	0.36	2	**2**	3	5	3	2	0.12
Fraxinus excelsior	2–4	0.12	3	**2**	3	3	1	2	0.12
Populus nigra	4			**1**	2			1	0.06
Populus tremula	3	0.12		**3**	3	3		3	0.18
Quercus petraea	2	0.36	2	**3**	4	5	3	3	0.18
Quercus pubescens	2		1	**4**	4		5	4	0.24
Quercus robur	3	0.24	1	**5**	3	4	5	5	0.30
Salix alba	4			**1**	2			1	0.06
Sorbus aria	2		2	**4**	4		3	4	0.24
Sorbus aucuparia	3	0.06	2	**4**	3	2	3	4	0.24
Tilia cordata	2	0.36	2	**4**	4	5	3	4	0.24
Tilia platyphyllos	3		2	**3**	3		3	3	0.18
Ulmus scabra	4	0.12	3	**3**	2	3	1	3	0.18

kBrow, kLy & kLa parameters

No coherent data could be found on the browsing susceptibility of tree species (except for scarce data in Ellenberg 1986 and Dengler et al. 1990); thus the values from Kienast (1987) were used (section 3.4, Tab. 3.11).

For deriving the light parameters (kLy, kLa), the following sources were consulted: Amann (1954), Landolt (1977), Bernatzky (1978), Ellenberg (1986) and Jahn (1991). Amann (1954) gives qualitative descriptions for a few species (see footnotes in Tab. A-11). Ellenberg (1986) is the only author who differentiates light tolerance values for saplings (pp. 915ff.) and older trees (p. 82) for most species used in FORCLIM (Tab. A-11). Hence, it was decided to use mainly Ellenberg's values, but to modify them where inconsistencies became apparent; for example, Amann (1954) and Prentice & Helmisaari (1991) agree that *Acer spp.* and *Fraxinus excelsior* are more shade tolerant as saplings than as adults, which is not reflected in Ellenberg (1986).

Tab. A-11: Shade tolerance of tree species according to various authors, all values scaled to the range [1…9] where 1 = shade-intolerant, 9 = shade-tolerant.

Species	Ellenberg (1986), p. 915ff.	Ellenberg (1986), p. 82	Landolt (1977)	Amann (1954)	Jahn (1991)	Bernatzky (1978)	kLy	kLa
Abies alba	3	1	1	1	1		3	1
Larix decidua	8	9	7	9	9	9	8	9
Picea excelsa	5	5	1	5	5	5	5	5
Pinus cembra	5	5	5	5[1]		5	6	5
Pinus montana	8	9	7				8	9
Pinus silvestris	7	9	7	9	9	9	7	9
Taxus baccata	4	3	3	1	9	1	4	3
Acer campestre	5		5	3	9		5	5
Acer platanoides	4	3	3	3[2]	5		2	4
Acer pseudoplatanus	4	3	3	3[2]	1		2	4
Alnus glutinosa	5	5	5	7	5	3	5	5
Alnus incana	6	7	5	7	9		6	7
Alnus viridis	7		7		9		7	7
Betula pendula	7	9	7	9	9	9	7	9
Carpinus betulus	4	3	3	3	1	1	4	3
Castanea sativa	5	5	5	5	5		5	5
Corylus avellana	6		5			1	6	6
Fagus silvatica	3	1	3	1	1	1	3	1
Fraxinus excelsior	4	3	5	7[3]	9	3	4	6
Populus nigra	5	5	5	7			5	5
Populus tremula	6	7	7	7			6	7
Quercus petraea	6	7	5	7	9		6	7
Quercus pubescens	7	7	5	7	9		7	7
Quercus robur	7	9	5	7	9		7	9
Salix alba	5	5	5				5	5
Sorbus aria	6	7	5	7	9		6	7
Sorbus aucuparia	6	7	5	7	9		6	7
Tilia cordata	5	5	3	3	5		5	5
Tilia platyphyllos	4	3	3	5	5		4	3
Ulmus scabra	4	3	3	5	5		4	3

[1] less shade tolerant when young

[2] less shade tolerant when adult

[3] more shade tolerant when young (Prentice & Helmisaari 1991)

kLQ parameter

Tab. A-12: Leaf litter quality (1 = fast decay, 2 = medium decay, 3 = recalcitrant) according to Ellenberg (1986, p. 93) and Berg & Staaf (1981, p. 168f.).

Species	Ellenberg (1986)	Berg & Staaf (1981)	kLQ
Abies alba			2
Larix decidua	3		3
Picea excelsa	3		3
Pinus cembra			3
Pinus montana			3
Pinus silvestris	3	3	3
Taxus baccata			2
Acer campestre	2		2
Acer platanoides	2		2
Acer pseudoplatanus	2		2
Alnus glutinosa	1	1	1
Alnus incana	1		1
Alnus viridis	1		1
Betula pendula	2		2
Carpinus betulus	1		1
Castanea sativa	1	2	2
Corylus avellana		1	1
Fagus silvatica	2	2	2
Fraxinus excelsior	1	1	1
Populus nigra	2		2
Populus tremula	2		2
Quercus petraea	2	1	2
Quercus pubescens	2		2
Quercus robur	2	1	2
Salix alba		2	2
Sorbus aria			1
Sorbus aucuparia			1
Tilia cordata	2	1	2
Tilia platyphyllos	2		2
Ulmus scabra	1	1	1

This parameter was determined from quantitative measurements of leaf nitrogen content (Berg & Staaf 1981, Ellenberg 1986) and descriptions by Ellenberg (1986) who quantified the relative duration of foliage decomposition depending on its initial C:N ratio. For FORCLIM, the following classification was adapted: Foliage with a C:N ratio of ≤30 whose decay takes less than two years “in an average brown earth” Ellenberg (1986, p. 93) is assigned to group 1 (fast decay); foliage with 30 < C:N ratio ≤ 60 whose decay takes 2 to 3 years is classified as group 2 (medium decay). The most recalcitrant foliage type (group 3, slow decay) has a C:N ratio of more than 60 and takes more than 3 years to decay (Tab. A-12).

The kLQ parameters of the species for which no data was available in Ellenberg (1986) and Berg & Staaf (1981), i.e. *Abies alba, Pinus cembra, P. montana,* and *Sorbus spp.*, were determined by evaluating the qualitative descriptions of leaf decomposition in Dengler et al. (1992).

Summary of all species parameters

A table containing all the species-specific parameters of the 30 European tree species is given in section 3.4.1 (Tab. 3.11).

III. Climatic input data sets for the European Alps

Tab. A-13 lists the general characteristics of the 12 sites used in the present study; the monthly climatic data at the sites were extracted from the database of the Swiss Meteorological Agency (1901-1990) according to Bantle (1989) and are given in Tab. A-14.

Tab. A-13: Characteristics of the European sites used in the present study. “Annual mean T” denotes the long-term annual mean temperature. “Annual P sum” stands for the long-term mean annual precipitation sum. “SMA no.” indicates the number of the climate station in the database of the Swiss Meteorological Agency (SMA 1901-1990, Bantle 1989).

Site	Latitude [°N]	Longitude [°E]	Elevation [m]	Annual mean T [°C]	Annual P sum [cm]	Observation period	SMA no.
Grande Dixence	46.1	7.4	2166	1.3	101.7	Jan 1965 - Sep 1985	7440
Bever	46.6	9.9	1712	1.5	84.1	Jan 1901 - Dec 1982	9850
Davos	46.8	9.8	1590	3.0	100.7	Jan 1901 - Dec 1989	460
Montana	46.3	7.5	1495	5.8	92.9	Jan 1931 - Dec 1989	7380
Adelboden	46.5	7.6	1325	5.5	135.1	Jan 1966 - Dec 1989	5270
Huttwil	47.1	7.8	639	8.1	128.7	May 1971 - Dec 1989	6600
Bern-Liebefeld	46.9	7.4	570	8.4	100.6	Jan 1901 - Dec 1989	5520
Schaffhausen	47.7	8.6	457	8.6	88.2	Jan 1931 - Dec 1989	1300
Basel Binningen	47.5	7.6	317	9.2	78.4	Jan 1901 - Dec 1989	1940
Sion	46.2	7.4	542	9.7	59.7	Jan 1901 - Dec 1977	7500
Airolo	46.5	8.6	1149	6.1	161.6	Jan 1931 - Dec 1980	9030
Locarno-Monti	46.2	8.8	379	11.8	184.6	May 1935 - Dec 1989	9400

Tab. A-14: Climatic parameters of the sites used in the present study (SMA 1901-1990, Bantle 1989). Symbols: μ(T): monthly mean temperature [°C]; σ(T): standard deviation of T; μ(P): monthly precipitation sum [cm/month]; σ(P): std. deviation of P; r: cross-correlation coefficient of T and P.

	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Grande Dixence (Cleuson)												
μ(T)	-5.8	-6.0	-4.2	-1.6	2.8	6.8	9.6	9.0	7.1	3.7	-1.5	-4.7
σ(T)	2.0	2.1	1.8	1.6	1.1	1.2	1.7	1.2	1.7	2.4	1.8	1.8
μ(P)	7.58	7.27	8.59	7.17	9.83	9.88	9.18	10.30	7.19	7.42	8.93	8.33
σ(P)	3.91	5.72	5.14	3.25	3.42	3.48	4.66	3.61	3.85	5.14	4.32	6.01
r	-0.23	0.04	-0.01	-0.13	-0.44	-0.40	-0.59	-0.49	-0.47	-0.54	-0.26	-0.29
Bever												
μ(T)	-9.2	-7.5	-3.6	0.9	6.1	9.7	11.5	10.8	7.7	2.7	-3.2	-7.9
σ(T)	2.1	2.4	1.7	1.5	1.3	1.3	1.3	1.1	1.4	1.5	1.5	1.9
μ(P)	4.16	3.92	5.09	5.24	7.50	8.95	10.14	10.97	8.07	7.59	7.20	5.28
σ(P)	2.90	3.37	3.59	2.89	3.10	3.94	3.71	4.57	5.27	5.74	5.35	3.78
r	0.34	0.33	0.07	-0.21	-0.09	-0.25	-0.37	-0.33	-0.16	-0.05	0.20	0.25
Davos												
μ(T)	-6.2	-5.3	-1.9	2.1	7.1	10.3	12.1	11.5	8.6	4.1	-1.2	-4.8
σ(T)	2.2	2.6	1.8	1.6	1.6	1.4	1.4	1.2	1.6	1.7	1.6	2.0
μ(P)	7.21	5.90	5.88	5.77	8.23	11.82	13.64	13.26	8.94	6.45	6.69	6.90
σ(P)	5.00	5.13	3.83	2.46	3.15	4.05	4.13	4.82	4.46	4.18	4.61	5.05
r	0.06	0.16	-0.18	-0.26	-0.32	-0.34	-0.46	-0.32	-0.35	-0.32	-0.09	-0.02
Montana												
μ(T)	-2.3	-1.8	1.0	4.4	8.8	12.3	14.6	13.8	11.3	6.9	1.9	-1.1
σ(T)	2.2	2.4	2.1	2.0	1.7	1.5	1.6	1.4	1.6	1.7	1.6	2.0
μ(P)	10.50	9.20	7.38	5.57	6.16	7.49	7.19	8.41	5.74	6.44	8.81	10.06
σ(P)	6.69	7.23	5.52	3.41	2.69	3.74	3.19	3.42	3.47	4.77	7.28	8.27
r	-0.17	0.12	-0.41	-0.29	-0.36	-0.47	-0.60	-0.52	-0.28	-0.58	-0.29	-0.28
Adelboden												
μ(T)	-2.1	-1.5	0.4	3.5	8.3	11.4	13.9	13.0	10.7	7.1	1.7	-0.8
σ(T)	2.2	2.2	2.1	1.7	1.4	1.2	1.5	1.1	1.5	1.9	1.7	2.1
μ(P)	9.98	9.12	10.10	10.15	11.00	14.96	15.22	16.02	8.94	8.70	10.95	9.99
σ(P)	6.80	5.45	5.67	4.29	3.02	4.51	5.45	4.66	4.46	5.65	6.68	5.74
r	-0.19	0.11	-0.10	-0.39	-0.23	-0.43	-0.49	-0.09	-0.25	-0.38	-0.30	-0.13
Huttwil												
μ(T)	-0.9	0.0	3.6	6.9	12.0	15.6	18.0	16.9	13.6	8.4	3.0	0.3
σ(T)	2.5	2.3	2.0	1.2	1.5	1.2	1.5	1.0	1.5	1.7	1.2	1.7
μ(P)	10.08	7.48	9.40	10.28	12.91	14.38	13.01	11.70	9.45	10.08	10.42	9.53
σ(P)	4.82	3.84	5.60	6.14	4.06	5.74	3.46	5.60	5.74	5.23	6.24	4.75
r	-0.14	0.24	-0.02	-0.28	-0.30	-0.48	-0.37	-0.07	0.10	-0.25	0.15	0.25

Tab. A-14 (continued)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Bern-Liebefeld												
μ(T)	-1.0	0.4	4.2	8.1	12.6	15.8	17.8	17.0	13.8	8.6	3.4	0.2
σ(T)	2.3	2.5	1.7	1.6	1.6	1.3	1.6	1.3	1.6	1.4	1.5	1.9
μ(P)	5.93	5.39	6.66	7.84	10.13	11.71	11.24	11.38	9.06	7.35	7.33	6.61
σ(P)	3.33	3.71	3.77	3.82	3.72	4.46	5.14	5.24	4.85	4.75	4.76	3.89
r	0.27	0.37	-0.13	-0.18	-0.33	-0.29	-0.63	-0.47	-0.16	-0.17	0.32	0.43
Schaffhausen												
μ(T)	-1.1	0.4	4.4	8.6	12.9	16.2	18.0	17.2	14.1	8.7	3.6	0.1
σ(T)	2.4	2.5	1.9	1.6	1.6	1.3	1.5	1.3	1.5	1.3	1.2	2.0
μ(P)	6.89	6.12	5.48	6.14	7.83	9.84	9.47	9.76	7.11	6.18	6.74	6.66
σ(P)	3.68	4.47	3.29	3.19	3.36	4.19	4.70	4.17	4.07	4.55	4.79	4.53
r	0.27	0.38	-0.27	-0.41	-0.42	-0.39	-0.56	-0.41	-0.25	-0.27	0.17	0.32
Basel Binningen												
μ(T)	0.3	1.5	5.1	8.8	13.1	16.3	18.3	17.5	14.3	9.4	4.5	1.5
σ(T)	2.6	2.8	1.7	1.6	1.5	1.4	1.7	1.4	1.6	1.5	1.6	2.1
μ(P)	4.75	4.42	4.98	6.11	8.00	8.87	8.45	9.02	7.15	5.81	5.77	5.09
σ(P)	2.37	2.69	2.66	3.37	3.54	3.85	4.49	4.30	3.60	3.63	3.65	2.75
r	0.24	0.31	-0.12	-0.15	-0.36	-0.21	-0.52	-0.42	-0.13	-0.10	0.29	0.40
Sion												
μ(T)	-0.4	1.6	5.9	9.9	14.5	17.6	19.2	18.2	15.0	9.9	4.4	0.4
σ(T)	2.1	2.4	1.7	1.6	1.4	1.3	1.6	1.4	1.6	1.5	1.4	1.8
μ(P)	5.18	4.98	4.08	3.87	3.92	4.91	5.12	6.38	4.50	4.64	5.90	6.19
σ(P)	3.68	4.95	3.06	2.92	2.24	2.55	2.58	2.79	2.65	3.47	4.85	5.08
r	0.24	0.32	-0.32	-0.28	-0.40	-0.32	-0.49	-0.46	-0.15	-0.28	0.00	0.11
Airolo												
μ(T)	-2.6	-1.1	1.6	5.0	9.3	13.2	15.4	14.6	11.6	6.8	1.6	-1.7
σ(T)	1.7	1.8	1.8	1.6	1.4	1.2	1.3	1.2	1.4	1.3	1.3	1.5
μ(P)	8.62	8.98	9.95	12.59	16.45	14.51	12.82	17.09	16.28	17.91	16.84	9.57
σ(P)	5.21	7.15	7.49	7.10	8.91	7.09	7.73	10.85	13.07	14.42	12.36	7.05
r	0.22	0.22	-0.18	-0.06	-0.29	-0.44	-0.62	-0.52	-0.21	-0.07	-0.03	0.11
Locarno-Monti												
μ(T)	2.6	4.1	7.6	11.5	15.1	18.9	21.2	20.2	17.1	12.0	6.9	3.8
σ(T)	1.5	1.7	1.7	1.4	1.5	1.2	1.3	1.1	1.3	1.2	0.9	1.3
μ(P)	7.01	7.32	10.60	17.08	21.68	18.71	19.88	21.19	20.57	17.97	14.60	8.04
σ(P)	6.45	7.17	8.66	12.48	10.01	10.84	11.84	13.92	16.80	14.22	12.59	6.85
r	0.05	0.06	-0.23	-0.43	-0.54	-0.55	-0.56	-0.49	-0.48	-0.15	0.17	-0.09

IV. Source code of the FORCLIM model

Module ForClim

```
MODULE ForClim;

  (*
        Implementation and Revisions:
        ============================

        Author  Date        Description
        ------  ----        -----------

        hb      17.12.92    First implementation (MacMETH_V3.2)
        af      08.07.93    About uses now FCResFileName
        hb      23. 9.93    Final purging for the thesis

  *)

  FROM ForestBase   IMPORT fMenu, configCmd, DeclForestBase, FCResFileName;

  FROM ForClimE     IMPORT DeclForClimE, RemoveForClimE;

  FROM ForClimP     IMPORT DeclForClimP, RemoveForClimP;

  FROM ForClimS     IMPORT DeclForClimS, RemoveForClimS;

  FROM SimMaster    IMPORT RunSimEnvironment;

  FROM DMMaster     IMPORT AddKeyboardHandler, RemoveKeyboardHandler;

  FROM DMMenus      IMPORT InstallMenu, InstallCommand, AccessStatus, Marking,
                           InstallAliasChar, InstallAbout, ExecuteAbout;

  FROM DMWindows    IMPORT Window, CreateModalWindow, ModalWindowKind, ScrollBars,
                           WindowFrame, AddWindowHandler, WindowHandlers, RemoveWindow,
                           RectArea, UseWindowModally;

  FROM DMWindowIO   IMPORT DisplayPredefinedPicture, BackgroundWidth,
                           BackgroundHeight;

  FROM DMEntryForms IMPORT FormFrame, WriteLabel, CheckBox, UseEntryForm;


  CONST
    windW = 500;
    windH = 315;

  VAR
    useFe, useFp, useFs: BOOLEAN;
    w: Window;

  PROCEDURE ConfigureForClim;
    CONST lem = 5;
    VAR ef: FormFrame;
      ok : BOOLEAN;
      cl: INTEGER;
  BEGIN
    cl := 2;
    WriteLabel(cl, lem-2, "Select the ForClim submodels you wish to use:"); INC(cl);
    CheckBox(cl,lem, "ForClim-E: Abiotic environment", useFe ); INC(cl);
    CheckBox(cl,lem, "ForClim-P: Plant population dynamics", useFp ); INC(cl);
    CheckBox(cl,lem, "ForClim-S: Soil organic matter turnover", useFs ); INC(cl);
    INC(cl);
    ef.x:= 0; ef.y:= -1; (* display entry form in middle of screen *)
    ef.lines:= cl+1; ef.columns:= 50;
    UseEntryForm(ef,ok);
    IF ok THEN
      IF useFe THEN DeclForClimE ELSE RemoveForClimE END;
      IF useFp THEN DeclForClimP ELSE RemoveForClimP END;
      IF useFs THEN DeclForClimS ELSE RemoveForClimS END;
    END; (* IF *)
  END ConfigureForClim;


  PROCEDURE PaintStartup( w : Window );
    VAR r : RectArea;
  BEGIN
    r.x := 1; r.y := 1;
    r.w := 0; r.h := 0;
    DisplayPredefinedPicture( FCResFileName, 2000, r );
  END PaintStartup;


  PROCEDURE CloseStartupWindow( w : Window );
  BEGIN RemoveWindow( w ) END CloseStartupWindow;

  PROCEDURE CloseStartupWindowByKeyboard;
  BEGIN
    RemoveWindow( w );
    RemoveKeyboardHandler( CloseStartupWindowByKeyboard );
  END CloseStartupWindowByKeyboard;


  PROCEDURE ShowStartupPicture;
    VAR f: WindowFrame;
      ok: BOOLEAN;
  BEGIN
    f.w := windW;
    f.h := windH;
    f.x := (BackgroundWidth() - windW) DIV 2;
    f.y := (BackgroundHeight() - windH) DIV 2;
    CreateModalWindow( w, SingleFrameShadowed, WithoutScrollBars, f, PaintStartup );
```

```
    AddWindowHandler( w, clickedInContent, CloseStartupWindow, 1 );
    AddKeyboardHandler( CloseStartupWindowByKeyboard, 1 );
    UseWindowModally( w , ok, ok );
  END ShowStartupPicture;


  PROCEDURE DeclForClim;
  BEGIN
    useFe := TRUE;
    useFp := TRUE;
    useFs := FALSE;
    InstallAbout( "About ForClim…", 0, 0, ShowStartupPicture );
    ExecuteAbout;
    InstallMenu( fMenu, "ForClim", enabled );
    InstallCommand( fMenu, configCmd, "Configure ForClim…", ConfigureForClim,
                    enabled, unchecked );
    InstallAliasChar( fMenu, configCmd, "F" );

    DeclForestBase;
    ConfigureForClim;
  END DeclForClim;


BEGIN
  RunSimEnvironment( DeclForClim );
END ForClim.
```

Module ForClimE

```
DEFINITION MODULE ForClimE;

  (*****************************************

    Module  ForClim-E     (Version 2.4)

              Copyright ©1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2   (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Provides a model of the abiotic forest environment,
              consisting of
              - the generation of weather data
              - the calculation of bioclimatic output variables

      Programming

          • Design
              H. Bugmann         18.1.1991

          • Implementation
              H. Bugmann         18.1.1991


          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  23.9.1993  hb

  *****************************************)


  PROCEDURE DeclForClimE;

  PROCEDURE RemoveForClimE;

END ForClimE.
```

```
IMPLEMENTATION MODULE ForClimE;

  (*
        Implementation and Revisions:
        =============================

        Author  Date        Description
        ------  ----        -----------

        hb      18. 1.1991  First implementation (V0.1, DM 2.02, MacMETH 2.6.2)
        hb      21. 3.1991  New structure for V0.4
        hb      12. 6.1991  V1.0 implemented including weather data from file
        hb      25. 3.1992  Inconsistencies with TableFunctions fixed (TabFs are now
                            removed when a new model is declared)
                            realistic values of uDD, kDryDays are calculated from site
                            data if the constant weather model is declared
        hb      26. 5.1992  calculation of new drought index (drIndx) introduced
        hb      17.12.1992  Adapted for usage within ForClim simulation system,
                            renamed from FCPInput to ForClimE
        hb      10. 3.1993  supports usage of StochStat and writing of sim results
                            to a text file (done by ForestBase)
        hb       6.12.1993  Reading of weather data from file implemented

  *)

FROM SimMaster     IMPORT CurrentSimNr, ExperimentRunning,
                          ExperimentAborted;
```

```
FROM SimBase       IMPORT DeclM, IntegrationMethod, NoDynamic, RTCType, DeclP,
                          StashFiling, DeclMV, Tabulation, NoAbout, Graphing, NoInput,
                          RemoveM, CurrentTime, MDeclared, GetGlobSimPars;

FROM TabFunc       IMPORT TabFUNC, DeclTabF, Yie, RemoveTabF;

FROM DMEntryForms  IMPORT FormFrame, WriteLabel, RadioButtonID, DefineRadioButtonSet,
                          RadioButton, UseEntryForm;

FROM DMFiles       IMPORT Lookup, ReadChar, GetReal, EOF, EOL, Close, TextFile,
                          Response, Reset, SkipGap, GetExistingFile, legalNum;

FROM DMStrings     IMPORT AssignString;

FROM DMMenus       IMPORT InstallCommand, InstallAliasChar, InstallSeparator,
                          Separator, AccessStatus, Marking, Command, SeparatorPosition,
                          RemoveSeparatorAtCommand, RemoveCommand, DisableCommand,
                          EnableCommand;

FROM DMMessages    IMPORT Warn;

FROM StochStat     IMPORT StatArray, Prob2Tail, DeclStatArray, notExistingStatArray,
                          PutValue, DeclDispMV, DisplayArray;

FROM SimGraphUtils IMPORT timeIsIndep;

FROM RandNormal    IMPORT InstallU;

FROM RandGen       IMPORT U;

FROM Jacobi        IMPORT Vector;

FROM MultiNormal   IMPORT MultiN;

FROM SYSTEM        IMPORT Exp;

FROM ForestBase    IMPORT Month, site, RemoveConstEnvironment, DeclConstEnvironment,
                          fe, uDD, uDrStr, uWiT, uAET, fMenu, Power, Rmax, Rmin, exp,
                          ExperimentType, DeclMonitoringProc, RemoveMonitoringProc,
                          DeclStatArrayForOutput, GetCurClimate, Climate;


CONST
  kDays = 30.5;
  modIdent = "ForClim-E";
  modDescrStoch = "ForClim-E: Abiotic environment";
  modDescrFileW = "ForClim-E: Weather data from file";
  modDescrFileE = "ForClim-E: Bioclimatic variables from file";


TYPE
  EnvironmentType = ( undefE, stochE, fileW, fileE );


VAR
  a, b, rTVect, rPVect, zeroSDVect: ARRAY [Jan..Dec] OF REAL;
  month: Month;

  uPET, k1, k2, k3, k4, k5, k6, k7, k8, kPM,
  tSuMod, tWiMod, tSDSuMod, tSDWiMod, pSuMod, pWiMod, pSDSuMod, pSDWiMod,
  tMod, pMod, tSDMod, pSDMod, currWater, kPMod,
  meanAET, meanDD, meanDrStr, meanWiT,

  tzero, hm: REAL;

  tSuTab, tWiTab, tSDSuTab, tSDWiTab, pSuTab, pWiTab, pSDSuTab, pSDWiTab,
  corrDDTab: TabFUNC;
  time, modifier: ARRAY [1..20] OF REAL;

  fileName: ARRAY [0..63] OF CHAR;
  inF: TextFile;

  declEMod: EnvironmentType;
  fceCmd, chooseEnvCmd: Command;

  uAETStatArray, uDDStatArray, uDrStrStatArray, uWiTStatArray: StatArray;


PROCEDURE EmptyProc; BEGIN END EmptyProc;


PROCEDURE RemoveAllWeatherTabFuncs;
BEGIN
  (* assumes that RemoveTabF will not inform on attempts to remove nonexisting TabFs *)
  RemoveTabF( corrDDTab );
  RemoveTabF( tSuTab   );   RemoveTabF( tWiTab );
  RemoveTabF( tSDSuTab );   RemoveTabF( tSDWiTab );
  RemoveTabF( pSuTab );     RemoveTabF( pWiTab );
  RemoveTabF( pSDSuTab );   RemoveTabF( pSDWiTab );
  tSuMod   := 0.0;  pSuMod   := 0.0;    tWiMod   := 0.0;    pWiMod   := 0.0;
  tSDSuMod := 1.0;  tSDWiMod := 1.0;    pSDSuMod := 1.0;    pSDWiMod := 1.0;
END RemoveAllWeatherTabFuncs;


PROCEDURE CalculateWeatherModifiers;
  VAR t: REAL;
BEGIN
  t := CurrentTime();
  tSuMod   := Yie( tSuTab,   t );
  pSuMod   := Yie( pSuTab,   t );
  IF declEMod = stochE THEN
    tWiMod   := Yie( tWiTab,   t );
    tSDSuMod := Yie( tSDSuTab, t );
    tSDWiMod := Yie( tSDWiTab, t );
    pWiMod   := Yie( pWiTab,   t );
    pSDSuMod := Yie( pSDSuTab, t );
    pSDWiMod := Yie( pSDWiTab, t );
  END; (* IF *)
END CalculateWeatherModifiers;
```

```
PROCEDURE CorrWeatherGenerator( VAR rTVect, rPVect: ARRAY OF REAL );
  (*
     A weather generator is used which draws samples from the joint distribution
     of temperature and precipitation. It takes into account the correlation between the
     two variates using the modules "Jacobi" and "MultiNormal" developed by
     D. Gyalistras, Systems Ecology, ETHZ

     Assumption of normality of T and P: see Botkin et al. (1972), Fliri (1974);
     the empirical correction formula for degree-days has been developed by Harald
     Bugmann based on SMA data
   *)
  VAR i: INTEGER;
    indx: Month;
    valueVect: Vector;
    cc: Climate;
BEGIN
  GetCurClimate( cc );          (* current climate from ForestBase *)
  CalculateWeatherModifiers;    (* TableFunctions with climatic change scenario *)

  FOR indx := Jan TO Dec DO
    i := ORD(indx);
    IF (i > 3) AND (i < 10) THEN    (* summer *)
      tMod := tSuMod; tSDMod := tSDSuMod;
      pMod := pSuMod; pSDMod := pSDSuMod;
    ELSE    (* winter *)
      tMod := tWiMod; tSDMod := tSDWiMod;
      pMod := pWiMod; pSDMod := pSDWiMod;
    END;

    MultiN( cc.mnDistr[indx], valueVect );
    rTVect[i] := tMod + cc.mTVect[indx] + tSDMod*cc.sdTVect[indx]*valueVect[1];
    rPVect[i] := Rmax( 0.0, pMod + cc.mPVect[indx] + pSDMod*cc.sdPVect[indx]*valueVect[2] );

  END; (* FOR *)
END CorrWeatherGenerator;


PROCEDURE DegreeDays( VAR uDD: REAL; VAR rTVect: ARRAY OF REAL );
  CONST kDTT = 5.5;
  VAR
    i: INTEGER;
    monthlyDD: REAL;
    indx: Month;
BEGIN
  uDD := 0.0;
  FOR indx := Jan TO Dec DO
    i := ORD(indx);
    monthlyDD := Rmax( (rTVect[i]-kDTT)*kDays, 0.0 ) + Yie(corrDDTab, rTVect[i]);
    uDD := uDD + monthlyDD;
  END; (* FOR *)
END DegreeDays;


PROCEDURE DeclSoilMoistureParameters;
BEGIN
  DeclP( k1, 0.2,       0.0, 1.0, rtc, "k1 (Heat index multiplier)", "k1" , "--" );
  DeclP( k2, 1.514,     0.0, 4.0, rtc, "k2 (Heat index exponent)", "k2" , "--" );
  DeclP( k3, 6.75E-7,   0.0, 1.0, rtc, "k3 (PET exponent coefficient)", "k3" , "--" );
  DeclP( k4, -7.71E-5, -1.0, 0.0, rtc, "k4 (PET exponent coefficient)", "k4" , "--" );
  DeclP( k5, 0.01792,   0.0, 1.0, rtc, "k5 (PET exponent coefficient)", "k5" , "--" );
  DeclP( k6, 0.49239,   0.0, 1.0, rtc, "k6 (PET exponent coefficient)", "k6" , "--" );
  DeclP( k7, 4.61E-4,   0.0, 1.0, rtc, "k7 (Retained water coefficient)", "k7" , "--" );
  DeclP( k8, 1.10559,   0.0, 2.0, rtc, "k8 (Retained water coefficient)", "k8" , "--" );
  DeclP( kPM, 1.6,      0.0, 3.0, noRtc, 'PET multiplier',  'kPM', '--');
END DeclSoilMoistureParameters;


PROCEDURE SoilMoisture( VAR uDrStr, uAET: REAL; rTVect, rPVect: ARRAY OF REAL );
  (* this simple calculation of the soil moisture balance is based on the model by
     Thornthwaite & Mather (1957) as modified by Pastor & Post (1984, 1985).
     It has been described in detail by Fischlin et al. (1993), including the new
     drought stress index which is based on Prentice & Helmisaari (1991).
   *)
  VAR accPWL, aa, heatIndx, prevWater, currDay, prevDay, PET, pWL,
    cSM, latPtr: REAL;
    k: Month;
    indx: CARDINAL;
BEGIN
  uAET := 0.0;
  uPET := 0.0;
  accPWL := 0.0;
  heatIndx := 0.0;

  FOR k:= Jan TO Dec DO (* calculate temperature efficiency index *)
    heatIndx := heatIndx + Power( k1*Rmax(0.0,rTVect[ORD(k)]), k2);
  END; (* FOR *)

  aa := k3*Power(heatIndx,3.0) + k4*heatIndx*heatIndx + k5*heatIndx + k6;

  prevDay := 0.0;
  currDay := 15.0;
  FOR k:= Jan TO Dec DO         (* main loop for annual water balance calculation *)
    indx := ORD(k);
    prevWater  := currWater;    (* help variable for previous month's water *)
    latPtr := a[k] + b[k]*site.kLat;
    PET  := kPMod * kPM * Power( 10.0*Rmax(0.0,rTVect[indx])/heatIndx, aa ) * latPtr;
    uPET := uPET + PET;
    pWL := rPVect[indx] - PET;  (* potential water loss pWL *)

    IF pWL < 0.0 THEN   (* rain does not satisfy PET, draw on soil water *)
      accPWL := accPWL + pWL;
      currWater := Rmax( 0.0, site.kFC*( Exp((k7 - k8/10.0/site.kFC)*(-10.0*accPWL)) ) );
      cSM := currWater - prevWater;         (* change in soil moisture *)
      uAET := uAET + rPVect[indx] - cSM;
    ELSE (* rain satisfies PET *)
      currWater := Rmin( site.kFC, prevWater + pWL);
      cSM := currWater - prevWater;
      accPWL := accPWL + cSM;
      IF currWater >= site.kFC THEN accPWL := 0.0 END;
      uAET := uAET + PET;
```

```
    END; (* IF *)

    prevDay := currDay;
    currDay := prevDay + kDays;
  END; (* FOR *)
  uAET := uAET * 10.0;       (* convert AET & PET from cm to mm *)
  uPET := uPET * 10.0;
  uDrStr := (uPET - uAET) / uPET;
END SoilMoisture;


(*****************************)
(*  Monitoring & statistics  *)
(*****************************)

PROCEDURE DeclareStatArrays( arrLen : INTEGER );
BEGIN
  uAETStatArray := notExistingStatArray;
  DeclStatArray( uAETStatArray, arrLen );
  DeclDispMV( uAETStatArray, fe, meanAET, fe, timeIsIndep );
  DeclStatArrayForOutput( uAETStatArray, "Actual evapotranspiration", "mm/yr", 0.0 );

  uDDStatArray := notExistingStatArray;
  DeclStatArray( uDDStatArray, arrLen );
  DeclDispMV( uDDStatArray, fe, meanDD, fe, timeIsIndep );
  DeclStatArrayForOutput( uDDStatArray, "Degree-days", "°C*days", 0.0 );

  uDrStrStatArray := notExistingStatArray;
  DeclStatArray( uDrStrStatArray, arrLen );
  DeclDispMV( uDrStrStatArray, fe, meanDrStr, fe, timeIsIndep );
  DeclStatArrayForOutput( uDrStrStatArray, "Drought stress", "%/100", 0.0 );

  uWiTStatArray := notExistingStatArray;
  DeclStatArray( uWiTStatArray, arrLen );
  DeclDispMV( uWiTStatArray, fe, meanWiT, fe, timeIsIndep );
  DeclStatArrayForOutput( uWiTStatArray, "Min. winter temperature", "°C", -100.0 );
END DeclareStatArrays;


PROCEDURE DisplayStatArrays;
BEGIN
  IF NOT ExperimentAborted() THEN
    DisplayArray( uAETStatArray,  TRUE, prob950 );
    DisplayArray( uDDStatArray, TRUE, prob950 );
    DisplayArray( uDrStrStatArray, TRUE, prob950 );
    DisplayArray( uWiTStatArray, TRUE, prob950 );
  END;
END DisplayStatArrays;


PROCEDURE Monitoring;
  VAR t: REAL;
    index: INTEGER;
BEGIN
  IF ExperimentRunning() THEN
    IF exp.type = estimEquil THEN
      t := 0.0;
      index := 1;
    ELSE
      t := CurrentTime();
      index := TRUNC( (t-tzero)/hm + 0.5 ) + 1;
    END;

    IF NOT ((exp.type = estimEquil) AND (CurrentTime() <= exp.startYear )) THEN
      PutValue( uAETStatArray,  index, t, uAET );
      PutValue( uDDStatArray, index, t, uDD );
      PutValue( uDrStrStatArray, index, t, uDrStr );
      PutValue( uWiTStatArray, index, t, uWiT );
    END; (* IF *)
  END; (* IF *)
END Monitoring;


(*  Stochastic model of the abiotic environment  *)
(*************************************************)

PROCEDURE Initialize;
  VAR tend, h, c, er: REAL;
    arrLen: INTEGER;
BEGIN
  DisableCommand( fMenu, chooseEnvCmd );

  currWater := site.kFC;     (* initial conditions in January of the first year *)
  IF site.kSlAsp > 0.0 THEN kPMod := 1.0 + site.kSlAsp*0.125;
                       ELSE kPMod := 1.0 + site.kSlAsp*0.063;
  END;

  IF ExperimentRunning() AND (CurrentSimNr() = 1 ) THEN
    IF exp.type = manyRuns THEN
      GetGlobSimPars(tzero, tend, h, er, c , hm);
      arrLen := TRUNC((tend-tzero)/hm+1.5);
      DeclareStatArrays( arrLen );
    ELSIF exp.type = estimEquil THEN
      DeclareStatArrays( 1 );
    ELSE
     (* do nothing *)
    END;
  END;
END Initialize;


PROCEDURE StochWeatherOutput;
BEGIN
  WITH site DO
    CorrWeatherGenerator( rTVect, rPVect );

    DegreeDays( uDD, rTVect );
    SoilMoisture( uDrStr, uAET, rTVect, rPVect );

    uWiT := rTVect[Jan];
    IF rTVect[Feb] < uWiT THEN uWiT := rTVect[Feb] END;
```

```
    IF rTVect[Dec] < uWiT THEN uWiT := rTVect[Dec] END;

  END;
END StochWeatherOutput;


PROCEDURE Terminate;
BEGIN
  IF ( (CurrentSimNr() MOD TRUNC(exp.nrRuns+0.5)) = 0 )
    AND ExperimentRunning() AND (exp.type = manyRuns) THEN
    DisplayStatArrays;
  END;
  EnableCommand( fMenu, chooseEnvCmd );
END Terminate;


PROCEDURE DeclareDDCorrectionTabF;
  VAR T, corrDD: ARRAY [0..11] OF REAL;
BEGIN
  T[0] := -20.0;    corrDD[0] :=  0.0;
  T[1] := -10.0;    corrDD[1] :=  0.0;
  T[2] := -5.0;     corrDD[2] :=  1.28;
  T[3] := -2.5;     corrDD[3] :=  3.3;
  T[4] :=  0.0;     corrDD[4] :=  8.52;
  T[5] :=  2.5;     corrDD[5] := 22.02;
  T[6] :=  5.24;    corrDD[6] := 62.56;
  T[7] :=  7.5;     corrDD[7] := 39.0;
  T[8] := 10.0;     corrDD[8] := 23.12;
  T[9] := 12.5;     corrDD[9] := 13.71;
  T[10]:= 16.11;    corrDD[10]:=  6.45;
  T[11]:= 17.5;     corrDD[11]:=  9.76;

  DeclTabF( corrDDTab, T, corrDD, 12, FALSE, "DD correction",
    "T", "corr", "T", "corr", -20.0, 30.0, 0.0, 70.0);
END DeclareDDCorrectionTabF;


PROCEDURE DeclStochWeatherObjects;
  VAR i: INTEGER;
BEGIN
  DeclMV( uAET, 0.0, 1000.0, "Actual evapotranspiration", "uAET" , "mm/y",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uPET, 0.0, 1000.0, "Potential evapotranspiration", "uPET" , "mm/y",
          notOnFile, notInTable, notInGraph);
  DeclMV( uDD, 0.0, 3000.0, "Degree-days", "uDD" , "d*°C",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uWiT, -30.0, 30.0, "Winter temperature", "uWiT" , "°C",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uDrStr, 0.0, 1.0, "Drought stress", "uDrStr" , "--",
          notOnFile, writeInTable, notInGraph);

  DeclMV( meanAET, 0.0, 1000.0, "Average AET", "meanAET" , "mm/y",
          notOnFile, notInTable, notInGraph);
  DeclMV( meanDD, 0.0, 3000.0, "Average degree-days", "meanDD" , "d*°C",
          notOnFile, notInTable, notInGraph);
  DeclMV( meanWiT, 0.0, 1.0, "Average winter temperature", "meanWiT" , "°C",
          notOnFile, notInTable, notInGraph);
  DeclMV( meanDrStr, 0.0, 1.0, "Average drought stress", "meanDrStr" , "--",
          notOnFile, notInTable, notInGraph);

  DeclSoilMoistureParameters;

  RemoveAllWeatherTabFuncs;

  DeclareDDCorrectionTabF;

  FOR i:= 1 TO 20 DO time[i] := FLOAT(i)*50.0; modifier[i] := 0.0 END;

  DeclTabF( tSuTab, time, modifier, 20, TRUE, "Summer T",
    "Year", "Δ (°C)", "year", "°C", 0.0, 5000.0, -10.0, 10.0);
  DeclTabF( tWiTab, time, modifier, 20, TRUE, "Winter T",
    "Year", "Δ (°C)", "year", "°C", 0.0, 5000.0, -10.0, 10.0);
  DeclTabF( pSuTab, time, modifier, 20, TRUE, "Summer P",
    "Year", "Δ (cm/month)", "year", "cm/month", 0.0, 5000.0, -5.0, 5.0);
  DeclTabF( pWiTab, time, modifier, 20, TRUE, "Winter P",
    "Year", "Δ (cm/month)", "year", "cm/month", 0.0, 5000.0, -5.0, 5.0);

  FOR i:= 1 TO 20 DO modifier[i] := 1.0 END;

  DeclTabF( tSDSuTab, time, modifier, 20,   TRUE, "Summer SD(T)",
    "Year", "Mult", "year", "--", 0.0, 5000.0, 0.5, 2.0);
  DeclTabF( tSDWiTab, time, modifier, 20,   TRUE, "Winter SD(T)",
    "Year", "Mult", "year", "--", 0.0, 5000.0, 0.5, 2.0);
  DeclTabF( pSDSuTab, time, modifier, 20,   TRUE, "Summer SD(P)",
    "Year", "Mult", "year", "--", 0.0, 5000.0, 0.5, 2.0);
  DeclTabF( pSDWiTab, time, modifier, 20,   TRUE, "Winter SD(P)",
    "Year", "Mult", "year", "--", 0.0, 5000.0, 0.5, 2.0);
  declEMod := stochE;
END DeclStochWeatherObjects;


PROCEDURE DeclStochEnvModel;
BEGIN
  DeclM(fe, discreteTime, Initialize, NoInput, StochWeatherOutput, NoDynamic, Terminate,
        DeclStochWeatherObjects, modDescrStoch, modIdent, NoAbout);
  DeclMonitoringProc( Monitoring );
END DeclStochEnvModel;


PROCEDURE SkipFileHeader;
  VAR ch: CHAR;
BEGIN
  ReadChar( inF, ch );
  WHILE NOT EOF(inF) AND (ch<>EOL) DO ReadChar( inF, ch ) END;
  ReadChar( inF, ch );
  WHILE NOT EOF(inF) AND (ch<>EOL) DO ReadChar( inF, ch ) END;
END SkipFileHeader;


(*  Weather data from file  *)
(***************************)
```

```
PROCEDURE InitializeFWM;
BEGIN
  DisableCommand( fMenu, chooseEnvCmd );

  currWater := site.kFC;    (* initial conditions in January of the first year *)
  IF site.kSlAsp > 0.0 THEN kPMod := 1.0 + site.kSlAsp*0.125;
                       ELSE kPMod := 1.0 + site.kSlAsp*0.063;
  END;

  Lookup( inF, fileName, FALSE );
  SkipFileHeader;
END InitializeFWM;


PROCEDURE FileWeatherOutput;
  VAR t: REAL;
    i: Month;

  PROCEDURE GetWeatherDataFromFile;
  BEGIN
    GetReal( inF, t );
    FOR i:= Jan TO Dec DO
      GetReal( inF, rTVect[i] );
    END;
    FOR i:= Jan TO Dec DO
      GetReal( inF, rPVect[i] );
    END;
    SkipGap( inF );
    IF EOF(inF) THEN
      Reset( inF );
      SkipFileHeader;
    END; (* IF *)
  END GetWeatherDataFromFile;

BEGIN
  GetWeatherDataFromFile;

  DegreeDays( uDD, rTVect );

  SoilMoisture( uDrStr, uAET, rTVect, rPVect );

  uWiT := rTVect[Jan];
  IF rTVect[Feb] < uWiT THEN uWiT := rTVect[Feb] END;
  IF rTVect[Dec] < uWiT THEN uWiT := rTVect[Dec] END;
END FileWeatherOutput;


PROCEDURE TerminateFWM;
BEGIN
  Close( inF );
  EnableCommand( fMenu, chooseEnvCmd );
END TerminateFWM;


PROCEDURE DeclFileWeatherObjects;
BEGIN
  RemoveAllWeatherTabFuncs;
  DeclareDDCorrectionTabF;
  DeclMV( uDD, 0.0, 2500.0, "Degree-days", "uDD" , "d*°C",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uDrStr, 0.0, 1.0, "Drought stress", "uDrStr" , "-",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uWiT, -30.0, 30.0, "Winter temperature", "uWiT" , "°C",
          notOnFile, writeInTable, notInGraph);
  DeclSoilMoistureParameters;
  declEMod := fileW;
END DeclFileWeatherObjects;


PROCEDURE DeclFileWeatherModel;
BEGIN
  IF declEMod = stochE THEN
    RemoveMonitoringProc( Monitoring );
  END;
  DeclM(fe, discreteTime, InitializeFWM, NoInput, FileWeatherOutput, NoDynamic,
        TerminateFWM, DeclFileWeatherObjects, modDescrFileW, modIdent, NoAbout);
END DeclFileWeatherModel;


(*  Bioclimatic data from file  *)
(********************************)

PROCEDURE TestTheBioclimaticFile( VAR allOK: BOOLEAN );
  VAR x: REAL;
    i: INTEGER;

  PROCEDURE TestNum;
  BEGIN
    IF NOT legalNum AND allOK THEN
      allOK := FALSE;
      Warn( "The file you specified contains illegal numbers!",
              "The stochastic environment model will be declared instead", "" );
    END;
  END TestNum;

BEGIN
  allOK := (inF.res = done);
  IF allOK THEN
    SkipFileHeader;
    WHILE NOT EOF(inF) DO
      FOR i:= 1 TO 4 DO GetReal( inF, x ); TestNum END;
      SkipGap( inF );
    END; (* WHILE *)
  ELSE
    Warn( "The file you specified could not be found or opened!",
          "The stochastic environment model will be declared instead", "" );
  END; (* IF *)
END TestTheBioclimaticFile;
```

```
PROCEDURE InitializeFEM;
BEGIN
  DisableCommand( fMenu, chooseEnvCmd );
  Lookup( inF, fileName, FALSE );
  SkipFileHeader;
END InitializeFEM;


PROCEDURE FileEnvironmentOutput;
  VAR t: REAL;
BEGIN
  GetReal( inF, t );
  GetReal( inF, uDD );
  GetReal( inF, uDrStr );
  GetReal( inF, uWiT );
  SkipGap( inF );
  IF EOF(inF) THEN
    Reset( inF );
    SkipFileHeader;
  END; (* IF *)
END FileEnvironmentOutput;


PROCEDURE TerminateFEM;
BEGIN
  Close( inF );
  EnableCommand( fMenu, chooseEnvCmd );
END TerminateFEM;


PROCEDURE DeclFileEnvObjects;
BEGIN
  RemoveAllWeatherTabFuncs;
  DeclMV( uDD, 0.0, 2500.0, "Degree-days", "uDD" , "d*°C",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uDrStr, 0.0, 1.0, "Drought stress", "uDrStr" , "-",
          notOnFile, writeInTable, notInGraph);
  DeclMV( uWiT, -30.0, 30.0, "Winter temperature", "uWiT" , "°C",
          notOnFile, writeInTable, notInGraph);
  declEMod := fileE;
END DeclFileEnvObjects;


PROCEDURE DeclFileEnvModel;
BEGIN
  IF declEMod = stochE THEN
    RemoveMonitoringProc( Monitoring );
  END;
  DeclM(fe, discreteTime, InitializeFEM, NoInput, FileEnvironmentOutput, NoDynamic,
        TerminateFEM, DeclFileEnvObjects, modDescrFileE, modIdent, NoAbout);
END DeclFileEnvModel;


PROCEDURE UseFileForBioclimaticInput( name: ARRAY OF CHAR );
BEGIN
  AssignString( name, fileName );
  IF MDeclared( fe ) THEN RemoveM( fe ) END;
  DeclFileEnvModel;
END UseFileForBioclimaticInput;


PROCEDURE SelectEnvModel;
  CONST lem = 5;
  VAR ef: FormFrame;
    ok: BOOLEAN;
    cl: INTEGER;
    envTypeB, stochBut, fileWBut, fileBBut: RadioButtonID;
BEGIN
  cl := 2;
  WriteLabel(cl, lem-2, "Select a model of the abiotic environment:"); INC(cl);
  DefineRadioButtonSet(envTypeB);
  RadioButton( stochBut, cl, lem, "Stochastic model, modified from Pastor & Post");
  INC(cl);
  RadioButton( fileWBut, cl, lem, "Weather data from text file");
  INC(cl);
  RadioButton( fileBBut, cl, lem, "Bioclimatic data from text file");
  INC(cl);
  ef.x:= 0; ef.y:= -1; (* display entry form in middle of screen *)
  ef.lines:= cl+2; ef.columns:= 55;
  UseEntryForm( ef,ok );
  IF ok THEN
    RemoveM( fe );
    IF envTypeB = stochBut THEN
      DeclStochEnvModel;
    ELSIF envTypeB = fileWBut THEN
      GetExistingFile( inF, "File to read weather data" );
      IF inF.res = done THEN
        AssignString( inF.filename, fileName );
        Close( inF );
        DeclFileWeatherModel;
      ELSE
        DeclStochEnvModel;
      END; (* IF *)
    ELSE
      GetExistingFile( inF, "File to read bioclimatic data" );
      TestTheBioclimaticFile( ok );
      IF (inF.res = done)  AND ok THEN
        AssignString( inF.filename, fileName );
        Close( inF );
        DeclFileEnvModel;
      ELSE
        DeclStochEnvModel;
      END; (* IF *)
    END; (* IF *)
  END; (* IF *)
END SelectEnvModel;


PROCEDURE DeclForClimE;
BEGIN
  IF NOT MDeclared( fe ) THEN
```

```
    InstallSeparator( fMenu, line );
    InstallCommand( fMenu, fceCmd, "ForClim-E:", EmptyProc,
                    enabled, unchecked );
    InstallCommand( fMenu, chooseEnvCmd, "  Select environment model…", SelectEnvModel,
                    enabled, unchecked );
    InstallAliasChar( fMenu, chooseEnvCmd, "W" );

    RemoveConstEnvironment;
    DeclStochEnvModel;
  END;
END DeclForClimE;


PROCEDURE RemoveForClimE;
BEGIN
  IF MDeclared( fe ) THEN
    IF declEMod = stochE THEN
      RemoveMonitoringProc( Monitoring );
    END;
    RemoveSeparatorAtCommand(fMenu, fceCmd, beforeCmd );
    RemoveCommand( fMenu, fceCmd );
    RemoveCommand( fMenu, chooseEnvCmd );
    RemoveM( fe );
    RemoveAllWeatherTabFuncs;
    DeclConstEnvironment;
  END;
END RemoveForClimE;


PROCEDURE InitializeForClimE;
BEGIN
  FOR month := Jan TO Dec DO zeroSDVect[month] := 0.0 END;

  a[Jan] := 1.1226; a[Feb] := 0.9859; a[Mar] := 1.0454;
  a[Apr] := 0.9708; a[May] := 0.9605; a[Jun] := 0.9185;
  a[Jul] := 0.9669; a[Aug] := 0.9892; a[Sep] := 0.9900;
  a[Oct] := 1.0600; a[Nov] := 1.0815; a[Dec] := 1.1444;

  b[Jan] := -7.3094E-3; b[Feb] := -3.8701E-3; b[Mar] := -4.9231E-4;
  b[Apr] := +3.5179E-3; b[May] := +7.1453E-3; b[Jun] := +8.4718E-3;
  b[Jul] := +7.6410E-3; b[Aug] := +4.9436E-3; b[Sep] := +1.2000E-3;
  b[Oct] := -2.6256E-3; b[Nov] := -6.3692E-3; b[Dec] := -8.6598E-3;

  InstallU( U );

  k1  := 0.2;
  k2  := 1.514;
  k3  := 6.75E-7;
  k4  := -7.71E-5;
  k5  := 0.01792;
  k6  := 0.49239;
  k7  := 4.61E-4;
  k8  := 1.10559;
  kPM := 1.6;
END InitializeForClimE;


BEGIN
  InitializeForClimE;
END ForClimE.
```

Module ForClimP

When the model FORCLIM-P is declared (see procedure DeclForClimP in module ForClimP), a text file with the default name “SpecPars.DAT” is read. It contains a matrix with the species-specific parameters (cf. section 3.4.1, Tab. 3.11). If this file can not be found, a dialog box is produced where the text file can be selected by the user.

```
DEFINITION MODULE ForClimP;

  (****************************************

    Module  ForClimP     (Version 2.4)

              Copyright (c) 1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              MacMETH_V3.2.1  (1-Pass Modula-2 implementation)

      Purpose Plant dynamics model for the ForClim model system

      Remarks none

      Programming

          o Design
              H. Bugmann         17.12.1992

          o Implementation
              H. Bugmann         17.12.1992


          Swiss Federal Institute of Technology Zurich ETHZ
          Department of Environmental Sciences
          Systems Ecology
          ETH-Zentrum
          CH-8092 Zurich
          Switzerland
```

```
          Last revision of definition:  17.12.1992  hb

  ****************************************)


  PROCEDURE DeclForClimP;

  PROCEDURE RemoveForClimP;

END ForClimP.





IMPLEMENTATION MODULE ForClimP;

  (****************************************

    Model:  ForClim-P V2.4 (ForClim Plant Succession Model)

          Copyright ©1992 by Harald Bugmann and Swiss
          Federal Institute of Technology Zurich (ETHZ)
          Department of Environmental Sciences
          Systems Ecology Group, ETH-Zentrum
          CH-8092 Zurich / Switzerland

      Version written for:
               'Dialog Machine' DM_V2.2  (User interface)
               MacMETH_V3.2        (1-Pass Modula-2 implementation)
               ModelWorks MW_V2.2  (Modelling & Simulation)


        Implementation and Revisions:
        ============================

        Author  Date        Description
        ------  ----        -----------

        hb      21. 1.1991  First implementation (DM 2.02, MacMETH 2.6.2)
        hb      30. 1.1991  Minor changes made
        hb      26. 2.1991  Implementation of V0.3 (cohorts instead of individuals)
        hb      18. 3.1991  Some minor changes made
        hb      23. 4.1991  Adaptation for V1.0
        hb      12. 6.1991  Dumping/reading of state vector implemented
        hb      17. 6.1991  Help window added
        hb      07. 8.1991  Test for ExperimentAborted introduced
        hb      24. 1.1992  Model now produces tree-ring chronologies
        hb      25. 2.1992  V1.1 with StochStat implemented
        hb      27. 2.1992  Estimation of equilibrium state introduced
        hb       2. 3.1992  Model now simulates also catastrophic disturbance
        hb      10. 3.1992  Demo and research version merged
        hb      12. 3.1992  Randomization at start of simulation introduced
        hb      20. 3.1992  Version 1.1 implemented (renaming & use of StochStat)
        hb       6. 4.1992  Support for Soppensee validation implemented
        hb       7. 4.1992  module FCPExp introduced, several procedures are
                            implemented there now
        hb      22. 4.1992  Demo version for FIA written
        hb       2. 6.1992  Version 1.1 completed, version 1.2 started
        hb      14. 8.1992  Adopted for version 2.0
        hb      10.11.1992  Version 2.0e finished
        hb      17.12.1992  Adapted for usage within the ForClim simulation system
        hb      22. 3.1993  Customization of statistical output introduced

  ****************************************)


  FROM SimMaster  IMPORT CurrentSimNr, ExperimentAborted, ExperimentRunning;

  FROM SimBase    IMPORT DeclM, IntegrationMethod, DeclP, DeclMV, RTCType, StashFiling,
                         Tabulation, Graphing, RemoveM, CurrentTime, SetSimTime,
                         SetMonInterval, NoAbout, MDeclared, GetGlobSimPars;

  FROM DMMenus    IMPORT InstallCommand, EnableCommand, DisableCommand, Command,
                         AccessStatus, Marking, InstallAliasChar, InstallSeparator,
                         Separator, RemoveCommand, RemoveSeparatorAtCommand,
                         SeparatorPosition;

  FROM DMSystem   IMPORT CurrentDMLevel, InstallTermProc;

  FROM DMConversions IMPORT IntToString;

  FROM DMStrings  IMPORT AssignString, Concat, AppendCh;

  FROM DMFiles    IMPORT GetExistingFile, TextFile, Close, CreateNewFile, Response;

  FROM DMEntryForms IMPORT FormFrame, WriteLabel, DefltUse, RealField, CheckBox,
                         UseEntryForm;

  FROM RandGen    IMPORT GetSeeds, U;


  FROM StochStat  IMPORT StatArray, Prob2Tail, DeclStatArray, notExistingStatArray,
                         PutValue, DeclDispMV, DisplayArray;

  FROM SimGraphUtils IMPORT timeIsIndep;

  FROM ForestBase IMPORT fp, site, SetRandomNumberSeeds, fMenu,
                         DeclMonitoringProc, RemoveMonitoringProc, DeclSiteProc,
                         RemoveSiteProc, uDD, uDrStr, uWiT, uLitt,
                         Litter, uAvN, DeclConstPlants, RemoveConstPlants,
                         kPatchSize, exp, ExperimentType, DeclStatArrayForOutput;

  FROM FCPBase    IMPORT SpeciesPtr, DeleteAllCohorts, EditParameters, firstSp, gLAI,
                         meanLAI, totalBiomass, meanTotBio, totalTrees, meanTotNr,
                         ResetAllSpeciesParameters, DeleteAllSpecies;

  FROM FCPMon     IMPORT ChooseSpeciesForHistograms, ChooseSpeciesForTreeRings,
                         CloseTreeRingFile, MakeAnimationWindow,
                         HistogramMonitoring, AnimationMonitoring;
```

```
FROM FCPFileIO  IMPORT DeclAllometricParameters, AssignAllometricParameters,
                       AssignMonitoringAttributes, DumpStateToFile,
                       ReadStateFromFile, undefSeed, ReadSpeciesFile,
                       CalcAndWriteLimFactorsToFile;

FROM FCPGrFact  IMPORT SoilNitrogenGrowthFactor, DegreeDayGrowthFactor,
                       StandCharacteristics, maxHeight, DroughtGrowthFactor;

FROM FCPDynamic IMPORT TreeDeathAndGrowth, TreeEstablishment, UpdateGap,
                       DeclSubMParameters, LitterInitialization;


CONST
  modIdent = "ForClim-P";
  modDescr = "ForClim-P: Plant dynamics model";
  noT = notInTable; noG = notInGraph; noF = notOnFile; isT = writeInTable;


VAR
  chooseSiteCmd, chooseWeatherCmd, editParsCmd, histoCmd, newSpeciesCmd,
  dumpStateCmd, readStateCmd, treeRingCmd, animCmd, statsCmd, fcpCmd: Command;
  sp: SpeciesPtr;
  kPDist, maxBioScaling: REAL;
  cumLA: ARRAY [1..maxHeight] OF REAL;
  pathAndFilename: ARRAY [0..63] OF CHAR;
  fn: ARRAY [0..31] OF CHAR;
  statArrLAI, statArrTotBio, statArrTotNr : StatArray;
  statArrLitt: ARRAY [MIN(Litter)..MAX(Litter)] OF StatArray;
  tzero, hm,
  minValBiom, minValNr : REAL;
  withBiom, withNr, ok: BOOLEAN;
  startupLevel: CARDINAL;
  meanLitt: ARRAY [MIN(Litter)..MAX(Litter)] OF REAL;

  (* for sensitivity analysis of species parameters only: *)
  sensFirstSp, sensSp, modelSp: SpeciesPtr;


PROCEDURE EmptyProc; BEGIN END EmptyProc;


PROCEDURE CreateStateFileName( VAR fn: ARRAY OF CHAR );
  VAR nrStr: ARRAY [0..7] OF CHAR;
BEGIN
  AssignString( "ForClim-P State.", fn );
  Concat( fn, site.name );
  IntToString( CurrentSimNr(), nrStr, 3 );
  Concat( fn, nrStr );
END CreateStateFileName;


(**************************)
(* Monitoring procedure   *)
(**************************)

PROCEDURE Monitoring;
  VAR t, convFBio, convFNr : REAL;
    index : INTEGER;
    sp : SpeciesPtr;
    i: Litter;
BEGIN
  HistogramMonitoring;
  AnimationMonitoring;

  IF ExperimentRunning() THEN
    IF exp.type = estimEquil THEN
      t := 0.0;
      index := 1;
    ELSE
      t := CurrentTime();
      index := TRUNC( (t-tzero)/hm + 0.5 ) + 1;
    END;

    IF NOT ((exp.type = estimEquil) AND (CurrentTime() <= exp.startYear )) THEN
      convFBio := 10.0 / kPatchSize;
      convFNr  := 1000.0 * convFBio;
      sp := firstSp;
      WHILE sp <> NIL DO
        PutValue( sp^.statArrB, index, t, sp^.biomass*convFBio );
        PutValue( sp^.statArrN, index, t, sp^.nrTrees*convFNr );
        sp := sp^.next;
      END; (* WHILE *)
      PutValue( statArrLAI,    index, t, gLAI );
      PutValue( statArrTotBio, index, t, totalBiomass*convFBio );
      PutValue( statArrTotNr,  index, t, totalTrees*convFNr );
      FOR i := MIN(Litter) TO MAX(Litter) DO
        PutValue( statArrLitt[i],  index, t, uLitt[i] );
      END;
    END; (* IF *)
  END; (* IF *)
END Monitoring;


(****************)
(* Statistics   *)
(****************)

PROCEDURE DeclareStatArrays( arrLen : INTEGER );
  VAR i: Litter;
BEGIN
  sp := firstSp;
  WHILE sp<> NIL DO   (* declare biomasses *)
    sp^.statArrB := notExistingStatArray;
    DeclStatArray( sp^.statArrB, arrLen );
    DeclDispMV( sp^.statArrB, fp, sp^.meanBio, fp, timeIsIndep );
    IF withBiom THEN
      DeclStatArrayForOutput( sp^.statArrB, sp^.name, "t/ha", minValBiom );
    END;
    sp := sp^.next;
  END;
```

```
  sp := firstSp;
  WHILE sp<> NIL DO   (* declare numbers *)
    sp^.statArrN := notExistingStatArray;
    DeclStatArray( sp^.statArrN, arrLen );
    DeclDispMV( sp^.statArrN, fp, sp^.meanNr, fp, timeIsIndep );
    IF withNr THEN
      DeclStatArrayForOutput( sp^.statArrN, sp^.longDescNr, "#/ha", minValNr );
    END;
    sp := sp^.next;
  END;

  statArrLAI := notExistingStatArray;
  DeclStatArray( statArrLAI, arrLen );
  DeclDispMV( statArrLAI, fp, meanLAI, fp, timeIsIndep );
  DeclStatArrayForOutput( statArrLAI, "Leaf area index", "m^2/m^2", 0.0 );

  statArrTotBio := notExistingStatArray;
  DeclStatArray( statArrTotBio, arrLen );
  DeclDispMV( statArrTotBio, fp, meanTotBio, fp, timeIsIndep );
  DeclStatArrayForOutput( statArrTotBio, "Total biomass", "t/ha", 0.0 );

  statArrTotNr := notExistingStatArray;
  DeclStatArray( statArrTotNr, arrLen );
  DeclDispMV( statArrTotNr, fp, meanTotNr, fp, timeIsIndep );
  DeclStatArrayForOutput( statArrTotNr, "Total number", "#/ha", 0.0 );

  FOR i:= MIN(Litter) TO MAX(Litter) DO
    statArrLitt[i] := notExistingStatArray;
    DeclStatArray( statArrLitt[i], arrLen );
    DeclDispMV( statArrLitt[i], fp, meanLitt[i], fp, timeIsIndep );
  END;
  DeclStatArrayForOutput( statArrLitt[leafFast], "Litterfall (foliage fast)", "t/ha", 0.0 );
  DeclStatArrayForOutput( statArrLitt[leafMedium], "Litterfall (foliage medium)", "t/ha", 0.0 );
  DeclStatArrayForOutput( statArrLitt[leafSlow], "Litterfall (foliage slow)", "t/ha", 0.0 );
  DeclStatArrayForOutput( statArrLitt[twigs], "Litterfall (twigs)", "t/ha", 0.0 );
  DeclStatArrayForOutput( statArrLitt[roots], "Litterfall (fine roots)", "t/ha", 0.0 );
  DeclStatArrayForOutput( statArrLitt[wood], "Litterfall (wood)", "t/ha", 0.0 );
END DeclareStatArrays;


PROCEDURE DisplayStatArrays;
  VAR i: Litter;
BEGIN
  IF NOT ExperimentAborted() THEN
    sp := firstSp;
    WHILE sp<> NIL DO
      DisplayArray( sp^.statArrB, TRUE, prob950 );
      DisplayArray( sp^.statArrN, TRUE, prob950 );
      sp := sp^.next;
    END;

    DisplayArray( statArrLAI,    TRUE, prob950 );
    DisplayArray( statArrTotBio, TRUE, prob950 );
    DisplayArray( statArrTotNr,  TRUE, prob950 );

    FOR i:= MIN(Litter) TO MAX(Litter) DO
      DisplayArray( statArrLitt[i],TRUE, prob950 );
    END;
  END;
END DisplayStatArrays;


(***********************************)
(*  Procedures for model dynamics  *)
(***********************************)

PROCEDURE Initialize;
  VAR  j, x0New, y0New, z0New, arrLen: INTEGER;
    tend, c, h, er: REAL;
    ok: BOOLEAN;

  (*
  PROCEDURE SetImmigPar( desc: ARRAY OF CHAR; kImmYrNew: REAL );
    VAR found: BOOLEAN;
  BEGIN
    found := FALSE;
    sp := firstSp;
    WHILE (sp <> NIL) AND NOT found DO
      IF CompareStrings( sp^.shortDescBio, desc ) = equal THEN
        found := TRUE;
        sp^.p.kImmYr := kImmYrNew;
      END;
      sp := sp^.next;
    END; (* WHILE *)
    IF NOT found THEN HALT END;
  END SetImmigPar;
  *)

  PROCEDURE SetSpeciesParameter( VAR sensSp, modelSp: SpeciesPtr; nrRun: INTEGER );
    VAR par: INTEGER;
  BEGIN
    par := nrRun MOD 14;
    ResetAllSpeciesParameters;

    IF (par = 1) AND (nrRun <> 1) THEN (* move to a new species *)
      sensSp  := sensSp^.next;
      modelSp := modelSp^.next;
    END;

    (* now assign a new species parameter *)
    IF    par =  1 THEN
      modelSp^.p.kA1 := sensSp^.p.kA1;
      modelSp^.p.kA2 := sensSp^.p.kA2;
      modelSp^.p.kC1 := sensSp^.p.kC1;
      modelSp^.p.kC2 := sensSp^.p.kC2;
    ELSIF par =  2 THEN
      modelSp^.p.kDm := sensSp^.p.kDm;
      modelSp^.p.kB2 := 2.0*(modelSp^.p.kHm - 137.0) / modelSp^.p.kDm;
      modelSp^.p.kB3 := modelSp^.p.kB2 / 2.0 / modelSp^.p.kDm;
    ELSIF par =  3 THEN
```

```
      modelSp^.p.kHm := sensSp^.p.kHm;
      modelSp^.p.kB2 := 2.0*(modelSp^.p.kHm - 137.0) / modelSp^.p.kDm;
      modelSp^.p.kB3 := modelSp^.p.kB2 / 2.0 / modelSp^.p.kDm;
    ELSIF par =  4 THEN
      modelSp^.p.kAm := sensSp^.p.kAm;
    ELSIF par =  5 THEN
      modelSp^.p.kG := sensSp^.p.kG;
    ELSIF par =  6 THEN
      modelSp^.p.kDDMin := sensSp^.p.kDDMin;
    ELSIF par =  7 THEN
      modelSp^.p.kDDMax := sensSp^.p.kDDMax;
    ELSIF par =  8 THEN
      modelSp^.p.kWiT := sensSp^.p.kWiT;
    ELSIF par =  9 THEN
      modelSp^.p.kDrT := sensSp^.p.kDrT;
    ELSIF par = 10 THEN
      modelSp^.p.kNTol := sensSp^.p.kNTol;
    ELSIF par = 11 THEN
      modelSp^.p.kBrow := sensSp^.p.kBrow;
    ELSIF par = 12 THEN
      modelSp^.p.kLy := sensSp^.p.kLy;
    ELSIF par = 13 THEN
      modelSp^.p.kLa := sensSp^.p.kLa;
    ELSE (* par 14 *)
      modelSp^.p.kLQ := sensSp^.p.kLQ;
    END;
  END SetSpeciesParameter;

BEGIN
  DisableCommand( fMenu, statsCmd );
  DisableCommand( fMenu, newSpeciesCmd );
  DisableCommand( fMenu, chooseSiteCmd );
  DisableCommand( fMenu, chooseWeatherCmd );
  DisableCommand( fMenu, treeRingCmd );

  AssignAllometricParameters;

  IF CurrentSimNr() = 1 THEN
    sp := firstSp;
    WHILE sp <> NIL DO
      FOR j := 1 TO 7 DO sp^.limCounter[j] := 0 END;
      sp^.sumALGF := 0.0; sp^.sumDDGF := 0.0;
      sp^.sumSMGF := 0.0; sp^.sumSNGF := 0.0; sp^.sumGF := 0.0;
      sp := sp^.next;
    END; (* WHILE *)
  END; (* IF *)

  GetGlobSimPars(tzero, tend, h, er, c , hm);

  IF ExperimentRunning() AND (CurrentSimNr() = 1 ) THEN
    IF exp.type = manyRuns THEN
      arrLen := TRUNC((tend-tzero)/hm+1.5);
      DeclareStatArrays( arrLen );
    ELSIF exp.type = estimEquil THEN
      DeclareStatArrays( 1 );

      (* for sensitivity analysis of species parameters only: *)
      IF exp.doSensAnalysis THEN
        (*. ReadSpeciesFile( sensFirstSp, "", ok ); .*)
        sensSp  := sensFirstSp;
        modelSp := firstSp;
      END;
    ELSE
      (* do nothing *)
    END;
  END;

  IF ExperimentRunning() AND (exp.type = estimEquil)
    AND exp.doSensAnalysis THEN (* experiment for parameter sensitivity *)
      (* execute this procedure only if the experiment is for the analysis
         of parameter sensitivity of tree species! *)
     (*. SetSpeciesParameter( sensSp, modelSp, CurrentSimNr() ); .*)
  END;

  IF exp.readState THEN
    AssignString( exp.inFileName, pathAndFilename );
    CreateStateFileName( fn );
    Concat( pathAndFilename, fn );
    ReadStateFromFile( ok, x0New, y0New, z0New, pathAndFilename );
    IF ok AND (x0New <> undefSeed) THEN
      SetRandomNumberSeeds( x0New, y0New, z0New );
    END;
  END;
END Initialize;


PROCEDURE Output;
BEGIN
  LitterInitialization( tzero, kPatchSize );
  UpdateGap( firstSp, uDD, uDrStr );
END Output;


PROCEDURE Input;
BEGIN
  StandCharacteristics( totalTrees, totalBiomass, gLAI, cumLA, firstSp );
  sp := firstSp;
  WHILE sp <> NIL DO
    DegreeDayGrowthFactor( sp, uDD );
    DroughtGrowthFactor( sp, uDrStr);
    SoilNitrogenGrowthFactor( sp, uAvN );
    sp := sp^.next;
  END; (* WHILE *)
END Input;


PROCEDURE Dynamic;
BEGIN
  IF U() < kPDist THEN (* catastrophic disturbance occurs, all trees die *)
    sp := firstSp;
    WHILE sp <> NIL DO
```

```
      DeleteAllCohorts( sp );
      sp := sp^.next;
    END; (* WHILE *)
  ELSE    (* normal year with all three submodels *)
    TreeDeathAndGrowth( firstSp, cumLA, gLAI );
    TreeEstablishment( firstSp, uWiT, uDD, gLAI, totalTrees, kPatchSize );
  END;
END Dynamic;


PROCEDURE Terminate;
  VAR x, y, z: INTEGER;
    fn : ARRAY [0..31] OF CHAR;
    ok: BOOLEAN;
BEGIN
  IF exp.writeState THEN
    GetSeeds( x, y, z );
    AssignString( exp.outFileName, pathAndFilename );
    CreateStateFileName( fn );
    Concat( pathAndFilename, fn );
    DumpStateToFile( ok, TRUNC(CurrentTime()), x, y ,z, site.name, pathAndFilename );
  END;

  sp := firstSp;
  WHILE sp <> NIL DO
    DeleteAllCohorts( sp );
    sp := sp^.next;
  END; (* WHILE *)
  CloseTreeRingFile;

  IF ExperimentRunning() AND ((CurrentSimNr() MOD TRUNC(exp.nrRuns+0.5)) = 0) THEN
    IF exp.type = manyRuns THEN
      DisplayStatArrays;
    END;

    IF exp.inBatchMode THEN
      AssignString( site.name, fn );
      Concat( fn, ".LF.DAT" );
    ELSE
      fn[0] := 0C;
    END;

    IF NOT exp.doSensAnalysis AND NOT ExperimentAborted() THEN
      CalcAndWriteLimFactorsToFile( fn, firstSp );
    END;
  END;

  EnableCommand( fMenu, statsCmd );
  EnableCommand( fMenu, newSpeciesCmd );
  EnableCommand( fMenu, chooseSiteCmd );
  EnableCommand( fMenu, chooseWeatherCmd );
  EnableCommand( fMenu, treeRingCmd );
END Terminate;


(************************************)
(* Procedures for model declaration  *)
(************************************)

PROCEDURE DeclModelObjects;
  VAR str: ARRAY [0..6] OF CHAR;
BEGIN
  sp := firstSp;  (* declare biomass MVs *)
  WHILE sp <> NIL DO
    WITH sp^ DO
      DeclMV( biomass, 0.0, maxBioScaling, longDescBio, shortDescBio, "kg/patch", noF, noT, mon.graphBio);
    END; (* WITH *)
    sp := sp^.next;
  END; (* WHILE *)
  DeclMV( totalBiomass, 0.0, maxBioScaling, "Total biomass", "totBio" , "kg/patch", noF, isT, noG);
  DeclMV( gLAI, 0.0, 20.0, "Leaf area index", "gLAI" , "--", noF, isT, noG);

  sp := firstSp;  (* declare tree number MVs *)
  WHILE sp <> NIL DO
    WITH sp^ DO
      DeclMV( nrTrees, 0.0, 100.0, longDescNr, shortDescNr,  "#/patch", noF, noT, mon.graphNr);
    END; (* WITH *)
    sp := sp^.next;
  END; (* WHILE *)
  DeclMV( totalTrees, 0.0, 200.0, "Total number of trees", "totNr" , "#/patch", noF, isT, noG);

  sp := firstSp;  (* declare average biomass MVs *)
  WHILE sp <> NIL DO
    WITH sp^ DO
      AssignString( shortDescBio, str ); AppendCh( str, "µ" );
      DeclMV( meanBio, 0.0, 400.0, longDescBio, str, "t/ha", noF, noT, noG);
    END; (* WITH *)
    sp := sp^.next;
  END; (* WHILE *)
  DeclMV( meanLAI, 0.0, 20.0, "Mean leaf area index", "µLAI" , "--", noF, noT, noG);
  DeclMV( meanTotBio, 0.0, 400.0, "Mean total biomass", "µtotBio" , "t/ha", noF, noT, noG);

  sp := firstSp;  (* declare average number MVs *)
  WHILE sp <> NIL DO
    WITH sp^ DO
      AssignString( shortDescNr, str ); AppendCh( str, "µ" );
      DeclMV( meanNr, 0.0, 100.0, sp^.longDescNr, str, "#/ha", noF, noT, noG);
    END; (* WITH *)
    sp := sp^.next;
  END; (* WHILE *)
  DeclMV( meanTotNr, 0.0, 200.0, "Mean total number of trees", "µtotNr" , "#/ha", noF, noT, noG);

  DeclMV( uLitt[leafFast], 0.0, 50.0, "Fast decaying foliage litter", "uLittLF", "t/ha", noF, noT, noG );
  DeclMV( uLitt[leafMedium], 0.0, 50.0, "Medium dec. foliage litter", "uLittLM", "t/ha", noF, noT, noG );
  DeclMV( uLitt[leafSlow], 0.0, 50.0, "Slowly dec. foliage litter", "uLittLS", "t/ha", noF, noT, noG );
  DeclMV( uLitt[roots],  0.0, 50.0, "Root litter", "uLittR", "t/ha", noF, noT, noG );
  DeclMV( uLitt[twigs],  0.0, 50.0, "Twig litter", "uLittT", "t/ha", noF, noT, noG );
  DeclMV( uLitt[wood],  0.0, 50.0, "Stemwood litter", "uLittW", "t/ha", noF, noT, noG );

  DeclMV( meanLitt[leafFast], 0.0, 50.0, "Fast decaying foliage litter", "µLittLF", "t/ha", noF, noT, noG );
  DeclMV( meanLitt[leafMedium], 0.0, 50.0, "Medium dec. foliage litter", "µLittLM", "t/ha", noF, noT, noG );
```

```
  DeclMV( meanLitt[leafSlow], 0.0, 50.0, "Slowly dec. foliage litter", "µLittLS", "t/ha", noF, noT, noG );
  DeclMV( meanLitt[roots],  0.0, 50.0, "Root litter", "µLittR", "t/ha", noF, noT, noG );
  DeclMV( meanLitt[twigs],  0.0, 50.0, "Twig litter", "µLittT", "t/ha", noF, noT, noG );
  DeclMV( meanLitt[wood],  0.0, 50.0, "Stemwood litter", "µLittW", "t/ha", noF, noT, noG );

  DeclP(kPDist, 0.0, 0.0, 1.0, noRtc, 'Disturbance probability',  'kPDist', '/year');

  DeclAllometricParameters;
  DeclSubMParameters;

END DeclModelObjects;


PROCEDURE DeclareGapModel;
BEGIN
  DeclM(fp, discreteTime, Initialize, Input, Output, Dynamic, Terminate,
        DeclModelObjects, modDescr, modIdent, NoAbout);
  SetSimTime( 0.0, 1200.0);
  SetMonInterval( 20.0 );
END DeclareGapModel;


(********************************************)
(* Procedures for site & species selection  *)
(********************************************)

PROCEDURE ChooseSpecies;
   VAR ok: BOOLEAN;
BEGIN
  ReadSpeciesFile( firstSp, "", ok );
  IF ok THEN
    RemoveM( fp );
    DeclareGapModel;
  END; (* IF *)
END ChooseSpecies;


PROCEDURE DumpTheState;
  VAR x, y, z: INTEGER;
    f: TextFile;
    ok: BOOLEAN;
BEGIN
  GetSeeds( x, y, z );
  CreateNewFile( f, "File to dump state vector", "ForClim-P State.DAT" );
  IF f.res = done THEN
    AssignString( f.path, pathAndFilename );
    Concat( pathAndFilename, f.filename );
    Close( f );
    DumpStateToFile( ok, TRUNC(CurrentTime()), x, y ,z, site.name, pathAndFilename );
  END;
END DumpTheState;


PROCEDURE ReadTheState;
  VAR ok: BOOLEAN;
    x0New, y0New, z0New: INTEGER;
    f: TextFile;
BEGIN
  GetExistingFile( f, "File to read state vector" );
  ok := f.res = done;
  IF ok THEN
    AssignString( f.path, pathAndFilename );
    Concat( pathAndFilename, f.filename );
    Close( f );
    ReadStateFromFile( ok, x0New, y0New, z0New, pathAndFilename );
    IF ok AND (x0New <> undefSeed) THEN
      SetRandomNumberSeeds( x0New, y0New, z0New );
    END;
  END;
END ReadTheState;


PROCEDURE DoTreeRings;
BEGIN
  ChooseSpeciesForTreeRings( site.name );
END DoTreeRings;


PROCEDURE CustomizeStats;
  CONST startLine = 3;
  VAR line, lem : INTEGER;
    ef : FormFrame;
    ok : BOOLEAN;
BEGIN
  line := startLine; lem := 2;
  WriteLabel( line-1, lem-1, "Customization of statistical output:" );
  INC( line );
  CheckBox( line, lem, "Write species biomasses higher than", withBiom );
  RealField(line, lem+34, 5, minValBiom, useAsDeflt, 0.0, 20.0 );
  WriteLabel( line, lem+40, "t/ha" ); INC( line );
  CheckBox( line, lem, "Write tree numbers higher than", withNr );
  RealField(line, lem+30, 5, minValNr, useAsDeflt, 0.0, 50.0 );
  WriteLabel( line, lem+36, "#/ha" );
  ef.x:= 0; ef.y:= -1; (* display entry form in middle of screen *)
  ef.lines:= 8; ef.columns:= 50;
  UseEntryForm( ef,ok );
END CustomizeStats;


PROCEDURE DeclForClimP;
  VAR ok: BOOLEAN;
BEGIN
  IF NOT MDeclared( fp ) THEN
    RemoveConstPlants;
    ReadSpeciesFile( firstSp, "SpecPars.DAT", ok );

    DeclMonitoringProc( Monitoring );
    DeclSiteProc( AssignMonitoringAttributes );
    AssignMonitoringAttributes;

    DeclareGapModel;
```

```
      InstallSeparator( fMenu, line );
      InstallCommand(fMenu, fcpCmd, "ForClim-P:", EmptyProc,
                     enabled, unchecked);
      InstallCommand(fMenu, statsCmd, "  Customize statistical output…", CustomizeStats,
                     enabled, unchecked);
      InstallCommand(fMenu, newSpeciesCmd, "  Choose other species…", ChooseSpecies,
                     enabled, unchecked);
      InstallCommand(fMenu, editParsCmd, "  Edit species parameters…", EditParameters,
                     enabled, unchecked);
      InstallAliasChar(fMenu, editParsCmd, "N" );
      InstallCommand(fMenu, histoCmd, "  Frequency distributions…", ChooseSpeciesForHistograms,
                     enabled, unchecked);
      InstallAliasChar(fMenu, histoCmd, "U" );
      InstallSeparator( fMenu, blank );
      InstallCommand(fMenu, animCmd, "  Animation", MakeAnimationWindow,
                     enabled, unchecked);

      InstallSeparator( fMenu, blank );
      InstallCommand(fMenu, dumpStateCmd, "  Dump current state…", DumpTheState,
                     enabled, unchecked);
      InstallCommand(fMenu, readStateCmd, "  Read state file", ReadTheState,
                     enabled, unchecked);
      InstallCommand(fMenu, treeRingCmd, "  Tree-rings…", DoTreeRings,
                     enabled, unchecked);
    END;
  END DeclForClimP;


  PROCEDURE RemoveForClimP;
  BEGIN
    IF MDeclared( fp ) THEN
      RemoveSiteProc( AssignMonitoringAttributes );
      RemoveMonitoringProc( Monitoring );
      RemoveM( fp );
      RemoveSeparatorAtCommand( fMenu, fcpCmd, beforeCmd );
      RemoveCommand( fMenu, fcpCmd );
      RemoveCommand( fMenu, statsCmd );
      RemoveCommand( fMenu, newSpeciesCmd );
      RemoveCommand( fMenu, editParsCmd );
      RemoveCommand( fMenu, histoCmd );
      RemoveSeparatorAtCommand( fMenu, animCmd, beforeCmd );
      RemoveCommand( fMenu, animCmd );
      RemoveSeparatorAtCommand( fMenu, dumpStateCmd, beforeCmd );
      RemoveCommand( fMenu, dumpStateCmd );
      RemoveCommand( fMenu, readStateCmd );
      RemoveCommand( fMenu, treeRingCmd );
      DeclConstPlants;
    END;
  END RemoveForClimP;


  PROCEDURE TermProc;
  BEGIN
    IF CurrentDMLevel() = startupLevel THEN
      DeleteAllSpecies( sensFirstSp );
    END;
    ok := TRUE;
  END TermProc;

  PROCEDURE InitModule;
  BEGIN
    maxBioScaling := 800.0 * kPatchSize/ 10.0;   (* conversion 800 t/ha -> kg/patch *)
    withBiom   := TRUE;
    withNr     := FALSE;
    minValBiom := 2.0;
    minValNr   := 0.0;
    sensFirstSp:= NIL;
    startupLevel := CurrentDMLevel();
    InstallTermProc( TermProc, ok );
  END InitModule;


BEGIN
  InitModule;
END ForClimP.
```

Module FCPDynamic

```
DEFINITION MODULE FCPDynamic;

  (****************************************

    Module  FCPDynamic     (Version 2.4)

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              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2   (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Dynamic Structure of the FORCLIM-P Model

      Programming

          • Design
              H. Bugmann        18.1.1991

          • Implementation
              H. Bugmann        18.1.1991
```

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          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  2.3.1992  hb

  ***************************************)

FROM FCPBase IMPORT SpeciesPtr;


  PROCEDURE DeclSubMParameters;
    (* declares ForClim-P parameters *)

  PROCEDURE LitterInitialization( t0,  kPatchSize: REAL );
    (* initializes litter production and assigns accumulated litter to the
       corresponding ForestBase variables;
       t0 is simulation start time (used for initialization);
       LitterInitialization is to be called in the Output proc
     *)

  PROCEDURE TreeDeathAndGrowth( VAR firstSp: SpeciesPtr; VAR cumLA: ARRAY OF REAL;
                                gLAI: REAL );
  PROCEDURE TreeEstablishment( VAR firstSp: SpeciesPtr;
                               uWiT: REAL; uDD, gLAI, totalTrees, kPatchSize: REAL );
  PROCEDURE UpdateGap( VAR firstSp: SpeciesPtr; uDD, uDrStr: REAL );
END FCPDynamic.




IMPLEMENTATION MODULE FCPDynamic;

  (*
        Implementation and Revisions:
        ============================

        Author  Date        Description
        ------  ----        -----------

        hb      18. 1.1991  First implementation (DM 2.02, MacMETH 2.6.2)
        hb      30. 1.1991  PROCs TreeDeath and TreeGrowth merged (V0.1)
        hb      26. 2.1991  Version 0.3 implemented
        hb      21. 3.1991  Version 0.4 implemented
        hb      28. 1.1992  More efficient establishment at the beginning of the
                            simulation introduced
        hb      30. 1.1992  List management changed in TreeDeathAndGrowth
        hb      11. 3.1992  Formulation of browsing changed
        hb      13. 8.1992  New formulation for light growth factor (kShaw = [1…9])
        hb      10.11.1992  Adaptation of limiting factor statistics to new equations
        hb       1. 3.1993  Adaptation for new gH-diameter relationship in maximum
                            growth equation
        hb       8. 6.1993  calculation of litter output fixed (twigs were too high)

  *)

FROM ForestBase   IMPORT Power, Rmax, uBrPr, Litter, uLitt;

FROM FCPBase      IMPORT SpeciesPtr, CohortPtr, CreateCohort, DeleteCohort,
                         MergeCohorts, SpeciesType;

FROM FCPMon       IMPORT WriteTreeRings;

FROM RandGen      IMPORT U;

FROM SYSTEM       IMPORT Exp;

FROM SimBase      IMPORT DeclP, RTCType, CurrentTime, GetGlobSimPars;


VAR kInitDBH, kMinAbsInc, kMinRelInc, kLAtt, kDeathP, kSlowGrP, kSlowGrYrs,
  kEstP, kEstNr, kTwig, kAFW, kRSR: REAL;
  littF: ARRAY [1..3] OF REAL;
  littW, littT, littR: REAL;
  kFRT: ARRAY [deciduous..coniferous] OF REAL;


PROCEDURE DeclSubMParameters;
BEGIN
  DeclP(kMinAbsInc, 0.03, 0.0, 1.0, noRtc, 'Min. abs. growth (vigorous tree)',  'kMinAbsInc', 'cm');
  DeclP(kMinRelInc, 0.1, 0.0, 1.0, noRtc, 'Min. rel. growth (vigorous tree)',  'kMinRelInc', '%');
  DeclP(kLAtt, 0.25, 0.0, 1.0, noRtc, 'Light attenuation coefficient',  'kLAtt', '--');
  DeclP(kDeathP, 4.605, 0.0, 10.0, noRtc, 'Death probability coefficient',  'kDeathP', '--');
  DeclP(kSlowGrP, 0.368, 0.0, 1.0, noRtc, 'Slow growth enhanced mortality',  'kSlowGrP', '--');
  DeclP(kSlowGrYrs, 2.0, 0.0, 10.0, noRtc, 'Nr of slow growth years required',  'kSlowGrYrs', '#');
  DeclP(kEstP, 0.1, 0.0, 1.0, noRtc, 'Probability of tree establishment',  'kEstP', '--');
  DeclP(kEstNr, 0.006, 0.0, 1.0, noRtc, 'Max. establishment per species',  'kEstNr', '#/m2*yr');
  DeclP(kInitDBH, 1.27, 0.0, 10.0, noRtc, 'DBH of new trees',  'kInitDBH', 'cm');
  DeclP(kFRT[coniferous], kFRT[coniferous], 0.0, 10.0, noRtc, 'Foliage retention time (conifers)',  'kFRT', 'years');
  DeclP(kTwig, 0.0025, 0.0, 0.1, noRtc, 'Twig litter production parameter',  'kTwig', 'kg/cm2');
  DeclP(kAFW, 0.92, 0.5, 1.0, noRtc, 'Ash-free weight of litter',  'kAFW', '--');
  DeclP(kRSR, 4.0, 0.0, 10.0, noRtc, 'Root:shoot ratio of litter',  'kRSR', '--');
END DeclSubMParameters;


PROCEDURE LitterInitialization( t0, kPatchSize: REAL );
  VAR conv: REAL;
BEGIN
  IF CurrentTime() = t0 THEN (* initialize variables *)
    littW    := 0.0;    littT    := 0.0;    littR    := 0.0;
    littF[1] := 0.0;    littF[2] := 0.0;    littF[3] := 0.0;
  END;

  (* assign ForestBase variables, and reset internal variables to zero *)
  conv := 10.0 / kPatchSize;    (* conversion factor kg/gap -> t/ha *)
  uLitt[leafFast]   := littF[1]*conv;   littF[1] := 0.0;
  uLitt[leafMedium] := littF[2]*conv;   littF[2] := 0.0;
  uLitt[leafSlow]   := littF[3]*conv;   littF[3] := 0.0;
  uLitt[wood]       := littW*conv;      littW    := 0.0;
  uLitt[twigs]      := littT*conv;      littT    := 0.0;
```

```
  uLitt[roots]      := littR*conv;      littR    := 0.0;
END LitterInitialization;


(**********************************)
(*  Procedure TreeDeathAndGrowth  *)
(**********************************)

PROCEDURE TreeDeathAndGrowth( VAR firstSp: SpeciesPtr; VAR cumLA: ARRAY OF REAL;
                              gLAI: REAL );
  VAR sp: SpeciesPtr;
      cohort, prevCohort: CohortPtr;
      gAL, gL1, gL9, slope, DIncMax, gF: REAL;
      iHT, i, cohortTrees: INTEGER;

  PROCEDURE CalculateLitterProduction( VAR sp: SpeciesPtr; VAR c: CohortPtr;
                                       nDead: REAL );
    (* calculates litter production of a tree cohort, including litter production
       if nTrees have died *)
    CONST
      pi4 = 3.141593/4.0;
    VAR
      nAlive: REAL;
  BEGIN
    nAlive := FLOAT( c^.nrTrees );

    (* normal annual litter production from living trees: *)

    (* foliage litter depends on foliage quality and foliage retention time *)
    littF[sp^.p.kLQ] := littF[sp^.p.kLQ] + c^.gFolW * nAlive/ kFRT[sp^.specType]*kAFW;
    (* twig litter is calculated from basal area according to Christensen (1977) *)
    littT := littT + pi4 * c^.D * c^.D * kTwig * nAlive * kAFW;
    (* root litter is calculated from foliage litter *)
    littR := littR + kRSR * c^.gFolW * nAlive/kFRT[sp^.specType] * kAFW;

    (* litter from the n dead trees *)
    IF nDead > 0.0 THEN
      (* foliage litter *)
      littF[sp^.p.kLQ] := littF[sp^.p.kLQ] + c^.gFolW*nDead*kAFW;
      (* twig litter *)
      littT := littT + pi4 * c^.D * c^.D * kTwig * nDead * kAFW;
      (* root litter *)
      littR := littR + kRSR * c^.gFolW * nDead * kAFW;
      (* woody litter *)
      littW := littW + c^.gSBio * nDead * kAFW;
    END;
  END CalculateLitterProduction;

BEGIN
  sp := firstSp;
  WHILE sp <> NIL DO
    WITH sp^ DO
      prevCohort := NIL;
      cohort := sp^.firstCohort;
      WHILE cohort <> NIL DO
        WITH cohort^ DO
          cohortTrees := nrTrees;
          FOR i:= 1 TO cohortTrees DO   (* mortality according to Shugart (1984) *)
            IF ( U() <= kDeathP/p.kAm ) OR
               ( (FLOAT(slowGrowth) >= kSlowGrYrs) AND (U() <= kSlowGrP) ) THEN
              DEC(nrTrees);
            END;
          END;
          CalculateLitterProduction( sp, cohort, FLOAT(cohortTrees-nrTrees) );
          IF nrTrees = 0 THEN
            DeleteCohort( firstCohort, cohort, prevCohort );
          ELSE (* this cohort can grow *)

            (* calculate light multiplier for this cohort; Botkin et al. (1972),
               Shugart & West (1977); for light attenuation see Monsi & Saeki (1953) *)
            iHT := TRUNC( gH - 137.0 ) DIV 10;
            gAL := Exp( -kLAtt*cumLA[iHT] );
            gL9 := 2.24*( 1.0 - Exp( -1.136*(gAL - 0.08) ) );
            gL1 :=        1.0 - Exp( -4.64 *(gAL - 0.05) );
            slope := (gL9 - gL1) / 8.0;
            gALGF := Rmax( gL1 + FLOAT(p.kLa - 1)*slope, 0.0 );

            (* calculate maximum ring width: Moore (1989) *)
            DIncMax  := p.kG * D * (1.0 - gH/p.kHm)
                      / (274.0 + 3.0*p.kB2*D - 4.0*p.kB3*D*D);

            (* calculate growth factor and reduce diameter increment *)
            gF := Power( gALGF*gSMGF*gDDGF*gSNGF, 0.333 );
            DInc := DIncMax * gF;

            (* update variables for calculating limiting factor statistics *)
            sumALGF := sumALGF + gALGF;
            sumSMGF := sumSMGF + gSMGF;
            sumDDGF := sumDDGF + gDDGF;
            sumSNGF := sumSNGF + gSNGF;
            sumGF := sumGF + gF;
            INC( limCounter[7] );   (* increment loop counter *)

            (* check if increment is less than required for growth: Kienast (1987),
               Solomon & Bartlein (1993) *)
            IF (DInc < kMinAbsInc) OR (DInc < kMinRelInc*DIncMax) THEN INC(slowGrowth);
            ELSE slowGrowth := 0 END;

            prevCohort := cohort;
            cohort := cohort^.next;
          END; (* IF *)
        END; (* WITH  cohort *)
      END; (* WHILE cohort *)
    END; (* WITH sp *)
    sp := sp^.next;
  END; (* WHILE sp *)
END TreeDeathAndGrowth;
```

```
(*********************************)
(*  Procedure TreeEstablishment  *)
(*********************************)

PROCEDURE TreeEstablishment( VAR firstSp: SpeciesPtr;
                               uWiT: REAL; uDD, gLAI, totalTrees, kPatchSize: REAL );
  VAR sp: SpeciesPtr;
      nrNewTrees: INTEGER;
      gAL, kThres, totTrees, browsU, gBirthNr, time: REAL;
      gWFlag, gLFlag, gBFlag, gDFlag, gIFlag, birthOK: BOOLEAN;
BEGIN
  gBirthNr := FLOAT( TRUNC(kEstNr*kPatchSize + 0.5) );
  gAL      := Exp( -kLAtt*gLAI );   (* available light on forest floor *)
  totTrees := totalTrees;
  time     := CurrentTime();

  browsU := U();    (* random number for browsing *)
  sp := firstSp;
  WHILE sp <> NIL DO
    WITH sp^ DO
      (* criterion 1: winter temperature (Woodward 1987, 1988, Prentice &
         Helmisaari 1991) *)
      gWFlag := uWiT  < p.kWiT;
      IF gWFlag THEN INC( limCounter[1] ) END;

      (* criterion 2: available light on forest floor (Ellenberg 1986) *)
      IF p.kLy < 5 THEN kThres := 0.025*FLOAT(p.kLy - 1);
      ELSE              kThres := 0.1*FLOAT(p.kLy) - 0.4;
      END;
      gLFlag := gAL < kThres;
      IF gLFlag THEN INC( limCounter[2] ) END;

      (* criterion 3: browsing (Kienast 1987, Dengler 1992) *)
      gBFlag := browsU < FLOAT(p.kBrow-1)*uBrPr/30.0;
      IF gBFlag THEN INC( limCounter[3] ) END;

      (* criterion 4: degree-days (Shugart 1984) *)
      gDFlag := (uDD < p.kDDMin) OR (uDD > p.kDDMax);
      IF gDFlag THEN INC( limCounter[4] ) END;

      (* criterion 5: immigration of species *)
      gIFlag := time < p.kImmYr;

      (* check if birth is inhibited *)
      birthOK := NOT gWFlag AND NOT gLFlag AND NOT gBFlag AND
                 NOT gDFlag AND NOT gIFlag;

      (* establish saplings if establishment is possible *)
      IF birthOK AND (U() < kEstP ) THEN
        nrNewTrees := TRUNC( U()*gBirthNr ) + 1;    (* determine number of trees *)
        IF (gLAI < 1.0) AND (firstNewCohort <> NIL) THEN
          firstNewCohort^.nrTrees := firstNewCohort^.nrTrees + nrNewTrees;
        ELSE
          CreateCohort( firstNewCohort, kInitDBH, nrNewTrees );
        END; (* IF *)
        totTrees := totTrees + FLOAT( nrNewTrees );
      ELSE
        INC( limCounter[5] );   (* count number of birth inhibitions *)
      END; (* IF *)
      INC( limCounter[6] );     (* count number of loops *)
    END; (* WITH *)
    sp := sp^.next;
  END; (* WHILE *)
END TreeEstablishment;


(************************)
(*  Procedure UpdateGap  *)
(************************)

PROCEDURE UpdateGap( VAR firstSp: SpeciesPtr; uDD, uDrStr: REAL );
  VAR sp: SpeciesPtr;
      cohort: CohortPtr;
      t, DInc: REAL;
BEGIN
  t := CurrentTime();
  sp := firstSp;
  WHILE sp <> NIL DO
    WITH sp^ DO
      cohort := firstCohort;
      WHILE cohort <> NIL DO
        cohort^.D := cohort^.D + cohort^.DInc;
        IF mon.monTreeRings THEN
          DInc := cohort^.DInc * 5.0;
            (* corresponds to /2 *10; ring width is half of diameter increment and is
               converted from cm to mm *)
          WriteTreeRings( sp, t, cohort^.nrOfCohort, DInc, uDD, uDrStr );
        END; (* IF *)
        INC(cohort^.age);
        cohort := cohort^.next;
      END;
    END; (* WITH *)
    MergeCohorts( sp );
    sp := sp^.next;
  END; (* WHILE *)
END UpdateGap;

BEGIN
  kFRT[deciduous]  := 1.0;
  kFRT[coniferous] := 5.0;  (* Bossel et al. 1985 *)
END FCPDynamic.
```

Module FCPGrFact

```
DEFINITION MODULE FCPGrFact;

  (****************************************

    Module  FCPGrFact     (Version 2.4)

              Copyright ©1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2   (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Provides growth factors for the ForClim-P model

      Programming

          • Design
              H. Bugmann         18.1.1991

          • Implementation
              H. Bugmann         18.1.1991


          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  14.1.1993  hb

  ****************************************)

FROM FCPBase IMPORT SpeciesPtr;


CONST maxHeight = 600;  (* in units of 10 cm, i.e. 60 m *)

  PROCEDURE SoilNitrogenGrowthFactor( VAR sp: SpeciesPtr; uAvN: REAL );

  PROCEDURE DegreeDayGrowthFactor( VAR sp: SpeciesPtr; uDD: REAL );

  PROCEDURE DroughtGrowthFactor( VAR sp: SpeciesPtr; uDrStr: REAL );

  PROCEDURE StandCharacteristics( VAR totalTrees, totalBiomass, gLAI: REAL;
                              VAR cumLA: ARRAY OF REAL; firstSp: SpeciesPtr );
END FCPGrFact.
```

```
IMPLEMENTATION MODULE FCPGrFact;

  (*
        Implementation and Revisions:
        ============================

        Author  Date        Description
        ------  ----        -----------

        hb      21. 3.1991  First implementation (V0.1, DM 2.02, MacMETH 2.6.2)
        hb      13. 8.1992  Adaptation for V2.0 (growth factors removed)
        hb       6.11.1992  Calculation of leaf weight changed (Burger data)
        hb      14. 1.1993  adapted for SNGF

  *)


FROM ForestBase   IMPORT kPatchSize, Rmax;

FROM FCPBase      IMPORT SpeciesPtr, CohortPtr;

FROM SYSTEM       IMPORT Exp, Ln, Sqrt;


VAR kN1, kN2: ARRAY [1..3] OF REAL;


PROCEDURE SoilNitrogenGrowthFactor( VAR sp: SpeciesPtr; uAvN: REAL );
  (* Mitchell & Chandler (1939), Aber et al. (1979), Pastor & Post (1985) *)

  VAR tol: INTEGER;
BEGIN
  tol := sp^.p.kNTol;
  sp^.gSNGF := Rmax( 1.0 - Exp( kN1[tol]*(uAvN-kN2[tol]) ) , 0.0 );
END SoilNitrogenGrowthFactor;


PROCEDURE DegreeDayGrowthFactor( VAR sp: SpeciesPtr; uDD: REAL );
  (* Hellmers (1962), Botkin et al. (1972), Shugart (1984),  Woodward (1987) *)

BEGIN
  WITH sp^ DO
    gDDGF := 4.0*(uDD-p.kDDMin)*(p.kDDMax-uDD)
             / ((p.kDDMax-p.kDDMin)*(p.kDDMax-p.kDDMin));
    gDDGF := Rmax( 0.0, gDDGF );
  END;
END DegreeDayGrowthFactor;


PROCEDURE DroughtGrowthFactor( VAR sp: SpeciesPtr; uDrStress: REAL );
  (* Bassett (1964), Prentice & Helmisaari (1991) *)

  VAR d: REAL;
```

```
BEGIN
  WITH sp^ DO
    d := Rmax( uDrStress, p.kDrT );
    gSMGF := Sqrt( 1.0 - uDrStress/d );
  END;
END DroughtGrowthFactor;


PROCEDURE StandCharacteristics( VAR totalTrees, totalBiomass, gLAI: REAL;
                            VAR cumLA: ARRAY OF REAL; firstSp: SpeciesPtr );
  CONST kB1 = 137.0;    (* diameter at breast height *)
  VAR sp: SpeciesPtr;
    cohort: CohortPtr;
    gFolA: REAL;
    i, iHT: INTEGER;
BEGIN
  totalBiomass := 0.0;
  totalTrees   := 0.0;

  (* initialize canopy leaf biomass profile *)
  FOR i:= 0 TO maxHeight-1 DO cumLA[i] := 0.0 END;

  (* calculate stemwood & foliage biomass and leaf area *)
  sp := firstSp;
  WHILE sp <> NIL DO
    WITH sp^ DO
      biomass := 0.0;
      nrTrees := 0.0;

      cohort := firstCohort;
      WHILE cohort <> NIL DO
        nrTrees := nrTrees + FLOAT(cohort^.nrTrees);
        WITH cohort^ DO
          (* dry stemwood biomass after Sollins et al. (1973), Burger (1945-53),
             Woods et al. (1991) *)
          gSBio := 0.12 * Exp( 2.4*Ln(D) );

          (* dry foliage biomass, leaf area and tree height after Burger (1945-53) *)
          gFolW := p.kA1 * Exp( p.kA2*Ln(D) ) * p.kC1;
          gFolA := p.kC2 * gFolW / p.kC1;
          gH    := kB1 + p.kB2*D - p.kB3*D*D;

          (* sum leaf area for all trees of similar height *)
          iHT := TRUNC( gH - kB1 ) DIV 10;
          cumLA[iHT] := cumLA[iHT] + gFolA*FLOAT(nrTrees);

          (* calculate species-specific biomass *)
          biomass := biomass + (gSBio+gFolW)*FLOAT(nrTrees);
        END; (* WITH *)
        cohort := cohort^.next;
      END; (* WHILE *)
      totalBiomass := totalBiomass + biomass;
      totalTrees := totalTrees + nrTrees;

      sp := sp^.next;
    END; (* WITH *)
  END; (* WHILE *)

  (* calculate cumulative leaf area index and leaf area index at forest floor*)
  FOR i:= maxHeight - 2 TO 0 BY -1 DO
    cumLA[i] := cumLA[i] + cumLA [i+1];
    cumLA[i+1] := cumLA[i+1] / kPatchSize;
  END; (* FOR *)
  cumLA[0] := cumLA[0] / kPatchSize;
  gLAI := cumLA[0];
END StandCharacteristics;

BEGIN
  (* initialize soil nitrogen multiplier parameters (Aber et al. 1979 as modified
     by Pastor & Post 1985) *)
  kN1[1] := -0.016; kN2[1] :=  2.245;
  kN1[2] := -0.022; kN2[2] := 30.605;
  kN1[3] := -0.016; kN2[3] := 43.973;
END FCPGrFact.
```

Definition module FCPMon

```
DEFINITION MODULE FCPMon;

  (****************************************

    Module  FCPMon     (Version 2.4)

              Copyright ©1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2  (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Monitoring of tree-ring chronologies and of tree frequency
              distributions in the ForClim-P model; animation of tree growth

      Programming

          • Design
              H. Bugmann         19.4.1991

          • Implementation
              H. Bugmann         19.4.1991


          Swiss Federal Institute of Technology Zurich ETHZ
```

```
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  15.4.1993  hb

  ****************************************)

  FROM FCPBase   IMPORT SpeciesPtr;


  PROCEDURE HistogramMonitoring;
  PROCEDURE ChooseSpeciesForHistograms;

  PROCEDURE AnimationMonitoring;
  PROCEDURE MakeAnimationWindow; (* if the window exists, it is brought to front *)

  PROCEDURE WriteTreeRings( VAR sp: SpeciesPtr; VAR year: REAL; VAR nr: INTEGER;
                          VAR rw, DD, DrStress: REAL );
  PROCEDURE ChooseSpeciesForTreeRings( site: ARRAY OF CHAR );
  PROCEDURE CloseTreeRingFile;

END FCPMon.
```

The code of the implementation module FCPMon is available upon request from the author.

Definition module FCPFileIO

```
DEFINITION MODULE FCPFileIO;

  (****************************************

    Module  FCPFileIO     (Version 2.4)

              Copyright ©1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2   (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Management of file input/output for the FORCLIM-P Model

      Programming

          • Design
              H. Bugmann        18.1.1991

          • Implementation
              H. Bugmann        18.1.1991


          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  17.12.1992  hb

  ****************************************)

FROM FCPBase     IMPORT SpeciesPtr;


CONST undefSeed = -9999;


VAR
  PROCEDURE DeclAllometricParameters;   (* ModelWorks declaration of kC1 and kC2 *)
  PROCEDURE AssignAllometricParameters; (* assignment of above parameters to the species *)
  PROCEDURE AssignMonitoringAttributes;

  PROCEDURE ReadSpeciesFile( VAR firstSp: SpeciesPtr; name: ARRAY OF CHAR;
                             VAR ok: BOOLEAN );

  PROCEDURE CalcAndWriteLimFactorsToFile( fn: ARRAY OF CHAR;
                                          VAR firstSp: SpeciesPtr );
    (* If fn[0] = 0C is passed to the procedure, a dialog box is produced for
       entering the destination file name; if a file name is passed, this
       file is written without dialog, which allows for batch mode in experiments *)

  PROCEDURE DumpStateToFile( VAR ok: BOOLEAN; t, x0, y0, z0: INTEGER; site,
                             fn: ARRAY OF CHAR );
  PROCEDURE ReadStateFromFile( VAR ok: BOOLEAN; VAR x0, y0, z0: INTEGER;
                              fn: ARRAY OF CHAR );

END FCPFileIO.
```

The code of the implementation module FCPFileIO is available upon request from the author.

Definition module FCPBase

```
DEFINITION MODULE FCPBase;

  (****************************************

    Module  FCPBase     (Version 2.4)

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              Federal Institute of Technology Zürich ETHZ

      Version written for:
              'Dialog Machine' DM_V2.2   (User interface)
              MacMETH_V3.2.1    (1-Pass Modula-2 implementation)
              ModelWorks_V2.2   (Modelling & Simulation)

      Purpose Data and list base for the FORCLIM-P Model

      Programming

          • Design
              H. Bugmann         10.1.1991

          • Implementation
              H. Bugmann         10.1.1991


          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  17.12.1992  hb

  ****************************************)

FROM SimBase      IMPORT Model, Graphing;
FROM DMWindows    IMPORT Window, RectArea;
FROM Histograms   IMPORT Histogram;
FROM StochStat    IMPORT StatArray;


TYPE
  SpeciesType = (deciduous, coniferous);

  SpeciesPtr = POINTER TO SpeciesNode;
  CohortPtr  = POINTER TO CohortNode;

  Monitoring = RECORD
    drawHisto, monTreeRings: BOOLEAN;
    histogram: Histogram;
    histoW: Window;
    freq: ARRAY [1..30] OF INTEGER;
    graphBio, graphNr: Graphing;
    resID: INTEGER;
  END;

  CohortNode = RECORD
    D,              (* diameter at breast height, cm *)
    gH,             (* tree height, cm *)
    DInc,           (* this year's diameter increment *)
    gSBio,          (* dry stemwood biomass *)
    gFolW,          (* dry foliage biomass *)
    gALGF: REAL;    (* cohort-specific growth factor *)
    age,            (* age of cohort *)
    slowGrowth,
    nrTrees, nrTreesOld: INTEGER; (* the latter is used only for animation *)
    nrOfCohort: INTEGER; (* used for tree-ring monitoring *)
    animXPos: ARRAY [1..5] OF REAL; (* random positions of trees *)
    oldRect: ARRAY [1..5] OF RectArea; (* for previous animated picture *)
    next: CohortPtr;
  END;

  Parameters = RECORD       (* species parameters *)
    kDm,    kHm,    kAm,     kB2,    kB3,    kG,
    kDDMin, kDDMax, kWiT,    kDrT,   kImmYr,
    kA1,    kA2,    kC1,     kC2              : REAL;
    kBrow,  kLy,    kLa,     kNTol,  kLQ      : INTEGER;
  END;

  SpeciesNode = RECORD
    name,                                   (* name & descriptors of the species *)
    longDescBio,  longDescNr : ARRAY [0..31] OF CHAR;
    shortDescBio, shortDescNr: ARRAY [0..5] OF CHAR;

    gDDGF, gSMGF, gSNGF,                    (* species-specific growth factors *)
    nrTrees, biomass, meanBio, meanNr,

    sumALGF, sumDDGF, sumSMGF, sumSNGF,
    sumGF: REAL;                            (* summation for average gFs *)
    limCounter: ARRAY [1..7] OF LONGINT;    (* counters for birth & growth limitation *)

    mon: Monitoring;                        (* histogram monitoring *)
    specSelected: BOOLEAN;                  (* selection in species list *)
    statArrB, statArrN: StatArray;          (* for calculation of statistics *)

    firstCohort, firstNewCohort: CohortPtr;
    next: SpeciesPtr;                       (* pointers for list management *)

    specType: SpeciesType;
    p, dfltP: Parameters;
  END;

VAR
  firstSp: SpeciesPtr;
  gLAI,    totalBiomass, totalTrees,
  meanLAI, meanTotBio,   meanTotNr : REAL;
  animationOn: BOOLEAN;
```

```
  littW,        (* woody litter *)
  littT,        (* twig litter *)
  littR: REAL;  (* root litter *)
  littF: ARRAY [1..3] OF REAL;  (* foliage litter *)

  PROCEDURE CreateSpecies( VAR first, newSp: SpeciesPtr );
  PROCEDURE CreateCohort( VAR first: CohortPtr; kInitDBH: REAL; nrTrees: INTEGER );
  PROCEDURE MergeCohorts( VAR sp: SpeciesPtr );

  PROCEDURE DeleteCohort( VAR first, cohort, prevCo: CohortPtr );
  PROCEDURE DeleteAllCohorts( VAR sp: SpeciesPtr );
  PROCEDURE DeleteAllSpecies( VAR first: SpeciesPtr );

  PROCEDURE SelectSpecies( title, checkBoxText: ARRAY OF CHAR;
                           VAR flag, okButtonPressed: BOOLEAN );
    (*
       Produces a modal window with 'title' as the title, a list of the
       currently present species, a check box labelled 'checkBoxText',
       a 'Cancel' and an 'OK' button.
       The selected species are flagged using the boolean variable sp^.specSelected,
       and the variable 'flag' contains the value of the check box.
       All variables should be ignored if okButtonPressed is FALSE!
     *)

  PROCEDURE EditParameters;
    (* produces entry forms where species can be selected and their parameters can
       be edited; allows also to perform a reset of species parameters
     *)
  PROCEDURE ResetSpeciesParameters( sp: SpeciesPtr );
  PROCEDURE ResetAllSpeciesParameters;

END FCPBase.
```

The code of the implementation module FCPBase is available upon request from the author.

Module ForClimS

```
DEFINITION MODULE ForClimS;

  (****************************************

    Module  ForClimS     (Version 2.4)

              Copyright (c) 1994 by Harald Bugmann and Swiss
              Federal Institute of Technology Zürich ETHZ

      Version written for:
              MacMETH_V3.2.1  (1-Pass Modula-2 implementation)

      Purpose Soil organic matter turnover model, adapted from the
              LINKAGES model by Pastor & Post (1985)

      Remarks none

      Programming

          o Design
              hb          23.12.1992

          o Implementation
              hb          23.12.1992


          Swiss Federal Institute of Technology Zurich ETHZ
          CH-8092 Zurich
          Switzerland

          Last revision of definition:  23.12.1992

  ****************************************)


  PROCEDURE DeclForClimS;

  PROCEDURE RemoveForClimS;

END ForClimS.
```

```
IMPLEMENTATION MODULE ForClimS;

  (****************************************

    Model:  ForClim-S

          Copyright ©1992 by Harald Bugmann and Swiss Federal Institute
          of Technology Zurich ETHZ, Department of Environmental Sciences
          Systems Ecology Group
          Grabenstr. 3
          CH-8952 Schlieren/Zurich

      Version written for:
              'Dialog Machine' DM_V2.2  (User interface)
              MacMETH_V3.2              (1-Pass Modula-2 implementation)
              ModelWorks MW_V2.2        (Modelling & Simulation)
```

```
    Purpose Simulation model for soil organic mass & nitrogen dynamics

    Remarks Based on the model by Pastor & Post (1985, 1986)


      Implementation and Revisions:
      ============================

      Author  Date        Description
      ------  ----        -----------

      hb       5. 2.1992   First implementation (DM 2.2, MacMETH 3.2)
      hb       7. 2.1992   Major bugs fixed; rewritten with mass as state var
      hb       9. 2.1992   Rewritten (dynamic lists)
      hb      19. 2.1992    Implementation finished
      hb      23. 3.1992   Model renamed to FORCLIM-S
      hb      23.12.1992   adapted for 6 litter types (usage within ForClim)
                           reverted to mass dynamics instead of mass
      hb       5. 3.1993   adapted for output of statistical data

****************************************)


  FROM SimMaster    IMPORT CurrentSimNr, ExperimentRunning, ExperimentAborted;

  FROM SimBase      IMPORT DeclM, IntegrationMethod, DeclSV, RTCType, DeclP,
                           StashFiling, DeclMV, Tabulation, NoAbout, Graphing,
                           GetGlobSimPars, RemoveM, MDeclared, CurrentTime;

  FROM DMSystem     IMPORT CurrentDMLevel, InstallTermProc;

  FROM DMMenus      IMPORT Command, AccessStatus, Marking, Separator, InstallCommand,
                           DisableCommand, EnableCommand, InstallSeparator,
                           RemoveSeparatorAtCommand, RemoveCommand, SeparatorPosition;

  FROM DMEntryForms IMPORT FormFrame, WriteLabel, RadioButtonID,
                           DefineRadioButtonSet, RadioButton, CheckBox, UseEntryForm;

  FROM DMMessages   IMPORT Warn, Abort;

  FROM DMStorage    IMPORT Allocate, Deallocate;

  FROM ForestBase   IMPORT fs, Litter, uLitt, uAvN, uAET, DeclConstSoil,
                           RemoveConstSoil, fMenu, exp, ExperimentType,
                           DeclStatArrayForOutput, DeclMonitoringProc,
                           RemoveMonitoringProc, Rmax, Rmin;

  FROM StochStat    IMPORT StatArray, Prob2Tail, DeclStatArray, notExistingStatArray,
                           DeclDispMV, DisplayArray, PutValue;

  FROM SimGraphUtils IMPORT timeIsIndep;


CONST
  modIdent = "ForClim-S";
  modDescr = "ForClim-S: Soil C/N turnover model";

TYPE
  LitterPtr = POINTER TO LitterNode;
  LitterNode = RECORD
                 LOM,                 (* litter organic matter *)
                 LOMNew,
                 LOMinit,             (* initial LOM *)
                 LN,                  (* litter nitrogen *)
                 LNNew,
                 gLign     : REAL;    (* lignin content *)
                 type: Litter;        (* litter type *)
                 next: LitterPtr;     (* pointer for list management *)
               END;

VAR
  startupLevel: CARDINAL;
  first, prev: LitterPtr;
  type: Litter;

  statArrAvN, statArrLitM, statArrHumM : StatArray;

  kInitN, kCritN: ARRAY [ MIN(Litter) .. MAX(Litter) ] OF REAL;
  kNC, kLignA, kLignB,
  gNMR, decMlt, kAET, kMin,
  k1, k2, k3, k4, k5, k6, mLoss, kLeach, litterM, litterN, totSOM,
  litterCO2, gLNC, gAETM, humusNMin, HOM, HOMNew, humCN,
  HN, HNNew, gImmob, totCO2, totNimmob, totNMin, kNAtm,

  meanAvN, meanLitM, meanHumM,

  tzero, hm: REAL;

  ok, allTypes, everyYear: BOOLEAN;

  fcsCmd, litterCmd: Command;


PROCEDURE EmptyProc; BEGIN END EmptyProc;


(************************************)
(*  Procedures for list management  *)
(************************************)

PROCEDURE CreateLitterCohort( VAR first: LitterPtr; m: REAL;
                              type: Litter );
  VAR litter: LitterPtr;
BEGIN
  Allocate( litter, SIZE(LitterNode) );
  IF litter = NIL THEN Abort( "", "Insufficient memory!", "" ) END;
  litter^.next := first;
  litter^.LOM := m;
  litter^.LOMNew := m;
  litter^.LOMinit := m;
```

```
  litter^.LN := kInitN[type] * m;
  litter^.LNNew := kInitN[type] * m;
  litter^.gLign := kLignA + kLignB;
  litter^.type := type;
  first := litter;
END CreateLitterCohort;


PROCEDURE DeleteLitterCohort( VAR first, cohort, prev: LitterPtr );
  (* for efficiency reasons, cohort = NIL is not tested *)
BEGIN
  IF prev = NIL THEN (* first element to be deleted *)
    first := cohort^.next;
    Deallocate( cohort );
    cohort := first;
  ELSE
    prev^.next := cohort^.next;
    Deallocate( cohort );
    cohort := prev^.next;
  END;
END DeleteLitterCohort;


PROCEDURE DeleteAllCohorts( VAR first: LitterPtr );
  VAR coh: LitterPtr;
BEGIN
  coh := first;
  WHILE coh <> NIL DO
    first := coh^.next;
    Deallocate( coh );
    coh := first;
  END; (* WHILE *)
END DeleteAllCohorts;


(*****************************************************)
(*  Procedures for decomposition and mineralization  *)
(*****************************************************)

PROCEDURE TransferLitterToHumus( VAR litter: LitterPtr );
BEGIN
  HNNew  := HNNew + litter^.LNNew;
  HOMNew := HOMNew + litter^.LOMNew;
  DeleteLitterCohort( first, litter, prev );
END TransferLitterToHumus;


PROCEDURE Immobilization;
  VAR lignToN, litMDelta, gLeach: REAL;
    litter: LitterPtr;
BEGIN
  prev := NIL;
  litter := first;
  WHILE litter <> NIL DO
    WITH litter^ DO

      IF (type = wood) OR (type = twigs) THEN
        IF type = wood THEN mLoss := 0.03;
        ELSE mLoss := 0.2;
        END;
        litMDelta := mLoss * LOM;
        gImmob    := kNC * litMDelta;        (* nitrogen immobilization *)
        litterCO2 := litMDelta;              (* CO2 evolution from litter *)
        totCO2    := totCO2 + litterCO2;

        LOMNew    := LOM - litMDelta;        (* update state variables *)
        LNNew     := LN + gImmob;            (* no nitrogen leaching *)
        totNimmob := totNimmob + gImmob;     (* net N immobilization *)
        gNMR      := (LN + gImmob) / (LOM - litMDelta); (* new nitrogen conc. *)
      ELSE
        gLeach    := kLeach * LN;            (* nitrogen leaching *)
        gNMR      := LN / LOM;               (* nitrogen concentration *)
        gLign     := kLignA + kLignB * LOM/LOMinit;
        lignToN   := gLign/gNMR;

        IF lignToN > k2/k4 THEN
          lignToN := k2/k4; (* avoid unreasonable decomposition *)
          Warn( "", "Lignin:N ratio is unrealistically high!", "" );
        END;

        mLoss := ( k1 + k2*uAET - (k3 + k4*uAET)*lignToN )/100.0 * decMlt;
        IF mLoss < 0.0 THEN Warn("","Negative decomposition!","") END;

        litMDelta := mLoss * LOM;             (* LOM change *)
        gImmob    := kNC * litMDelta;         (* nitrogen immobilization *)
        gNMR      := (LN - gLeach + gImmob) / (LOM-litMDelta); (* new N conc. *)

        IF gNMR >= kCritN[type] THEN          (* recalculate weight loss *)
          mLoss := (kCritN[type] - LN/LOM)
                   / (gNMR       - LN/LOM) * mLoss;
          litMDelta := mLoss * LOM;
          gImmob := kNC * litMDelta;          (* nitrogen immobilization *)
        END;

        litterCO2 := litMDelta;               (* CO2 evolution from litter *)
        totCO2    := totCO2 + litterCO2;

        LOMNew    := LOM - litMDelta;        (* state variables *)
        LNNew     := LN - gLeach + gImmob;

        totNimmob := totNimmob - gLeach + gImmob; (* net N immobilization *)
      END;

      IF gNMR >= kCritN[type] THEN
        TransferLitterToHumus( litter );
      ELSE
        prev := litter;           (* pointer management *)
        litter := litter^.next;
      END;
    END; (* WITH *)
  END; (* WHILE *)
```

```
END Immobilization;


PROCEDURE Mineralization;
  VAR humMDelta: REAL;
BEGIN
  IF HOM <> 0.0 THEN
    gAETM := Rmin( uAET / (kAET-uAET), 1.0 );

    IF gLNC <> 0.0 THEN
      (* new formulation based on data in Pastor et al. (1984), avoids occurrence
         of mineralization values of ±∞ (pole in Pastor & Post formulation *)
      humusNMin := Rmax( k5 + k6/gLNC, 0.0005 ) * decMlt * gAETM * HOM;
    ELSE
      humusNMin := HN * kMin * decMlt * gAETM;
    END; (* IF *)

    HNNew   := HN - humusNMin;
    humMDelta := HOM * humusNMin / HN;
    IF HOM < humMDelta THEN HALT END;
    HOMNew  := HOM - humMDelta;
    totCO2  := totCO2 + humMDelta;
    totNMin := totNMin + humusNMin;
  ELSE
    HOMNew  := 0.0;
    HNNew   := 0.0;
  END; (* IF *)
END Mineralization;


(*****************************)
(*  Monitoring & statistics  *)
(*****************************)

PROCEDURE DeclareStatArrays( arrLen : INTEGER );
BEGIN
  statArrAvN := notExistingStatArray;
  DeclStatArray( statArrAvN, arrLen );
  DeclDispMV( statArrAvN, fs, meanAvN, fs, timeIsIndep );
  DeclStatArrayForOutput( statArrAvN, "Available nitrogen", "kg/ha", 0.0 );

  statArrLitM := notExistingStatArray;
  DeclStatArray( statArrLitM, arrLen );
  DeclDispMV( statArrLitM, fs, meanLitM, fs, timeIsIndep );
  DeclStatArrayForOutput( statArrLitM, "Litter mass", "t/ha", 0.0 );

  statArrHumM := notExistingStatArray;
  DeclStatArray( statArrHumM, arrLen );
  DeclDispMV( statArrHumM, fs, meanHumM, fs, timeIsIndep );
  DeclStatArrayForOutput( statArrHumM, "Humus mass", "t/ha", 0.0 );
END DeclareStatArrays;


PROCEDURE DisplayStatArrays;
BEGIN
  IF NOT ExperimentAborted() THEN
    DisplayArray( statArrAvN,  TRUE, prob950 );
    DisplayArray( statArrLitM, TRUE, prob950 );
    DisplayArray( statArrHumM, TRUE, prob950 );
  END;
END DisplayStatArrays;


PROCEDURE Monitoring;
  VAR t: REAL;
    index: INTEGER;
BEGIN
  IF ExperimentRunning() THEN
    IF exp.type = estimEquil THEN
      t := 0.0;
      index := 1;
    ELSE
      t := CurrentTime();
      index := TRUNC( (t-tzero)/hm + 0.5 ) + 1;
    END;

    IF NOT ((exp.type = estimEquil) AND (CurrentTime() <= exp.startYear )) THEN
      PutValue( statArrAvN,  index, t, uAvN );
      PutValue( statArrLitM, index, t, litterM );
      PutValue( statArrHumM, index, t, HOM );
    END; (* IF *)
  END; (* IF *)
END Monitoring;


PROCEDURE UpdateLitterCohorts;
  VAR litter: LitterPtr;
BEGIN
  litter := first;
  WHILE litter <> NIL DO
    litter^.LOM := litter^.LOMNew;
    litter^.LN  := litter^.LNNew;
    litter := litter^.next;
  END;
END UpdateLitterCohorts;


(*************************************************)
(*  ModelWorks procedures Initialize - Terminate  *)
(*************************************************)

PROCEDURE Initialize;
  VAR i: Litter;
    tend, h, c, er: REAL;
    arrLen: INTEGER;

  PROCEDURE CalculateLigninParameters;
  BEGIN
    kLignA := 0.4929  + 19.1784 * kNC;
    kLignB := 0.01558 -  0.673  * kLignA;
  END CalculateLigninParameters;
```

```
BEGIN
  DisableCommand( fMenu, litterCmd );

  IF ExperimentRunning() AND (CurrentSimNr() = 1 ) THEN
    IF exp.type = manyRuns THEN
      GetGlobSimPars(tzero, tend, h, er, c , hm);
      arrLen := TRUNC((tend-tzero)/hm+1.5);
      DeclareStatArrays( arrLen );
    ELSIF exp.type = estimEquil THEN
      DeclareStatArrays( 1 );
    ELSE
      (* do nothing *)
    END;
  END;

  CalculateLigninParameters;
  DeleteAllCohorts( first );
  IF NOT everyYear THEN
    IF allTypes THEN
      FOR i:= MIN(Litter) TO MAX(Litter) DO
        IF uLitt[i] <> 0.0 THEN CreateLitterCohort( first, uLitt[i], i )  END;
      END; (* FOR *)
    ELSE
      CreateLitterCohort( first, uLitt[type], type )
    END;
  END;
END Initialize;


PROCEDURE Input;
  VAR litter: LitterPtr;
    i: Litter;
BEGIN
  IF everyYear THEN
    IF allTypes THEN
      FOR i:= MIN(Litter) TO MAX(Litter) DO
        IF uLitt[i] <> 0.0 THEN CreateLitterCohort( first, uLitt[i], i )  END;
      END; (* FOR *)
    ELSE
      CreateLitterCohort( first, uLitt[type], type );
    END;
  END;

  totCO2 := 0.0;
  totNimmob := 0.0;
  totNMin := 0.0;

  litterM := 0.0;
  litterN := 0.0;
  litter := first;
  WHILE litter <> NIL DO (* summation of total leaf litter *)
    WITH litter^ DO
      IF (type = leafFast) OR (type = leafMedium) OR (type = leafSlow) THEN
        litterM := litterM + LOM;
        litterN := litterN + LN;
      END;
    END; (* WHILE *)
    litter := litter^.next;
  END; (* WHILE *)
  IF litterM <> 0.0 THEN gLNC := litterN / litterM / 0.48;
  ELSE gLNC := 0.0;
  END; (* IF *)

  litterM := 0.0;
  litterN := 0.0;
  litter := first;
  WHILE litter <> NIL DO (* summation of total litter *)
    WITH litter^ DO
      litterM := litterM + LOM;
      litterN := litterN + LN;
    END; (* WHILE *)
    litter := litter^.next;
  END; (* WHILE *)

  totSOM := litterM + HOM;     (* total soil organic matter *)
END Input;


PROCEDURE Dynamic;
BEGIN
  Mineralization;
  Immobilization;
  uAvN := kNAtm + Rmax(totNMin - totNimmob, 0.0) * 1000.0;
END Dynamic;


PROCEDURE Output;
BEGIN
  UpdateLitterCohorts;
END Output;


PROCEDURE Terminate;
BEGIN
  DeleteAllCohorts( first );

  IF ( (CurrentSimNr() MOD TRUNC(exp.nrRuns+0.5)) = 0 )
    AND ExperimentRunning() AND (exp.type = manyRuns) THEN
    DisplayStatArrays;
  END;

  EnableCommand( fMenu, litterCmd );
END Terminate;


(******************)
(*  Menu command  *)
(******************)

PROCEDURE LitterInput;
```

```
  CONST lem = 3;
  VAR ef: FormFrame;
    ok: BOOLEAN;
    cl: INTEGER;
    button: ARRAY [MIN(Litter)..MAX(Litter)] OF RadioButtonID;
    allTypesB, selectedbutton: RadioButtonID;
BEGIN
  cl := 2;
  WriteLabel(cl, lem-2, "Select litter type :"); INC(cl);
  DefineRadioButtonSet(selectedbutton);
  IF NOT allTypes THEN selectedbutton := button[type] END;
  RadioButton( allTypesB, cl, lem, "All types"); INC(cl,2);

  RadioButton( button[leafFast], cl, lem, "Fast decaying foliage"); INC(cl);
  RadioButton( button[leafMedium], cl, lem, "Medium decaying foliage"); INC(cl);
  RadioButton( button[leafSlow], cl, lem, "Slowly decaying foliage"); INC(cl);
  RadioButton( button[roots], cl, lem, "Roots"); INC(cl);
  RadioButton( button[twigs], cl, lem, "Twigs"); INC(cl);
  RadioButton( button[wood], cl, lem, "Wood"); INC(cl);
  INC(cl);
  CheckBox( cl, lem, "Every year", everyYear );
  INC(cl);
  ef.x := 0; ef.y := -1; (* display entry form in middle of screen *)
  ef.lines := cl+1; ef.columns := 30;
  UseEntryForm(ef,ok);
  IF ok THEN
    IF selectedbutton = allTypesB THEN allTypes := TRUE;
    ELSE allTypes := FALSE;
    END;

    IF    selectedbutton = button[leafFast]   THEN type := leafFast;
    ELSIF selectedbutton = button[leafMedium] THEN type := leafMedium;
    ELSIF selectedbutton = button[leafSlow]   THEN type := leafSlow;
    ELSIF selectedbutton = button[roots]      THEN type := roots;
    ELSIF selectedbutton = button[twigs]      THEN type := twigs;
    ELSIF selectedbutton = button[wood]       THEN type := wood;
    END; (* IF *)
  END; (* IF *)
END LitterInput;


(*********************************)
(*  Procedure ModelObjects  *)
(*********************************)

PROCEDURE ModelObjects;
  VAR i: Litter;
BEGIN
  DeclSV( HOM, HOMNew, 0.0, 0.0, 100.0,
    'Humus organic matter', 'HOM', 't/ha');
  DeclSV( HN, HNNew, 0.0, 0.0, 10.0,
    'Humus nitrogen', 'HN', 't/ha');

  DeclMV( uAvN, 0.0, 500.0, 'Available nitrogen','uAvN','kg/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( litterM, 0.0, 500.0, 'Litter organic matter','LOM','t/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( litterN, 0.0, 50.0, 'Litter nitrogen','LN','t/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( HOM, 0.0, 500.0, 'Humus organic matter','HOM','t/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( HN, 0.0, 50.0, 'Humus nitrogen','HN','t/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( gLNC, 0.0, 0.05, 'Litter N:C ratio','gLNC','--',
    notOnFile,notInTable,notInGraph);
  DeclMV( humCN, 0.0, 100.0, 'Humus C:N ratio','gHCN','--',
    notOnFile,notInTable,notInGraph);
  DeclMV( totCO2, 0.0, 25.0, 'total C(O2) emission','CO2(tot)','t/ha*yr',
    notOnFile,notInTable,notInGraph);
  DeclMV( totSOM, 0.0, 500.0, 'total soil organic matter','totSOM','t/ha',
    notOnFile,writeInTable,notInGraph);
  DeclMV( meanAvN, 0.0, 500.0, 'average available nitrogen','meanAvN','t/ha',
    notOnFile,notInTable,notInGraph);
  DeclMV( meanLitM, 0.0, 500.0, 'average litter organic matter','meanLOM','t/ha',
    notOnFile,notInTable,notInGraph);
  DeclMV( meanHumM, 0.0, 500.0, 'average humus organic matter','meanHOM ','t/ha',
    notOnFile,notInTable,notInGraph);

  DeclP( kNAtm, 5.0, 0.0, 100.0, rtc,
    'Atmospheric N input',  'kNAtm', 'kg/ha*yr');
  DeclP( kAET, 1200.0, 0.0, 2000.0, rtc,
    'AET multiplier parameter',  'kAET', 'mm/yr');
  DeclP( kMin, 0.035, 0.0, 1.0, rtc,
    'Humus decay in absence of litter', 'kMin', '%');
  DeclP( kLeach, 0.16, 0.0, 1.0, rtc,
    'Leaching from leaf litter',  'kLeach', '%');
  DeclP( decMlt, 1.0, 0.0, 1.0, rtc,
    'Decay multiplier',  'decMlt', '--');
  DeclP( k1, 0.9804, 0.0, 10.0, rtc,
    'Regression parameter',  'k1', '--');
  DeclP( k2, 0.09352, 0.0, 1.0, rtc,
    'Regression parameter',  'k2', '--');
  DeclP( k3, -0.4956, -1.0, 1.0, rtc,
    'Regression parameter',  'k3', '--');
  DeclP( k4, 0.00193, 0.0, 1.0, rtc,
    'Regression parameter',  'k4', '--');
  DeclP( k5, 0.0079702, 0.0, 1.0, rtc,
    'Regression parameter',  'k5', '--');
  DeclP( k6, -1.3173E-4, -1.0, 0.0, rtc,
    'Regression parameter',  'k6', '--');
  DeclP( kNC, 0.005, 0.0, 0.1, rtc,
    'N immobilized per unit weight loss',  'kNC', '--');
  FOR i := MIN(Litter) TO MAX(Litter) DO
    DeclP( kInitN[i], kInitN[i], 0.0, 0.05, rtc,
      'Initial nitrogen percentage',  'kInitN', '%/100');
    DeclP( kCritN[i], kCritN[i], 0.0, 0.1, rtc,
      'Critical N percentage',  'kCritN', '%/100');
  END;
END ModelObjects;
```

```
  (*************************************************)
  (*  Model declaration and module initialization  *)
  (*************************************************)

  PROCEDURE DeclForClimS;
  BEGIN
    IF NOT MDeclared( fs ) THEN
      RemoveConstSoil;
      DeclMonitoringProc( Monitoring );
      DeclM(fs, discreteTime, Initialize, Input, Output, Dynamic, Terminate,
            ModelObjects, modDescr, modIdent, NoAbout);
      InstallSeparator( fMenu, line );
      InstallCommand( fMenu, fcsCmd, "ForClim-S:", EmptyProc,
                      enabled, unchecked );
      InstallCommand( fMenu, litterCmd, "  Litter input…", LitterInput,
                      enabled, unchecked );
    END;
  END DeclForClimS;


  PROCEDURE RemoveForClimS;
  BEGIN
    IF MDeclared( fs ) THEN
      RemoveMonitoringProc( Monitoring );
      RemoveSeparatorAtCommand(fMenu, fcsCmd, beforeCmd );
      RemoveCommand( fMenu, fcsCmd );
      RemoveCommand( fMenu, litterCmd );
      DeleteAllCohorts( first );
      RemoveM( fs );
      DeclConstSoil;
    END;
  END RemoveForClimS;


  PROCEDURE TermProc;
  BEGIN
    IF CurrentDMLevel() = startupLevel THEN
      DeleteAllCohorts( first );
      ok := TRUE;
    END;
  END TermProc;


  PROCEDURE InitModule;
  BEGIN
    first := NIL;
    prev := NIL;
    ok := FALSE;
    allTypes := TRUE;
    everyYear := TRUE;
    startupLevel := CurrentDMLevel();
    InstallTermProc( TermProc, ok );
  END InitModule;


  PROCEDURE InitDecayParameters;
  BEGIN
    kInitN[leafFast]   := 0.016;
    kInitN[leafMedium] := 0.01;
    kInitN[leafSlow]   := 0.006;
    kInitN[twigs]      := 0.003;
    kInitN[roots]      := 0.0093;
    kInitN[wood]       := 0.003;

    kCritN[leafFast]   := 0.02;
    kCritN[leafMedium] := 0.017;
    kCritN[leafSlow]   := 0.015;
    kCritN[twigs]      := 0.009;
    kCritN[roots]      := 0.015;
    kCritN[wood]       := 0.02;
  END InitDecayParameters;


BEGIN
  InitModule;
  InitDecayParameters;
END ForClimS.
```

Definition module ForestBase

At the startup of the module ForestBase, a text file with the default name “Bern.DAT” is read. It contains the site-specific parameters (kFC, kSlAsp, and 60 monthly climatic parameters: μ(T), σ(T), μ(P), σ(P), and r, cf. Tab. A-14). If this file can not be found, a dialog box is produced where the text file can be selected by the user. For convenience, the file “Bern.DAT” is listed in the following section.

```
DEFINITION MODULE ForestBase;

  (****************************************

    Module  ForestBase     (Version 2.4)

            Copyright (c) 1994 by Harald Bugmann and Swiss
            Federal Institute of Technology Zürich ETHZ

      Version written for:
            MacMETH_V3.2.1  (1-Pass Modula-2 implementation)
```

```
    Purpose Provides the basis for the ForClim model system

    Programming

        o Design
            H. Bugmann         16.12.1992

        o Implementation
            H. Bugmann         16.12.1992


        Swiss Federal Institute of Technology Zurich ETHZ
        Department of Environmental Sciences
        Systems Ecology
        Grabenstr. 3
        CH-8952 Schlieren
        Switzerland

        Last revision of definition:  23.9.1993  hb

****************************************)


FROM SimBase       IMPORT Model;
FROM DMMenus       IMPORT Menu, Command;
FROM MultiNormal   IMPORT MultiNDistr;
FROM StochStat     IMPORT StatArray;



VAR
  kPatchSize: REAL;   (* size of a forest patch [m^2] *)



(*****************************)
(*  Objects defining a site  *)
(*****************************)

CONST maxMonSpec = 20; (* maximum number of species variables for monitoring *)


TYPE
  SiteRec = RECORD
    name: ARRAY [1..32] OF CHAR;
    kFC,              (* soil field capacity           [cm]        *)
    kLat,             (* latitude of the site          [°]          *)
    kSlAsp,           (* slope & aspect qualifier      [-2..2]     *)

    (* the following parameters are optional since calculated also by ForClim-E *)
    kDD,              (* average annual degree-days    [°C*days]    *)
    kAET,             (* average annual evapotransp.  [mm]         *)
    kWiT,             (* minimum winter temperature    [°C]         *)
    kDrStr: REAL;     (* average drought stress        [-]         *)
  END; (* RECORD *)


VAR
  site: SiteRec;
  specIdent: ARRAY [1..maxMonSpec],[0..7] OF CHAR; (* for monitoring *)

PROCEDURE SelectSite( fn: ARRAY OF CHAR; VAR ok: BOOLEAN );
  (* reads site data from a text file; the routine tries to open the
     file named 'fn'; if this is not successful or fn is an empty string,
     a dialog box is produced where a file can be selected
   *)

PROCEDURE SetSiteParameters( kFC, kLat, kSlAsp: REAL );
PROCEDURE ResetSiteParameters;
  (* sets / resets the site parameters kFC, kLat & kSlAsp to the values
     assigned the last time SelectSite was called
   *)

PROCEDURE DeclSiteProc( p: PROC );
PROCEDURE RemoveSiteProc( p: PROC );
  (* procedure to be executed every time SelectSite [see above] is executed;
     useful e.g. for updating a model's setup upon switching of sites *)



(***************************************************************)
(*  Objects for defining and manipulating climatic parameters  *)
(***************************************************************)

TYPE
  Month = (Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec);

  Climate = RECORD
              mTVect, sdTVect,    (* T mean, st.dev. *)
              mPVect, sdPVect,    (* P mean, st.dev. *)
              corrVect            (* T,P cross-correl. coeff. *)
              : ARRAY [Jan..Dec] OF REAL;
              mnDistr: ARRAY [Jan..Dec] OF MultiNDistr;
                (* multiple normal distributions for cross-correlations *)
            END(*RECORD*);


PROCEDURE GetMonth(m: Month; VAR name: ARRAY OF CHAR);

PROCEDURE GetCurClimate( VAR cc: Climate );
PROCEDURE SetCurClimate( VAR cc: Climate );
PROCEDURE GetDfltClimate( VAR dc: Climate );
PROCEDURE SetDfltClimate( dc: Climate );
PROCEDURE ResetClimate; (* resets current values to the default *)



(**********************************************************)
(*  Objects used for communication between the submodels  *)
(**********************************************************)
```

```
  TYPE
    Litter = (leafFast, leafMedium, leafSlow, roots, twigs, wood );


  VAR
    (* Variables linking the submodels *)
    (*---------------------------------*)

    (* output of ForClim-E: *)
    uDD,          (* annual sum of degree-days    [°C*days]   *)
    uDrStr,       (* drought stress index         [-]         *)
    uWiT,         (* minimum winter temperature   [°C]        *)
    uAET: REAL;   (* evapotranspiration           [mm/yr]     *)

    (* output of ForClim-P: *)
    uLitt: ARRAY [ MIN(Litter)..MAX(Litter) ] OF REAL;
                  (* litter production            [t/ha]      *)

    (* output of ForClim-S: *)
    uAvN: REAL;   (* available nitrogen           [kg/ha]     *)

    (* output of ForClim-D: *)
    uBrPr: REAL;  (* browsing pressure            [0…10]      *)


    (* The following procedures serve to declare output variables
       as parameters when the corresponding model is not present,
       i.e. the Remove procedure should be called when a model is installed,
       and the Declare procedure when it is removed *)
  PROCEDURE DeclConstEnvironment;    PROCEDURE RemoveConstEnvironment;
  PROCEDURE DeclConstPlants;         PROCEDURE RemoveConstPlants;
  PROCEDURE DeclConstSoil;           PROCEDURE RemoveConstSoil;
  PROCEDURE DeclConstBrowsing;       PROCEDURE RemoveConstBrowsing;



  (********************************************)
  (*  Objects required for technical reasons  *)
  (********************************************)

  TYPE
    ExperimentType = ( manyRuns, estimEquil );

    Experiment = RECORD
      type: ExperimentType;
      writeState, readState,
      inBatchMode, doSensAnalysis: BOOLEAN;
      outFileName, inFileName, batchFileName: ARRAY [0..127] OF CHAR;
      nrPoints, delta: INTEGER; (* for equilibrium estimation *)
      startYear,                (* for equilibrium estimation *)
      nrRuns: REAL;             (* for many runs *)
    END; (* RECORD *)


  VAR
    fe,         (* ForClim-E *)
    fp,         (* ForClim-P *)
    fs: Model;  (* ForClim-S *)

    exp: Experiment;

    fMenu: Menu; (* ForClim menu *)
    configCmd: Command; (* Configure command *)

    FCResFileName: ARRAY [0..63] OF CHAR;


  PROCEDURE Power( base, exp: REAL ): REAL;
    (* straightforward and efficient implementation *)
  PROCEDURE Imax( i1,i2: INTEGER ): INTEGER;
  PROCEDURE Imin( i1,i2: INTEGER ): INTEGER;
  PROCEDURE Rmax( x1,x2: REAL ): REAL;
  PROCEDURE Rmin( x1,x2: REAL ): REAL;


  PROCEDURE SetRandomNumberSeeds( x, y, z: INTEGER );
    (* use this procedure and NOT SetSeeds from RandGen because of consistency
       in the ModelWorks parameter window!
     *)


  PROCEDURE DeclMonitoringProc( p: PROC );
  PROCEDURE RemoveMonitoringProc( p: PROC );
    (* procedure for ModelWorks client monitoring, must be declared here because
       ModelWorks does not support several simultaneous monitoring procedures *)


  PROCEDURE DeclStatArrayForOutput( sa: StatArray; labelStr, unitStr: ARRAY OF CHAR;
                                    minV: REAL );
    (* if the average of sa is below minV, this StatArray is not used for
       displaying the equilibrium estimate *)
  PROCEDURE RemoveStatArrayFromOutput( sa: StatArray );
    (* to declare / remove StatArrays from a list common to all models *)
  PROCEDURE WriteStatArraysToFile( fn: ARRAY OF CHAR );
    (* writes StatArrays declared by means of DeclStatArrayForOutput to a text file *)


  PROCEDURE DisplayEquilibriumValues;
  PROCEDURE SaveEquilibriumState( fn : ARRAY OF CHAR );
    (* if fn is an empty string, a dialog box is produced prompting for the filename *)


  PROCEDURE DeclForestBase;
    (* to be be called by master program *)
END ForestBase.
```

The code of the implementation module ForestBase is available upon request from the author.

Example of a text file containing site-specific data

The site-specific data files (see “Bern.DAT” as an example below) contain the following:

- Three site-specific parameters, i.e. kLat, kFC, and kSlAsp
- Four parameters describing the average output data of FORCLIM-E at the site. These values are used to provide a constant input to the submodels FORCLIM-P and FORCLIM-S when FORCLIM-E is not present (i.e. not declared)
- 60 long-term mean monthly climatic parameters obtained from the Swiss Meteorological Agency (SMA)
- Optionally, the identifiers of those species that are to be displayed on the ordinate in the ModelWorks graph window.

```
Site-specific data frame for the ForClim model
**********************************************

General parameters and output variables for Bern
------------------------------------------------
Latitude of the site [NB]         46.9
Field capacity [cm water]         30
Slope/aspect qualifier [-]         0
Annual degree-days [°C*days]    1933.4
Annual evapotranspiration [mm]   591.9
Minimum winter temperature [°C]   -2.17
Average drought stress [-]         0.023

Climatic parameters (T in °C, P in cm/month)
--------------------------------------------
        Jan     Feb     Mar     Apr     May     Jun     Jul     Aug     Sep     Oct     Nov     Dec
mT      -1.0     0.4     4.2     8.1    12.6    15.8    17.8    17.0    13.8     8.6     3.4     0.2
sdT      2.3     2.5     1.7     1.6     1.6     1.3     1.6     1.3     1.6     1.4     1.5     1.9
mP       5.93    5.39    6.66    7.84   10.13   11.71   11.24   11.38    9.06    7.35    7.33    6.61
sdP      3.33    3.71    3.77    3.82    3.72    4.46    5.14    5.24    4.85    4.75    4.76    3.89
r        0.27    0.37   -0.13   -0.18   -0.33   -0.29   -0.63   -0.47   -0.16   -0.17    0.32    0.43

Variables for monitoring
------------------------
Aalb B
Apse B
Qpet B
Qrob B
Fsil B
Pexc B
```

V. Sensitivity analysis: Species parameters and detailed results

Tab. A-15 & A-16 list the lower and upper end of the plausibility interval of the species parameters, respectively. For some parameters of some species, it was not possible to derive these values because of the following restrictions:

1) For some parameters of a few species, no measure of variability could be derived from the literature (e.g. kDm and kAm of *Pinus montana*)

2) It was not possible to determine plausible uncertainty ranges of the $kWiT_S$ parameter for those species that have no susceptibility to low winter temperature ($kWiT_S$ = N).

3) For parameters whose default value for a given species is already at the lower or upper boundary of the definition range (e.g. sType, kNTol, kBrow, kLy, kLa, kLQ), the sensitivity could not be determined because the definition range of the parameters would have been exceeded

4) For parameters whose default value for a given species is closer to the lower or upper boundary of the definition range than half the size of their plausibility interval (e.g. kLy of *Larix decidua*), the parameter was set to the minimum or maximum of the definition range, respectively.

In the cases 1) to 3) above, no simulation studies were conducted. These cases are marked by empty cells in Tab. A-15 & A-16.

Taking into account the above restrictions, it was possible to derive a lower boundary of the plausibility interval for 364 species parameters and an upper boundary for 368 species parameters (Tab. A-15 & A-16).

Tab. A-17 & A-18 give the percentage similarity coefficients between the steady state species composition of the FORCLIM-E/P/S model with the default parameter set and the steady states as estimated with each of the parameters changed according to Tab. A-15 and A-16, respectively.

In Tab. A-19 & A-120 the change in the biomass of those species whose parameters were lowered or increased are listed. Empty cells denote either missing parameters (cf. Tab. A-15 & A-18) or that no significant change (α = 5%) of the biomass occurred.

Tab. A-15: Lower end of the plausibility interval of the species-specific parameters. Empty cells denote missing values.

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba	C4	150	45	300	81.9	512.8	2694.6	-8	0.08	1	2	1		1
Larix decidua	D1	100	35	300	119	258.4	1395	-13	0.02		1	6	7	2
Picea excelsa	C4	100	36	200	119.7	308	1395		0.001	1	1	3	3	2
Pinus cembra	C4	105	20	600	80.5	258.4	674.4	-13	0.2		2	4	3	2
Pinus montana	C4		15		96.6	348.8	1155		0.2		1	6	7	2
Pinus silvestris	C3	100	35	400	83.3	488	1666.2		0.2		1	5	7	2
Taxus baccata	C4	50	15	1000	32.9	808.8	2694.6	-7	0.14	1	2	2	1	1
Acer campestre	D1	40	9	100	109.2	849.6	2694.6		0.14	1		3	3	1
Acer platanoides	D2	100	20	150	99.4	833.6	2860.8	-19	0.08	1		1	2	1
Acer pseudoplatanus	D2	200	30	350	87.5	718.4	2694.6		0.08	1		1	2	1
Alnus glutinosa	D1	50	19	100	175	718.4	3138	-18	0.001	1	1	3	3	
Alnus incana	D1	40	10	50	186.2	488	2522.4		0.001	1	1	4	5	
Alnus viridis	D1		2.5		371.7	217.6	742.2		0.02	1	1	5	5	
Betula pendula		60	18	100	194.6	488	2793		0.02			5	7	1
Carpinus betulus	D2	50	19	150	123.9	718.4	2793	-11	0.08	1	2	2	1	
Castanea sativa	D2	100	20	600	99.4	989.6	2866.8		0.14		1	3	3	1
Corylus avellana	D2		5	50	66.5	718.4	2793	-19	0.14	1	2	4	4	
Fagus silvatica	D2	150	30	300	133.7	578.4	2793	-6	0.02		2	1		1
Fraxinus excelsior	D1	100	30	250	123.9	784	2694.6	-19	0.02	2	1	2	4	
Populus nigra	D1	127	30	200	199.5	529.6	3243		0.001	2	2	3	3	1
Populus tremula	D1	60	15	100	217	488	2793		0.08		2	4	5	1
Quercus petraea	D2	250	30	500	136.5	628	2793	-7	0.08		1	4	5	1
Quercus pubescens	D2		16		103.6	808.8	2793		0.14	1	1	5	5	1
Quercus robur	D2	200	30	500	136.5	833.6	2793	-19	0.2		1	5	7	1
Salix alba			20	100	194.6	849.6	3243		0.001	2		3	3	1
Sorbus aria	D1	40	12	100	57.4	718.4	3205.8		0.14	1	1	4	5	
Sorbus aucuparia		30	15	90	116.9	398.4	2522.4		0.14		1	4	5	
Tilia cordata	D2	100	22	500	79.8	1071.2	2694.6	-23	0.14	1	1	3	3	1
Tilia platyphyllos	D2	185	30	500	77	1071.2	2694.6		0.08	1	1	2	1	1
Ulmus scabra	D2	100	30	400	107.1	849.6	3138	-18	0.08	2		2	1	

Tab. A-16: Upper end of the plausibility interval of the species-specific parameters. Empty cells denote missing values.

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba		250	65	800	152.1	769.2	6287.4	-4	0.28	3		5	3	3
Larix decidua	D3	200	57	1000	221	387.6	3255	-9	0.22	2	3	9		
Picea excelsa		250	63	1200	222.3	462	3255		0.16	3	3	7	7	
Pinus cembra		200	27	1200	149.5	387.6	1573.6	-9	0.4	2		8	7	
Pinus montana			25		179.4	523.2	2695		0.4	2	3	9		
Pinus silvestris	C5	190	48	900	154.7	732	3887.8		0.4	2	3	9		
Taxus baccata		450	25	2500	61.1	1213.2	6287.4	-3	0.34	3		6	5	3
Acer campestre	D3	95	26	200	202.8	1274.4	6287.4		0.34	3	2	7	7	3
Acer platanoides	D4	190	35	500	184.6	1250.4	6675.2	-15	0.28	3	2	4	6	3
Acer pseudoplatanus	D4	223	40	600	162.5	1077.6	6287.4		0.28	3	2	4	6	3
Alnus glutinosa	D3	180	35	300	325	1077.6	7322	-14	0.16	3	3	7	7	2
Alnus incana	D3	200	25	200	345.8	732	5885.6		0.16	3	3	8	9	2
Alnus viridis	D3		5		690.3	326.4	1731.8		0.22	3	3	9	9	2
Betula pendula	D2	150	31	300	361.4	732	6517		0.22	2	2	9		3
Carpinus betulus	D4	127	30	250	230.1	1077.6	6517	-7	0.28	3		6	5	2
Castanea sativa	D4	410	35	2000	184.6	1484.4	6689.2		0.34	2	3	7	7	3
Corylus avellana	D4		12	80	123.5	1077.6	6517	-15	0.34	3		8	8	2
Fagus silvatica	D4	260	50	500	248.3	867.6	6517	-2	0.22	2		5	3	3
Fraxinus excelsior	D3	220	45	400	230.1	1176	6287.4	-15	0.22		3	6	8	2
Populus nigra	D3	200	40	300	370.5	794.4	7567		0.16			7	7	3
Populus tremula	D3	150	35	160	403	732	6517		0.28	2		8	9	3
Quercus petraea	D4	300	50	1000	253.5	942	6517	-3	0.28	2	3	8	9	3
Quercus pubescens	D4		30		192.4	1213.2	6517		0.34	3	3	9	9	3
Quercus robur	D4	382	60	1200	253.5	1250.4	6517	-15	0.4	2	3	9		3
Salix alba	D2		30	200	361.4	1274.4	7567		0.16		2	7	7	3
Sorbus aria	D3	60	25	200	106.6	1077.6	7480.2		0.34	3	3	8	9	2
Sorbus aucuparia	D2	80	20	120	217.1	597.6	5885.6		0.34	2	3	8	9	2
Tilia cordata	D4	270	32	1000	148.2	1606.8	6287.4	-19	0.34	3	3	7	7	3
Tilia platyphyllos	D4	500	41	1000	143	1606.8	6287.4		0.28	3	3	6	5	3
Ulmus scabra	D4	223	48	500	198.9	1274.4	7322	-14	0.28		2	6	5	2

Tab. A-17: Percentage similarity coefficients (PS) between the conjectured "true" steady state species composition of the ForClim model with default species parameters and the species composition as simulated when setting the species parameters to the lower end of their plausibility interval. The threshold for significant differences ($\alpha = 5\%$) corresponds to PS = 0.871. Empty cells denote missing values (cf. Tab. A-12).

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba	0.770	0.932	0.930	0.732	0.806	0.880	0.893	0.853	0.788	0.789	0.873	0.919		0.885
Larix decidua	0.908	0.882	0.919	0.906	0.895	0.872	0.805	0.906	0.843		0.932	0.885	0.910	0.836
Picea excelsa	0.871	0.877	0.935	0.916	0.829	0.898	0.900		0.807	0.837	0.882	0.924	0.912	0.884
Pinus cembra	0.907	0.882	0.929	0.884	0.941	0.928	0.896	0.934	0.927		0.924	0.958	0.925	0.871
Pinus montana	0.926		0.932		0.921	0.895	0.936		0.913		0.942	0.949	0.897	0.887
Pinus silvestris	0.915	0.933	0.924	0.928	0.953	0.880	0.919		0.872		0.901	0.890	0.885	0.963
Taxus baccata	0.923	0.938	0.925	0.895	0.937	0.922	0.883	0.884	0.913	0.938	0.870	0.943	0.890	0.937
Acer campestre	0.943	0.923	0.929	0.913	0.922	0.906	0.931		0.930	0.880		0.938	0.848	0.954
Acer platanoides	0.960	0.904	0.951	0.933	0.920	0.927	0.880	0.908	0.875	0.932		0.925	0.878	0.919
Acer pseudoplatanus	0.905	0.942	0.908	0.858	0.888	0.907	0.910		0.928	0.888		0.905	0.858	0.909
Alnus glutinosa	0.941	0.900	0.889	0.892	0.946	0.944	0.894	0.900	0.923	0.888	0.919	0.940	0.907	
Alnus incana	0.931	0.935	0.885	0.939	0.942	0.910	0.893		0.954	0.905	0.925	0.917	0.878	
Alnus viridis	0.886		0.902		0.925	0.918	0.971		0.894	0.940	0.921	0.897	0.914	
Betula pendula		0.943	0.896	0.949	0.910	0.935	0.888		0.887			0.929	0.880	0.887
Carpinus betulus	0.919	0.945	0.946	0.910	0.887	0.862	0.905	0.930	0.900	0.906	0.912	0.943	0.944	
Castanea sativa	0.948	0.893	0.967	0.938	0.937	0.879	0.943		0.946		0.933	0.942	0.878	0.940
Corylus avellana	0.945		0.899	0.878	0.960	0.874	0.904	0.890	0.909	0.913	0.924	0.911	0.917	
Fagus silvatica	0.872	0.846	0.770	0.797	0.775	0.895	0.848	0.834	0.641		0.931	0.863		0.966
Fraxinus excelsior	0.970	0.881	0.914	0.898	0.950	0.949	0.917	0.892	0.936	0.902	0.938	0.929	0.929	
Populus nigra	0.949	0.905	0.929	0.894	0.933	0.924	0.926		0.903	0.864	0.887	0.875	0.933	0.906
Populus tremula	0.928	0.956	0.934	0.906	0.880	0.888	0.894		0.918		0.937	0.929	0.920	0.895
Quercus petraea	0.854	0.930	0.876	0.923	0.849	0.854	0.857	0.943	0.902		0.936	0.853	0.917	0.918
Quercus pubescens	0.871		0.891		0.902	0.918	0.923		0.939	0.875	0.870	0.885	0.927	0.935
Quercus robur	0.859	0.928	0.906	0.889	0.890	0.908	0.919	0.912	0.871		0.910	0.875	0.968	0.914
Salix alba			0.928	0.943	0.878	0.939	0.907		0.876	0.951		0.905	0.897	0.926
Sorbus aria	0.957	0.894	0.904	0.927	0.919	0.928	0.938		0.931	0.864	0.935	0.945	0.921	
Sorbus aucuparia		0.922	0.888	0.932	0.892	0.924	0.936		0.919		0.914	0.910	0.872	
Tilia cordata	0.863	0.937	0.932	0.948	0.904	0.904	0.920	0.936	0.950	0.915	0.921	0.860	0.922	0.858
Tilia platyphyllos	0.933	0.907	0.919	0.885	0.924	0.910	0.939		0.931	0.926	0.929	0.877	0.937	0.927
Ulmus scabra	0.859	0.954	0.932	0.966	0.836	0.899	0.902	0.902	0.914	0.920		0.930	0.889	

Tab. A-18: Percentage similarity coefficients (PS) between the conjectured "true" steady state species composition of the ForClim model with default species parameters and the species composition as simulated when setting the species parameters to the upper end of their plausibility interval. The threshold for significant differences ($\alpha = 5\%$) corresponds to PS = 0.871. Empty cells denote missing values (cf. Tab. A-13).

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba		0.940	0.945	0.926	0.861	0.945	0.885	0.899	0.954	0.841		0.758	0.866	0.904
Larix decidua	0.907	0.918	0.888	0.897	0.866	0.886	0.912	0.920	0.906	0.845	0.877	0.953		
Picea excelsa		0.905	0.932	0.853	0.887	0.936	0.955		0.775	0.914	0.922	0.832	0.856	
Pinus cembra		0.903	0.873	0.920	0.897	0.906	0.913	0.912	0.960	0.932		0.891	0.941	
Pinus montana			0.861		0.952	0.958	0.916		0.930	0.883	0.962	0.931		
Pinus silvestris	0.946	0.912	0.946	0.919	0.880	0.929	0.895		0.942	0.882	0.827	0.935		
Taxus baccata		0.930	0.941	0.938	0.924	0.902	0.904	0.925	0.852	0.873		0.888	0.918	0.911
Acer campestre	0.922	0.918	0.920	0.942	0.905	0.921	0.952		0.909	0.910	0.921	0.927	0.926	0.926
Acer platanoides	0.912	0.908	0.901	0.875	0.891	0.915	0.927	0.902	0.862	0.887	0.899	0.895	0.912	0.932
Acer pseudoplatanus	0.912	0.904	0.943	0.892	0.897	0.901	0.934		0.873	0.866	0.915	0.941	0.937	0.927
Alnus glutinosa	0.947	0.920	0.955	0.927	0.905	0.868	0.919	0.909	0.931	0.903	0.881	0.951	0.961	0.923
Alnus incana	0.893	0.925	0.923	0.954	0.901	0.896	0.906		0.938	0.889	0.912	0.935	0.922	0.893
Alnus viridis	0.930		0.914		0.925	0.947	0.916		0.921	0.928	0.896	0.918	0.882	0.923
Betula pendula	0.937	0.946	0.896	0.928	0.909	0.958	0.910		0.919	0.905	0.921	0.893		0.961
Carpinus betulus	0.926	0.911	0.914	0.923	0.918	0.914	0.914	0.839	0.859	0.837		0.927	0.894	0.889
Castanea sativa	0.933	0.925	0.951	0.918	0.933	0.929	0.948		0.883	0.930	0.921	0.915	0.942	0.945
Corylus avellana	0.950		0.956	0.945	0.945	0.899	0.875	0.913	0.884	0.910		0.935	0.914	0.923
Fagus silvatica	0.880	0.866	0.903	0.836	0.765	0.903	0.880	0.722	0.886	0.838		0.788	0.883	0.916
Fraxinus excelsior	0.912	0.888	0.906	0.920	0.883	0.892	0.950	0.926	0.850		0.935	0.903	0.928	0.877
Populus nigra	0.868	0.916	0.947	0.927	0.882	0.929	0.950		0.917			0.899	0.943	0.901
Populus tremula	0.941	0.935	0.894	0.937	0.933	0.891	0.884		0.919	0.916		0.934	0.927	0.878
Quercus petraea	0.916	0.874	0.920	0.846	0.784	0.889	0.890	0.922	0.933	0.832	0.958	0.845	0.936	0.921
Quercus pubescens	0.945		0.876		0.919	0.815	0.907		0.916	0.862	0.955	0.907	0.893	0.932
Quercus robur	0.899	0.956	0.899	0.900	0.776	0.858	0.878	0.940	0.905	0.866	0.923	0.877		0.945
Salix alba	0.924		0.866	0.909	0.922	0.943	0.897		0.947		0.933	0.950	0.928	0.906
Sorbus aria	0.907	0.899	0.903	0.882	0.894	0.866	0.872		0.923	0.903	0.919	0.916	0.893	0.952
Sorbus aucuparia	0.939	0.912	0.917	0.920	0.937	0.921	0.910		0.896	0.806	0.939	0.910	0.849	0.931
Tilia cordata	0.927	0.883	0.882	0.944	0.902	0.892	0.907	0.912	0.904	0.900	0.955	0.921	0.905	0.941
Tilia platyphyllos	0.929	0.899	0.913	0.834	0.915	0.926	0.939		0.897	0.909	0.945	0.950	0.863	0.940
Ulmus scabra	0.884	0.909	0.905	0.910	0.933	0.909	0.913	0.903	0.936		0.899	0.921	0.864	0.876

Tab. A-19: Significant (α = 5%) percentage changes of the biomass of the species whose parameters were set to the lower end of the plausibility interval. Empty cells denote missing values (cf. Tab. A-12) or insignificant change. Reading example: When kG of *Abies alba* is set to the lower end of the plausibility interval, the biomass of this species decreases significantly by 37%.

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba	114	-23		-82	-37		26	-22	-18	52	24			43
Larix decidua		-77	-72	-83	-97	84	-100	-56	-100			72	-35	47
Picea excelsa	59	-51	-34	-96	-87	-24	-100		-100	116		35		-61
Pinus cembra														
Pinus montana					-62		-100							-64
Pinus silvestris		-60	-67	-77	-96							318		-51
Taxus baccata		-93			-61		238			188			194	
Acer campestre		-39		-76	-69		139			111		55		
Acer platanoides		-49		-87	-86	57	145		-65	72			186	
Acer pseudoplatanus	58		-48	-71	-91		129		-45	81			88	-51
Alnus glutinosa		-81		-91	-75		115		-100	108		57	92	
Alnus incana	-69	-92		-91	-94				-100	400		209		
Alnus viridis														
Betula pendula		-82		-87	-61				-99			115		
Carpinus betulus		-74		-46	-75		50		-54	64		39	74	
Castanea sativa		-75			-71	1109						140		
Corylus avellana			-67		-67							400		
Fagus silvatica		-52	-17	-62	-60		47	44	-100					
Fraxinus excelsior		-60	-41		-95		217		-99				174	
Populus nigra		-35		-58	-91				-100	100		134	101	
Populus tremula		-73		-41	-42							82		-40
Quercus petraea	135		-66	-39	-70	93	86		-42			97		
Quercus pubescens	-61		-56		-67					1539		1106	-72	
Quercus robur	204		-93	-64	-97		127		-78		140	251		
Salix alba				-72	-75		115		-100			104		
Sorbus aria										400		500		
Sorbus aucuparia		-74		-52	-84							150		
Tilia cordata	-50	-50			-50	4788			-50					
Tilia platyphyllos		-58			-53	8511			-47					
Ulmus scabra		-43	-54	-48	-91		193	-45	-79	125		131	170	

Tab. A-20: Significant (α = 5%) percentage changes of the biomass of the species whose parameters were set to the upper end of the plausibility interval. Empty cells denote missing values (cf. Tab. A-13) or insignificant change. Reading example: When kG of *Abies alba* is set to the upper end of the plausibility interval, the biomass of this species increases significantly by 41%.

Species	sType	kDm	kHm	kAm	kG	kDDMin	kDDMax	kWiT	kDrT	kNTol	kBrow	kLy	kLa	kLQ
Abies alba					41		-38			-38		-61	-50	
Larix decidua				78	87	46				-91	-56			
Picea excelsa		59			130				322	-50		-87		
Pinus cembra														
Pinus montana					271					-92				
Pinus silvestris				-92	1024	-72	-87				-73	-86		
Taxus baccata						-62		-66		-36		-83	-53	-38
Acer campestre					211	-86				-52	-30	-90	-46	
Acer platanoides	-26	52		135	272	-91	-50			-58	-31	-63	-43	
Acer pseudoplatanus	118				249	-68	-55			-63		-60	-77	
Alnus glutinosa					119		-71		114	-76	-54	-91		
Alnus incana	-51		-62			-73			355	-89	-55	-95	-76	
Alnus viridis														
Betula pendula					96	-44	-37			-70	-57			
Carpinus betulus	-33				130	-47	-32			-55		-80	-32	
Castanea sativa				-55		-100				-79	-49	-85	-53	
Corylus avellana	-67			-67	-100				-67			-100		
Fagus silvatica	-15			34	70		-21	-70		-27		-62	-26	
Fraxinus excelsior			-39		367	-80	-68					-85		
Populus nigra			64				-52		202			-97		
Populus tremula										-42			-48	-41
Quercus petraea					137	-30	-37	-39		-92		-59		
Quercus pubescens	-56		-56				-89		-83		-78	-100		
Quercus robur			64	135	378	-97	-51			-81		-80		
Salix alba					214	-91	-48		172			-94		
Sorbus aria			-67				-67				-67	-67		
Sorbus aucuparia										-87			-46	
Tilia cordata						-100				-50		-100	-38	
Tilia platyphyllos						-100	-37		-37	-47	-47	-95	-47	
Ulmus scabra					312	-97	-70	-48				-98	-85	

VI. Derivation of parameters for eastern North American tree species

The 14 species-specific parameters were derived according to the following conversion rules for the 72 most important tree species of eastern North America (Pastor & Post 1985, Solomon 1986), which are used in the FORENA model:

sType parameter:
The sType parameter was derived from the parameters FWT (a foliage production parameter), SLTA (an allometric parameter), and FRT (the foliage retention time in years) of the 72 tree species given in Pastor & Post (1985, pp. 30ff.). These three parameters determine the amount of foliage weight per tree in function of its diameter at breast height. There are 9 combinations of values for these three parameters in the data set by Pastor & Post (1985). They were mapped to the five types of allometric relationships between DBH and foliage weight in FORCLIM as indicated in Eq. A-2.

$$
\text{sType} = \begin{cases}
\text{D1} & (\text{FWT} = 248 \wedge \text{SLTA} = 0.804 \wedge \text{FRT} = 1) \vee \\
 & (\text{FWT} = 173 \wedge \text{SLTA} = 0.729 \wedge \text{FRT} = 1) \\[2ex]
 & (\text{FWT} = 440 \wedge \text{SLTA} = 0.804 \wedge \text{FRT} = 1) \vee \\
\text{D2} & (\text{FWT} = 440 \wedge \text{SLTA} = 0.814 \wedge \text{FRT} = 1) \vee \\
 & (\text{FWT} = 440 \wedge \text{SLTA} = 0.428 \wedge \text{FRT} = 1) \\[2ex]
\text{C3} & (\text{FWT} = 248 \wedge \text{SLTA} = 0.804 \wedge \text{FRT} = 3) \\[2ex]
\text{C4} & (\text{FWT} = 440 \wedge \text{SLTA} = 0.804 \wedge \text{FRT} = 2) \\[2ex]
\text{D4} & (\text{FWT} = 440 \wedge \text{SLTA} = 0.904 \wedge \text{FRT} = 1) \\[2ex]
\text{C5} & (\text{FWT} = 440 \wedge \text{SLTA} = 0.804 \wedge \text{FRT} = 3)
\end{cases} \tag{A-2}
$$

kDm, kHm, kAm, and kDrT parameters:
The FORENA and FORCLIM parameters kDm, kHm, kAm, and kDrT are identical.

kG parameter:
The kG parameters of FORENA were recalculated according to Eq. A-1 (Appendix II) to conform to the requirements of the maximum growth equation according to Moore (1989).

kDDMin and kDDMax parameters:
Both parameters were calculated based on the regression equation given in Fig. A-2.

kWiT parameter:
The calculation of the kWiT parameter is given in Eq. A-3 (cf. Appendix II).

$$kWiT_{FORCLIM} = kWiT_{FORENA} - 1 \tag{A-3}$$

kNTol parameter:
The kNTol parameter of FORCLIM was derived from the CM1 parameter in the LINKAGES model (Pastor & Post 1985), which describes the nitrogen response function of the tree species (Eq. A-4):

$$kNTol_s = \begin{cases} 1 & CM1 = 2.79 \\ 2 & CM1 = 2.94 \\ 3 & CM1 = 2.99 \end{cases} \tag{A-4}$$

kBrow parameter:
The kBrow parameter was determined based on the boolean variable SWITCH4 in FORENA, which determines the susceptibility of the tree species to browsing (Eq. A-5):

$$kBrow_s = \begin{cases} 1 & \text{SWITCH4} = \text{FALSE} \\ 3 & \text{SWITCH4} = \text{TRUE} \end{cases} \tag{A-5}$$

kL_y and kL_a parameters:
The light requirement parameters were determined from the two light tolerance classes distinguished in FORENA (Eq. A-6). It should be noted that no differentiation between saplings and older trees was possible due to the lack of data in FORENA.

$$kL_{y,s} = kL_{a,s} = \begin{cases} 3 & ITOL = 1 \\ 7 & ITOL = 2 \end{cases} \tag{A-6}$$

kLQ parameter:
The kLQ parameter was assigned by mapping the 12 leaf litter classes distinguished in the LINKAGES model by Pastor & Post (1985, p. 34, parameter TL) to the three types of leaf litter distinguished in FORCLIM (Eq. A-7):

$$kLQ_s = \begin{cases} 1 & 1 \le TL \le 4 \\ 2 & 5 \le TL \le 9 \\ 3 & 10 \le TL \le 12 \end{cases} \tag{A-7}$$

Tab. A-21 gives an overview of the values of the 14 species parameters for each of the 72 eastern North American tree species.

Tab. A-21: Species-specific parameter values of eastern North American tree species as used in the FORCLIM-P model.

Species	sType	Dm	Hm	Am	G	DDMin	DDMax	WiT	DrT	NTol	Brow	Ly	La	LQ
Abies balsamea	C5	50	1500	200	108	785	2660	-26	0.165	1	1	3	3	3
Abies fraseri	C5	100	3500	200	208	2944	3047	-8	0.025	1	1	7	7	3
Acer rubrum	D2	100	3000	150	244	1504	6986	-19	0.23	1	3	3	3	1
Acer saccharinum	D2	120	3000	125	295	1853	5035	-13	0.268	1	1	7	7	1
Acer saccharum	D2	150	3000	300	123	1465	3393	-19	0.193	2	3	3	3	1
Aesculus octandra	D2	100	3000	100	366	2941	3876	-2	0.175	3	3	3	3	2
Betula alleghaniensis	D1	50	2500	300	104	1339	2982	-19	0.343	2	3	3	3	1
Betula lenta	D1	75	2100	265	104	1649	3358	-3	0.177	2	3	3	3	1
Betula papyrifera	D1	100	2500	140	227	707	2300	-29	0.347	1	3	7	7	1
Betula populifolia	D1	25	1000	250	64	1244	3167	-12	0.292	1	3	7	7	1
Carpinus caroliniana	D1	25	1000	150	107	1590	6381	-13	0.382	3	1	3	3	2
Carya cordiformis	D1	100	3000	300	122	2171	5421	-13	0.32	2	1	3	3	1
Carya glabra	D1	100	3000	300	122	2171	7355	-8	0.294	2	1	3	3	1
Carya laciniosa	D1	100	3000	300	122	2769	4948	-5	0.254	2	1	3	3	1
Carya ovata	D1	100	3000	275	133	1925	5856	-8	0.389	2	1	3	3	1
Carya texana	D1	100	3000	300	122	2941	5421	-2	0.478	2	1	3	3	1
Carya tomentosa	D1	100	2800	300	116	2171	6363	-5	0.385	2	1	3	3	1
Castanea dentata	D2	150	3500	300	140	2171	4903	-3	0.3	3	1	3	3	1
Celtis laevigata	D2	75	3000	200	182	2941	7355	-2	0.3	3	1	3	3	1
Cornus florida	D2	25	1000	100	160	2171	6363	-5	0.387	3	1	3	3	1
Fagus grandifolia	D4	100	3000	366	100	1571	5894	-13	0.331	2	1	3	3	2
Fraxinus americana	D2	100	3000	300	122	1645	6363	-13	0.414	3	3	3	3	1
Fraxinus nigra	D2	100	2500	300	106	1237	2531	-19	0.022	3	3	7	7	1
Fraxinus pennsylvanica	D2	100	3000	150	244	1288	5838	-24	0.114	3	1	7	7	1
Fraxinus quadrangulata	D2	100	3000	300	122	2516	4042	-5	0.241	3	3	7	7	1
Ilex opaca	C5	75	2000	200	134	2941	6363	1	0.36	2	1	3	3	2
Juglans cinerea	D2	100	3000	100	366	2130	3564	-13	0.333	2	1	3	3	2
Juglans nigra	D2	150	3500	250	168	2171	4903	-9	0.429	2	1	7	7	2
Juniperus virginiana	C4	75	2000	300	89	1977	5894	-11	0.397	1	1	7	7	2
Larix laricina	D2	75	2000	335	98	498	2941	-30	0.267	1	3	7	7	3
Liquidambar styraciflua	D2	125	3500	250	167	2941	6363	-2	0.423	3	3	7	7	1
Liriodendron tulipifera	D2	150	3500	300	140	2171	6363	-3	0.327	3	3	7	7	1
Nyssa sylvatica	D2	100	3000	300	122	2171	7355	-3	0.301	3	1	7	7	1
Ostrya virginiana	D1	50	1500	100	215	1522	5914	-19	0.36	2	1	3	3	2
Picea glauca	C5	50	2500	200	155	498	2172	-31	0.309	1	1	3	3	3
Picea mariana	C5	40	2000	250	104	464	2172	-31	0.17	1	1	3	3	3
Picea rubens	C5	100	3000	400	92	1490	2738	-13	0.237	1	1	7	7	3
Pinus banksiana	C4	50	2500	150	311	1062	2485	-31	0.511	1	3	7	7	3
Pinus echinata	C4	100	3000	300	122	2941	5421	-2	0.423	1	1	7	7	3
Pinus resinosa	C4	75	2500	310	102	1339	2299	-21	0.385	1	1	7	7	3
Pinus rigida	C4	75	2000	200	134	2202	3393	-8	0.307	1	1	7	7	3
Pinus strobus	C4	150	3500	450	93	1339	3459	-21	0.267	1	1	7	7	3
Pinus taeda	C4	100	3500	350	119	3459	6363	3	0.36	1	1	7	7	3
Pinus virginiana	C4	50	1500	250	86	2941	3979	-4	0.226	1	1	7	7	3
Platanus occidentalis	D4	175	3500	500	84	2187	5838	-8	0.12	2	1	7	7	2
Populus balsamifera	D1	75	2500	200	158	780	2767	-31	0.267	1	3	7	7	2
Populus grandidentata	D1	75	2500	70	450	1339	3463	-19	0.267	1	3	7	7	2
Populus tremuloides	D1	75	2200	200	143	973	2737	-31	0.267	1	3	7	7	2
Prunus serotina	D1	100	3000	200	183	2399	6363	-11	0.387	3	3	7	7	1
Quercus alba	D4	100	3500	400	104	1977	5894	-13	0.406	2	1	3	3	2
Quercus borealis	D4	50	2500	250	124	1339	2469	-18	0.258	1	1	3	3	2
Quercus coccinea	D4	75	2500	400	108	2302	4903	-8	0.286	1	1	3	3	2
Quercus ellipsoidalis	D4	75	2500	200	158	1523	2504	-16	0.318	1	3	7	7	2
Quercus falcata	D4	100	3500	400	104	2941	6363	1	0.423	2	1	3	3	2
Quercus lyrata	D4	80	2500	250	126	3214	5666	3	0.031	1	3	7	7	2
Quercus macrocarpa	D4	80	2500	300	105	1398	5500	-21	0.487	1	1	3	3	2
Quercus marilandica	D4	50	1500	400	53	2769	5894	-2	0.422	1	1	7	7	2
Quercus muehlenbergii	D4	100	3000	300	122	2220	5188	-8	0.383	2	1	7	7	2
Quercus nuttallii	D4	75	2500	250	126	3671	5610	3	0.03	1	3	7	7	2
Quercus palustris	D4	75	2500	200	158	2486	5500	-7	0.013	1	1	7	7	2
Quercus prinus	D4	100	3000	267	137	2171	4429	-8	0.285	1	1	3	3	2
Quercus rubra	D4	100	3000	400	92	2263	4903	-18	0.225	2	1	3	3	2
Quercus shumardii	D4	100	3500	300	138	2667	6363	-4	0.484	1	1	7	7	2
Quercus stellata	D4	75	2500	400	79	2941	6363	-5	0.555	1	1	7	7	2
Quercus velutina	D4	100	3000	300	122	2068	5421	-11	0.36	1	1	3	3	2
Quercus virginiana	D4	150	2000	300	91	5188	7062	6	0.512	1	1	3	3	2
Thuja occidentalis	C3	100	3500	400	61	1237	2456	-21	0.35	1	3	3	3	2
Tilia americana	D2	100	3000	140	262	1647	3431	-18	0.27	3	3	3	3	1
Tilia heterophylla	D2	100	3000	150	244	2941	4903	-2	0.211	3	1	3	3	1
Tsuga canadensis	C5	150	3500	650	64	1569	4111	-13	0.288	1	3	3	3	2
Ulmus alata	D2	75	2000	125	214	2941	6363	1	0.345	1	1	7	7	2
Ulmus americana	D2	80	2500	300	105	1446	7355	-21	0.457	2	1	7	7	2

VII. Climatic input data sets for eastern North America

Tab. A-22: Latitude and climatic parameters of the sites and climatic divisions used for simulating eastern North American conditions. Symbols: μ(T): monthly mean temperature [°C]; σ(T): standard deviation of T; μ(P): monthly precipitation sum [cm/month]; σ(P): standard deviation of P; r: cross-correlation coefficient of T and P. Data from A.M. Solomon (pers. comm., also used by Solomon 1986).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Churchill, Manitoba												58 °N
μ(T)	-27.6	-26.7	-20.3	-11	-2.3	6.1	12	11.5	5.7	-1	-11.9	-21.8
σ(T)	3	3	2.5	2	1.5	1.3	1.3	1.3	1.5	2	2.5	3
μ(P)	1.4	1.3	1.8	2.4	2.8	4	4.9	5.8	5.2	4	4	2
σ(P)	0.7	0.9	0.9	1.3	1.1	1.6	2.2	2.2	2.6	2.5	1.8	1.2
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
Shefferville, Quebec												55 °N
μ(T)	-22.7	-21.1	-14.8	-6.9	0.9	8.5	12.6	10.8	5.6	-0.9	-8.7	-18.1
σ(T)	3	2.5	3	2	1.5	1	1	1.3	1.3	1.5	2.5	3
μ(P)	4.1	3.7	3.7	3.5	4.5	7.9	8.9	9.8	8.3	7	6.4	4.6
σ(P)	1.5	1.4	1.4	1.1	2.1	3.4	3.5	4.9	3.6	3.4	2.2	1.6
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
Armstrong, Ontario												50 °N
μ(T)	-20.7	-18.1	-10.8	-0.5	6.4	12.9	16.4	14.7	9.2	3.6	-6.5	-16.2
σ(T)	3	3	2.5	2	1.5	1.3	1.3	1.3	1.5	2	2.5	3
μ(P)	4.1	3.3	3.3	4.8	6.3	8.8	9.4	8.3	8.8	6.3	6.2	4.3
σ(P)	2	2.2	1.6	2.6	2.5	3.6	4.1	3.2	4.4	4	2.8	2.5
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
West Upper Division, Michigan												47 °N
μ(T)	-9.2	-8.8	-4.2	3.9	10.7	15.9	18.9	18.1	13.5	7.9	-0.6	-6.8
σ(T)	2.4	2.5	2.6	2.1	1.7	1.5	1.2	1.5	1.3	1.9	2.1	2.2
μ(P)	4.8	3.9	4.4	5.9	8.1	10.2	8.7	9.4	8.7	6.1	7	4.5
σ(P)	1.8	1.8	2	2.8	2.8	4	3.5	3.1	3.8	2.8	2.1	1.4
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
Central Lower Division, Michigan												44 °N
μ(T)	-4.9	-4.9	-0.4	7.2	13.7	19.3	21.7	20.8	16.2	10.4	3.1	-2.9
σ(T)	2.4	2.3	2.7	1.9	1.6	1.5	1.2	1.4	1.4	1.7	1.9	2.1
μ(P)	4.4	4	4.9	6.5	7.8	8.2	6.6	7.8	8.1	6.7	6.4	4.6
σ(P)	2	1.9	2.1	3	3.3	3.3	3.6	3.5	3.9	4.4	2.5	2.1
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0

Tab. A-22 (continued)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
West Central Division, Ohio												40 °N
μ(T)	-1.5	-0.8	3.6	10	16	21.3	23.4	22.5	18.7	12.4	5.1	-0.5
σ(T)	3	2.5	2.9	1.8	1.6	1.5	1.3	1.2	1.5	1.6	1.8	2.5
μ(P)	7.4	5.6	7.9	8.8	9.5	11	9.1	7.9	7.4	6.3	6.3	5.8
σ(P)	6.3	2.6	3.7	3.6	4.1	5.3	3.8	3.3	3.9	3.5	3.1	2.8
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
West Ozarks Division, Missouri												37 °N
μ(T)	1.5	3.3	7.4	13.8	18.5	23.5	25.7	25.1	21	15	7.5	2.8
σ(T)	2.6	2.5	2.9	1.6	1.3	1.5	1.4	1.5	1.7	0.5	1.8	2.2
μ(P)	7.6	7.2	9.5	11	12.7	11.3	8.5	8.7	8.7	8.4	8.7	7.2
σ(P)	6.2	4	5.5	5.4	6.3	6.8	4.2	4.2	5.4	5.3	4.6	3.7
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
Cumberland Plateau Division, Tennessee												36 °N
μ(T)	4	4.9	8.5	14	18.7	22.8	24.4	23.9	20.9	15	8.4	4.5
σ(T)	3.1	2.8	2.9	1.4	1.4	1.3	1	1.1	1.5	1.7	1.7	2.5
μ(P)	15	14.4	14.3	11.1	9.9	10.7	12.8	10.3	8.6	6.9	10.3	13.5
σ(P)	9.2	7.4	4.6	3.7	4	4	4.4	3.9	5	4.3	6	6.4
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
South Central Division, Arkansas												34 °N
μ(T)	7.4	9.1	12.7	17.8	22	26.4	28.1	28	24.5	18.7	11.8	8.2
σ(T)	2.3	2.2	2.4	1.2	1.2	1.1	0.9	1.4	1.4	1.7	1.5	1.9
μ(P)	13.3	11.7	13	13.8	12.4	9	10.5	7.3	7.6	7.9	12.1	12.6
σ(P)	7.9	6	4.7	6.8	5.6	5.2	5.3	4.5	4.9	5.8	6.9	6.9
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0
Southwest Division, Georgia												31 °N
μ(T)	11.4	12.4	15.2	19.3	23.6	26.9	27.5	27.3	25.3	20.3	14.5	11.4
σ(T)	2.9	2.6	2.2	1.2	1.1	0.8	0.7	0.7	0.9	1.4	1.5	2.2
μ(P)	9.6	11	13.5	12	9.4	11.3	16.1	13.4	10.9	5.2	6.4	10.2
σ(P)	5	5.4	6.9	5.5	4.3	4.2	3.8	4.3	5.9	4.6	6	6.3
r	0	0	0	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	0	0	0

Curriculum vitae

Harald Karl Matthias BUGMANN

born 11th April, 1965 in Solothurn, Switzerland
citizen of Döttingen/AG, Switzerland

1972-1977	Primary school in Oberdorf/SO, Switzerland
1977-1984	High school and college in Solothurn
1984-1985	Six months of practical work as a trainee student with the software department of the Autophon company (now Ascom) in Solothurn
1985	Military service as a radio operator
1985-1989	Studies of systematic and ecological biology at the Swiss Federal Institute of Technology Zürich (ETHZ) in the Department of Natural Sciences
1989	Diploma thesis (M.Sc.): *“Effects of a phosphorus ester (insecticide Ekamet) on the plankton biocoenosis of Lake Greifen: A modelling study”* under the supervision of Prof. H. Ambühl (Institute of Water Protection and Water Technology) Dr. A. Fischlin (Systems Ecology)
1989-1990	ETHZ diploma as a biology teacher at college level
1990-1993	Post-graduate study course in biology at ETHZ with diploma
1990-1994	Ph.D. thesis at the Institute of Terrestrial Ecology ETHZ: *“On the ecology of mountainous forests in a changing climate: A simulation study”* under the supervision of Prof. H. Flühler (Soil Physics) Dr. A. Fischlin (Systems Ecology)

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