

## Model convergence and state variable update in forest gap models

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### Abstract

During the last 25 years, models of the JABOWA/FORET type ('gap models') were increasingly applied to study forest succession. By adding more and more details, they have grown to rather complex systems, but little is known about the importance of the numerous ecological processes included in the models and about their exact mathematical properties from a systems theoretical point of view.

Based on the stochastic gap model FORECE developed for European forests we analysed two generally relevant aspects of gap models: (1) the sample size needed to reliably compute the statistical properties of the model behaviour; (2) inconsistencies in the mechanism used to update the state variables.

It was found that 150–200 simulation runs are required to warrant the convergence of the average species-specific biomass values. This sample size is considerably larger than that used in most previous studies. The analysis of the mechanism used for updating the state variables revealed that it does not conform to the requirements of systems theory. A new consistent update mechanism is presented, which even leads to more efficient calculations. While the FORECE model produces only minor differences of the simulated species-specific biomass values when using the old vs. the new update mechanism, the frequency distribution of stem numbers may be affected significantly.

It is concluded that rigorous systems theoretical and statistical investigations of the properties of forest gap models are required to render the application of those models more robust. It is proposed to revise the update mechanism for the state variables in the existing forest gap models as outlined in the present study. The design of future simulation studies with these models should be improved so as to sample sufficiently large numbers of about 200 simulation runs.

*Keywords:* Forest ecosystems; Statistics; Succession; Systems theory; Vegetation dynamics

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### 1. Introduction

Forests are highly complex ecosystems, and field investigations on their long-term behaviour are hindered considerably by many stochastic in-

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fluences as well as the spatial and temporal scales involved. Ecological modelling has been increasingly applied in forest science to overcome the limits imposed on field investigations and to make long-term projections of forest dynamics possible (e.g. Shugart et al., 1973; Sollins et al., 1976; Shugart, 1984). Another important role of modelling is the synthesis of information and the generation of hypotheses on the systems under study in order to gain a better understanding of important ecological processes.

The forest gap model approach has proven to be useful in many respects (cf. Shugart, 1984). The first models (Botkin et al., 1972) have been rather simple, but subsequent research has led to more complicated models, culminating in models including detailed information such as soil processes (Pastor and Post, 1985), phytosociological concepts (Kienast, 1987), explicit modelling of tree crown structure (Leemans and Prentice, 1989), and detailed treatment of ecophysiological (Friend et al., 1993) and biophysical processes (Bonan and van Cleve, 1992; Martin, 1992). The increasing complexity of forest gap models may have helped to make detailed and presumably more accurate projections of forest succession, but it has little furthered the analysis of forests to better understand their dynamics.

Forest gap models are stochastic models. Therefore, it is a standard practice to perform many independent simulation runs and to average the resulting species-specific biomasses and stem numbers. It is evident that the choice of an appropriate sample size is important in order to be able to derive typical model behaviour. Moreover, many studies involving forest gap models have dealt with the assessment of the effects of a change in environmental factors, such as air pollution or climate change (e.g., Solomon et al., 1981; Shugart and Emanuel, 1985; Solomon, 1986; Dale and Franklin, 1989; Kienast, 1991; Urban et al., 1993; Bugmann, 1994). Due to the complexity of gap models, which refutes any analytical approach, significant differences between two sets of model runs can not be derived easily. Are the different results from two simulation experiments caused by the different environmental conditions

or merely by the stochastic nature of the model? Hence the convergence behaviour of the output of a forest gap model is crucial for the analysis as well as the application of these models.

Although ecological models usually are built in a straightforward way oriented toward some problem of theoretical or practical relevance, they are inevitably based on systems theory, e.g. through the choice of either a discrete or a continuous-time system, which imposes certain restrictions on the formulation of equations as well as the estimation of parameters. A consistent formulation and use of an ecological model has to adhere to the formal restrictions imposed by the underlying systems theoretical approach; otherwise incorrect or completely artificial simulation results may be obtained. The use of ad-hoc simulation tools for studying complex systems increases the likelihood of obtaining numerical artefacts due to inconsistencies between the numerical implementation and the true mathematical properties of the model (Cellier and Fischlin, 1982; Cellier, 1984; Fischlin, 1991).

The investigations presented in this paper are part of a larger effort aimed at providing the systems theoretical basis for simplifying forest gap models and to make them accessible to a detailed statistical and ecological analysis (cf. Bugmann, 1994). Focusing on the FORECE model (Kienast, 1987) as a case study, we first investigate the convergence of model output, i.e. how many simulation runs have to be performed to allow for meaningful calculation of statistical properties of the model output. We then examine the state variable update in the model as a first step toward model simplification and present a more efficient forest gap model for central European conditions. The findings from the case study are generalized by comparison with other studies where gap models were developed and/or applied (Botkin et al., 1972; Shugart and West, 1977; Pastor and Post, 1985; Solomon, 1986; Leemans and Prentice, 1989; Martin, 1992). Our analysis reveals that many forest gap models, although formulated as discrete-time systems, do not conform to the formal requirements defined by systems theory.

## 2. Methods

### 2.1. Modelling approach

The forest simulator FORECE (Kienast, 1987) used for the present study is a gap model of the JABOWA/FORET type (Shugart and West, 1980) based on previous models of Botkin et al. (1972), Shugart and West (1977), Dale and Hemstrøm (1984), and Pastor and Post (1985). A detailed description of the model is given in Kienast (1987) and Kienast and Kuhn (1989a). The simulator runs on the basis of 1/12-ha patches, which is equivalent to forest succession models developed for the Appalachian region of the Eastern United States (Shugart, 1984). Stand development on a forest patch is simulated by calculating establishment, growth, and death of individual trees as a mixture of deterministic and stochastic processes. To obtain forest development at the ecosystem level, the successional patterns of patches from many simulation runs are averaged. This concept is supported by various plant succession studies which show that a forest ecosystem may be described by the average growth dynamics of a multitude of patches with different successional ages (Watt, 1947; Bray, 1956; Curtis, 1959; Forman and Godron, 1981).

Forest succession is driven by extrinsic and intrinsic variables of the species and the stand. Variables extrinsic to the stand are summer warmth, spring frost, soil moisture, and browsing. Variables intrinsic to the species are maximum potential growth rate and mortality, while shading and crowding are variables intrinsic to the stand. Each model starts with a randomly selected number of saplings in a patch to simulate tree establishment. Unfavourable environmental factors and site conditions control the exclusion of species from the establishment process.

Growth of each individual tree is simulated by decreasing the maximum potential diameter growth rate at its respective age by environmental factors that are less than optimum. To do so, growth multipliers for each limiting factor are calculated, and the maximum growth rate is reduced according to the difference between the smallest growth multiplier and its optimum value

(often called 'Liebig's Law of the Minimum'). The form of the maximum growth equation is similar to a logistic equation; it is based on the assumption that annual biomass increment is proportional to the amount of sunlight the leaves receive (Botkin et al., 1972).

Death of the trees is determined by a Poisson process parameterized by allowing only 1% of all individuals to reach the maximum physiological age, which is a model parameter. Furthermore, trees are also removed from the patch if they are growing slower than a certain threshold of relative or absolute minimum growth.

The growth curve for optimum diameter growth of each species was obtained by fitting the maximum growth equation to data from yield tables (Kienast, 1987). The species-specific parameters describing shade tolerance, soil moisture requirements, maximum age etc. were derived from silvics books and phytosociological vegetation descriptions (Amann, 1954; Mitscherlich, 1970; Bernatzky, 1978; Ellenberg, 1986).

### 2.2. Model convergence

At a given point in time species biomass and the numbers of trees sampled from multiple simulation runs of forest gap models are rarely normally distributed (Bugmann, 1994). Therefore, the coefficient of variation (Zar, 1984) does not provide a robust estimate of model convergence. For highly skewed distributions, a more robust statistical measure such as the quotient  $q$  is needed (Eq. 1): the interval between the 10% and the 90% percentile ( $p_{90} - p_{10}$ ) is a robust measure for the range of the samples, and the median (med) characterizes their location. Note that  $q$  should converge toward a non-zero value as the sample size approaches infinity.

$$q = \frac{p_{90} - p_{10}}{\text{med}} \quad (1)$$

For the present case study we chose the site Bern in Switzerland (Kienast, 1987); it is representative of beech forests, which cover a large area of central Europe (Ellenberg, 1986). The site-specific parameters were taken from Kienast (1987). The  $q$  value was calculated for three key

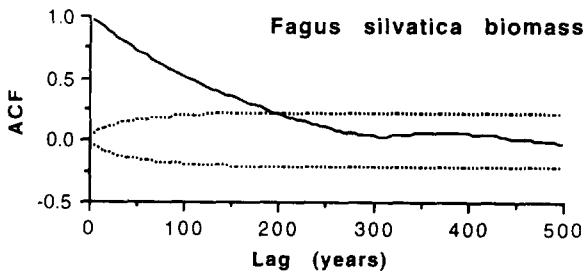


Fig. 1. Typical autocorrelation function (ACF) in the forest gap model FORECE V1.0, showing the ACF of the biomass of *Fagus silvatica* at the site Bern (Switzerland). The dotted lines indicate the 95% confidence limits for ACF = 0.

species, i.e. *Abies alba* with a low abundance at the beginning and intermediate abundance during the 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; plant nomenclature is according to Hess et al., 1980). The analysis was performed at three disparate points in time, i.e. the simulation years 400, 800 and 1200, where autocorrelation becomes negligible (Fig. 1).

Since the original implementation of the FORECE model (Kienast, 1987) does not support flexible simulation studies, e.g. it does not allow for performing more than 50 simulation runs at a time, it was re-implemented using the simulation software ModelWorks (Fischlin et al., 1994) within the RAMSES simulation environment on Apple Macintosh computers (Fischlin, 1991). Hereby the model had to be translated into the programming language Modula-2 (Wirth, 1985; Wirth et al., 1992), which facilitated the access to the programming library DialogMachine (Fischlin et al., 1987) supporting interactive simulations in a research situation. With this model version, called FORECE V1.0, we performed 4000 simulation runs on an Apple Macintosh II computer. From this data base random samples of size  $n$  were taken to calculate the quotient from Eq. 1. The procedure was repeated 10 times for each of the following sample sizes:  $n = 5, 10, 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 400$ . Finally, the statistical properties of the full sample of 4000 runs were calculated.

### 2.3. State vector update

Typically forest gap models are implemented as discrete-time models ( $t = 0, 1, 2, \dots$ ) with a time step ( $\Delta t$ ) of one year (cf. Bugmann, 1994). This means that establishment, growth and death of trees must depend only on the current state vector  $x(t)$  and input vector  $\underline{u}(t)$  (Zeigler, 1976; Fischlin et al., 1994; Eq. 2).

$$\underline{x}(t + \Delta t) = f(\underline{x}(t), \underline{u}(t)) \quad (2)$$

Eq. 2 implies that in the implementation of such a model no parts of the state vector must be updated continually during the calculation of a single time step. For example, if a state variable  $x_1$  currently has the value  $x_1(t)$  and is updated immediately to  $x_1(t + \Delta t)$  before the new value  $x_2(t + \Delta t)$  of another state variable  $x_2$ , being a function of  $x_1$ , is calculated, Eq. 2 is violated because

$$x_2(t + \Delta t) = f(x_1(t + \Delta t), x_2(t), \dots, x_n(t), \underline{u}(t)) \quad (2')$$

whereas the state transition function for state variable  $x_1$  is formally correct, since

$$x_1(t + \Delta t) = f(x_1(t), x_2(t), \dots, x_n(t), \underline{u}(t)) = f(\underline{x}(t), \underline{u}(t)) \quad (2'')$$

Unfortunately, many gap models work on state and auxiliary variables which are continually being updated (e.g. Botkin et al., 1972; Shugart and West, 1977; Pastor and Post, 1985; Kienast, 1987; Leemans and Prentice, 1989). For example, 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 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

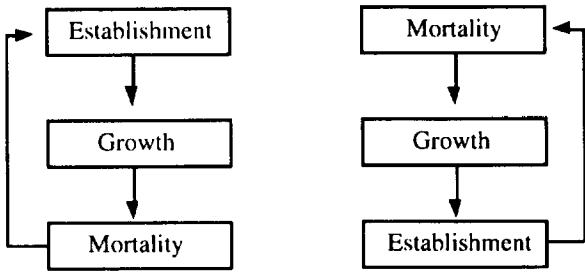


Fig. 2. Sequence of procedure calculations as incorporated in the simulation model FORECE V1.0 (left) leading to systems theoretical inconsistencies, and a corrected sequence (FORECE V1.1 right). Arrows to the left and the right symbolize the transition from one time step of the simulation model to the next; the other arrows indicate the sequence of calculation within a single time step.

growth increment of the trees which will survive, and (3) establishment of saplings within  $\Delta t$  (Fig. 2 right). However, most forest gap models do not conform to this scheme (Table 1). Since a correct update mechanism avoids repeated calculation of some variables within the same  $\Delta t$ , 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. This correct updating mechanism was implemented in a successor of FORECE 1.0, i.e. FORECE version 1.1.

Another correct and more general solution to the update problem is of course to assign during a time step new state values temporarily only to a

separate storage location, which holds the new state vector  $x(t + \Delta t)$ ; all updates to the state vector  $x(t)$  must be deferred and reserved to the end of all time step calculations (e.g., Fischlin et al., 1994).

#### 2.4. Quantitative comparison of model versions

Modifying the state vector update is one of many possible alterations of interest that can be made to the stochastic process underlying a forest gap model. In all these cases the question arises whether the two stochastic processes yield ecologically different results at the level of stand dynamics. Earlier studies (e.g. Kienast, 1991) dealing with the quantitative comparison of several model versions have relied on the t-test although its assumptions, e.g. the normal distribution of the variables, often are not met in forest gap models (Bugmann, 1994). Furthermore, the frequency distribution of most variables of interest changes over time. Therefore nonparametric tests appear more appropriate for comparing model versions. In this study, the following set of methods were used to detect differences between FORECE V1.0 and FORECE V1.1 along a transect:

1. Graphical eye-ball comparison of time series of species-specific biomass values; of course this allowed an overall qualitative evaluation of model behaviour only.
2. Starting in the simulation year 100, the non-

Table 1

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

Model name	Number of simulations	Patch size (m <sup>2</sup> )	Equilibrium landscape size (ha)	State vector update	Reference
JABOWA	100	100	1.0	E–M–G	Botkin et al. (1972)
FORET	100	833	8.3	M–E–G	Shugart and West (1977)
LINKAGES	20	833	1.7	E–G–M	Pastor and 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 and Prentice (1989)
EXE	10	833	0.8	E–G–M	Martin (1992)
	200	833	16.7	M–G–E	this study

parametric Mann–Whitney U-test (Sokal and Rohlf, 1981) was used to compare frequency distributions of key species every 200 years.

The time interval was chosen to minimize autocorrelation (cf. Fig. 1). Not all species were compared in this way, since biomass values

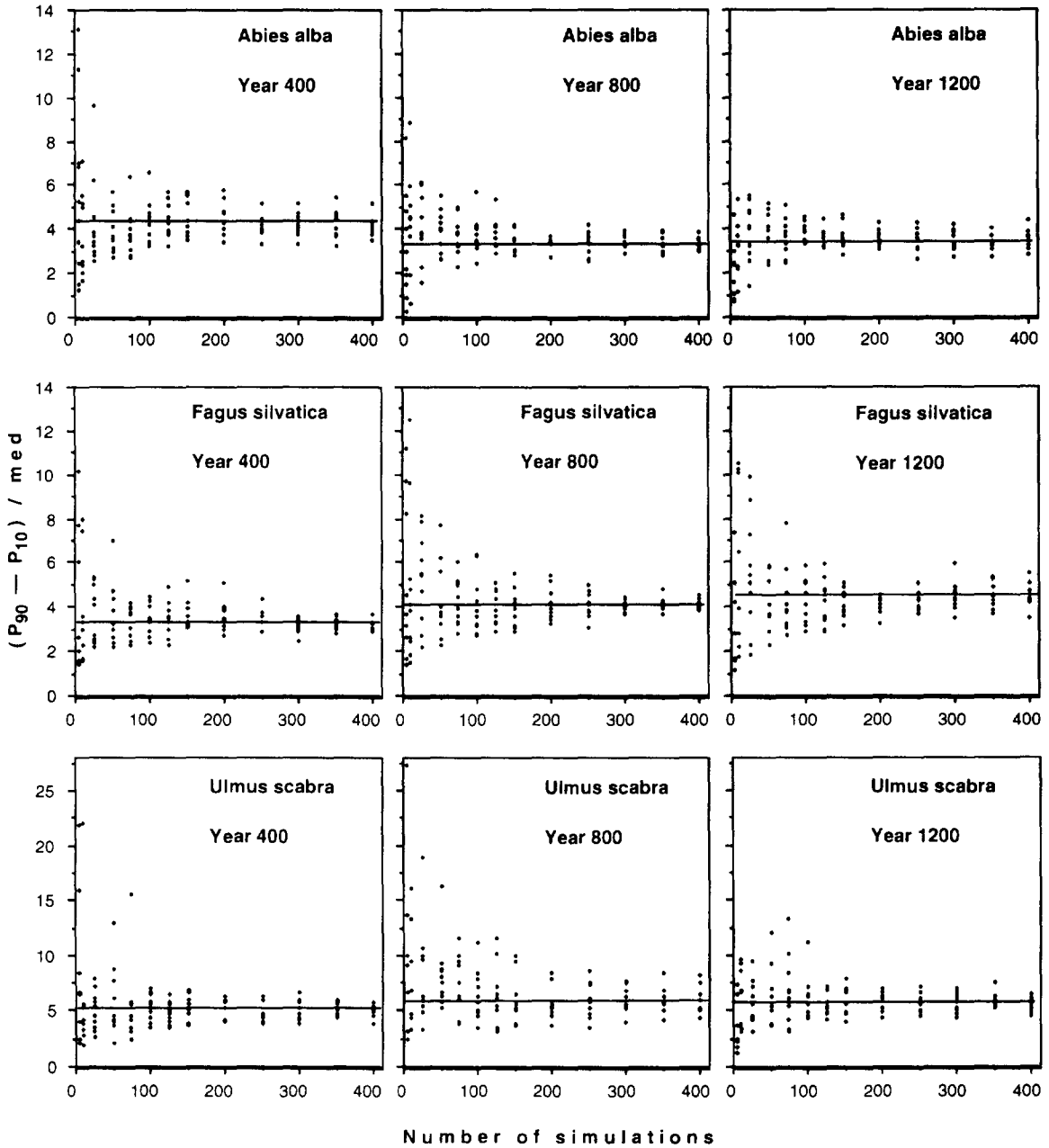


Fig. 3. Convergence of the FORECE model V1.0, estimated by the coefficient  $q$  (Eq. 1) as a function of the number of simulation runs  $n$ . The horizontal line in each panel is the value of  $q$  for  $n = 4000$ , which is the best estimate of a conjectured boundary value. For each value of  $n$ ,  $q$  was calculated 10 times independently. For small  $n$ , some extremely large values of  $q$  had to be clipped for convenience.

and numbers of a species are not independent from that of all the others due to light limitation and the maximum carrying capacity assumed in the model (Kienast, 1987).

3. Eye-ball comparison of the frequency distribution of those variables for which the U-test yielded significant differences ( $P < 0.05$ ).

Model comparisons were made at the sites Airolo, Basel, Bern, Locarno, Sion and Zermatt (all located in Switzerland; Kienast, 1987; Kienast and Kuhn, 1989a, b; Bugmann, 1994), which are representative of typical forest communities along an altitudinal transect in the European Alps (Ellenberg and Klötzli, 1972; Kienast and Kuhn, 1989a, b). At each site two hundred simulation runs were performed for each model version. The data were analysed using the statistics package SYSTAT on an Apple Macintosh IIfx.

### 3. Results and discussion

#### 3.1. Model convergence

For all three key species we found similar patterns of the  $q$  values in all analysed years (Eq. 1; Fig. 3): For small sample sizes ( $n < 100$ ),  $q$  is highly variable, and only larger sample sizes ( $100 < n < 200$ ) show a clear tendency of convergence. Beyond a sample size of  $n = 200$ ,  $q$  appears to have converged and no further significant reductions in  $q$  can be detected. The funnel-shaped function (Fig. 3) of  $q$  corresponds to theoretical expectations, but model convergence is slow, reflecting the highly stochastic nature of gap models.

Hence the FORECE model requires approximately 200 simulation runs to calculate reliable model outputs such as means of species specific biomass, a result similar to that obtained in a pilot study (Bugmann and Fischlin, 1992). We surmise that this result is also valid for many other forest gap models because their structure is quite similar to that of FORECE (Botkin, 1993; Bugmann et al., 1996). The recommended sample size  $n = 200$  is markedly larger than that of  $n \leq 50$ , which appears to have become a generally accepted standard (Table 1).

The quasi-equilibrium landscape concept holds that the vegetation attributes exhibit constancy at the landscape level when the size of the typical disturbance is small relative to the size of the landscape (Whittaker, 1953; Bormann and Likens, 1979). Shugart (1984, p. 165) quantified this concept and suggested that the minimum landscape area required for the quasi-equilibrium is about 50 times the size of a disturbance. The size of a patch in forest gap models is chosen so as to represent the typical disturbance size (Shugart and West, 1979), from which Shugart (1984) concluded that 50 patches should be sufficient to calculate the properties of the quasi-equilibrium landscape in forest gap models. However, the present study indicates that such a small sample size can be regarded as an absolute minimum at best, and that only larger sample sizes warrant the desired precision (Fig. 3, Table 1).

Busing and 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 Shugart's 50:1 rule. However, the species composition at the landscape level, i.e. the relative basal area of the species, did not yet equilibrate at an area 50 times the disturbance size (Busing and White, 1993). Hence their findings corroborate the results of the present convergence analysis. Generally our findings do not question the principle of a quasi-equilibrium landscape (Bormann and Likens, 1979); they just modify its quantification (Shugart, 1984).

For many gap models, e.g. FORECE, it is time-consuming to perform more than 50 simulation runs due to their complexity. It would therefore be desirable to simplify the models in order to allow for more efficient calculations. Attempts in this direction have been undertaken e.g. by Reed (1980), Fulton (1991), and Bugmann (1994).

#### 3.2. State vector update

The graphical comparisons of the simulation results did not reveal any striking differences between FORECE 1.0 and 1.1 at any of the study sites. The results from the statistical analysis, however, suggest that the sites can be grouped

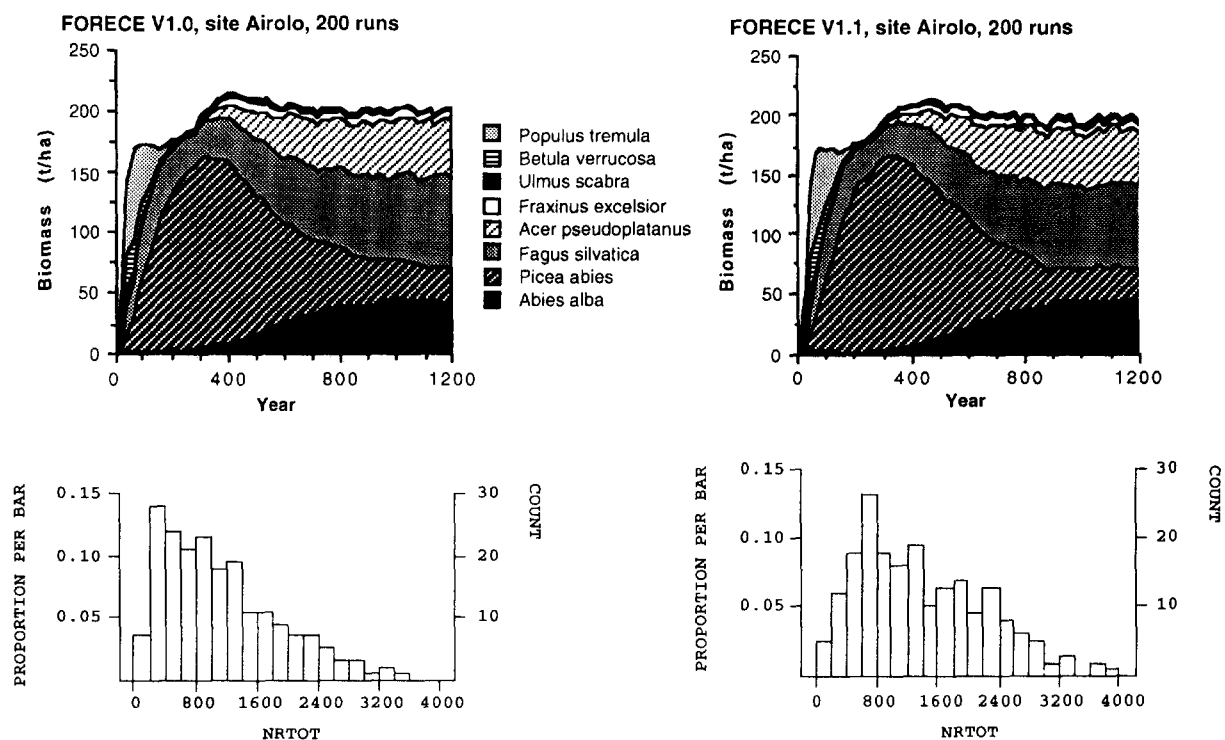


Fig. 4. Top: Forest succession as simulated for the site Airolò, starting from a bare patch. Cumulative species-specific biomass values are shown for the original model FORECE 1.0 (left, Kienast, 1987) and FORECE 1.1 incorporating an improved state vector update (this study, right). Bottom: Frequency distribution of the total number of stems per hectare (NRTOT) at the site Airolò in the simulation year 500 from the original (left) and the modified FORECE model (right). The distributions are significantly different at  $P < 0.01$ . The modified model is characterized by a higher occurrence of stem numbers between 1500 and 2500  $\text{ha}^{-1}$ , but the overall shape of the distributions remains quite similar.

into two classes: Airolò, Basel and Bern showed only few significant differences between the two model versions, whereas Locarno, Sion and Zermatt exhibit a larger number of differences.

### 3.2.1. Sites with small differences

A typical example from this group is the site Airolò (Fig. 4). Both models exhibit similar species composition, and total aboveground biomass is almost identical (Fig. 4 top). The comparison of the frequency distributions by means of the U-test is given in Table 2. Out of the 66 investigated cases, only 5 (7.6%) show differences that are significant at  $P < 0.05$  (Table 2). The individual examination of each of the latter 5 cases revealed no striking differences between the two model versions, nor was it possible to detect a consistent pattern of the deviations. Only in two cases, i.e.

Table 2

Results of the Mann–Whitney U-test comparing the two model versions FORECE 1.0 and 1.1 with respect to the species-specific biomass of the eight most abundant tree species, total biomass, total number, and leaf area index (LAI) for the site Airolò

Species	Year					
	100	300	500	700	900	1100
<i>Abies alba</i>	◦					
<i>Picea abies</i>		◦				
<i>Fagus sylvatica</i>		*				
<i>Acer pseudoplatanus</i>						
<i>Fraxinus excelsior</i>	*					
<i>Ulmus scabra</i>						*
<i>Betula verrucosa</i>						
<i>Populus tremula</i>						
Total biomass						
Total number			**		*	
LAI						

Significance levels: ◦:  $P < 0.1$ ; \*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ .



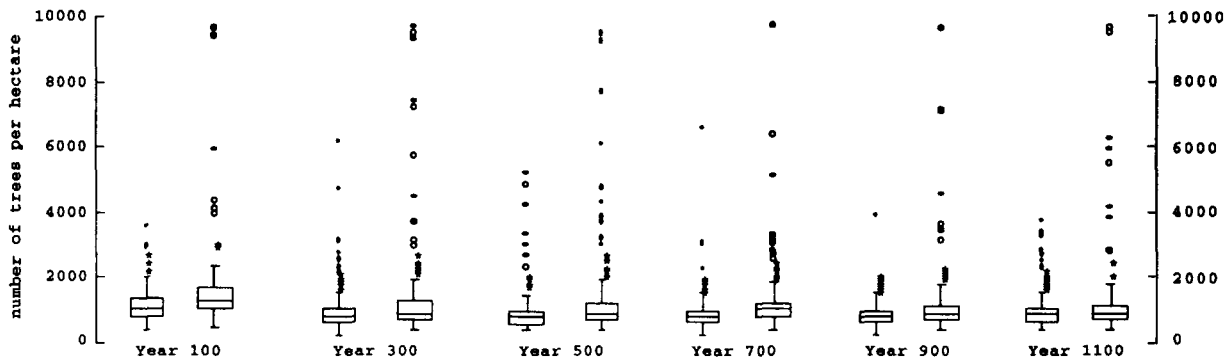


Fig. 5. Notched box plots of total tree numbers at the site Sion for all years of the analysis (original model FORECE V1.0, left; modified model FORECE V1.1, right). The same pattern governs the distributions throughout: the modified model version exhibits an increase of medium tree numbers and an increased but still episodic occurrence of very high tree numbers.

in the years 500 (Table 2, Fig. 5 bottom) and 900, did total stem numbers differ significantly and according to a similar pattern. The differences for the sites Basel and Bern are even smaller (cf. Table 3). Thus, for this class of sites the modified update mechanism seems to have little effect on model behaviour.

### 3.2.2. Sites with larger differences

The site Sion showed the largest number of significant differences of all the sites (Table 4, Fig. 5). Although the composition of the species-poor pine forest at Sion remains unaffected by the changed update mechanism, the statistical analysis revealed that large differences occur with tree numbers (Table 4). Out of the 30 cases investigated, 10 showed significant differences at  $P < 0.05$ . The significant differences in the biomass of *Pinus silvestris* in the year 500 (Table 4) and of total tree numbers throughout the simu-

lation (Fig. 5) are the most pronounced effects. The highly significant difference in total biomass and LAI in the year 500 (Table 4) is brought about by the biomass distribution of *P. silvestris*, since the forest consists almost entirely of this species. The sites Locarno and Zermatt also exhibit a marked number of significant differences (Table 5). Thus, for this class of sites the modified update mechanism has a significant effect on model behaviour (between 10% and 33% out of all cases, Table 5).

## 4. Conclusions

The stochastic nature and the large scale in space and time of forest ecosystems is encapsulated in forest gap models, which have consequently grown to complex models showing complex, stochastic behaviour that is difficult to anal-

Table 3  
Summary of results from the Mann–Whitney U-test at the sites with small numbers of significant differences due to a changed state vector updating mechanism in the FORECE model

Site	No. cases analysed	Number of cases significant at			% of cases at $P < 0.05$
		$0.05 > P \geq 0.01$	$0.01 > P \geq 0.001$	$P < 0.001$	
Airolo	66	4	1	0	7.6
Basel	78	1	0	0	1.3
Bern	78	3	0	0	3.8

Table 4

Results of the Mann–Whitney U-test comparing the two model versions FORECE 1.0 and 1.1 with respect to the species-specific biomass of the eight most abundant tree species, total biomass, total number, and leaf area index (LAI) for the site Sion

Species	Year					
	100	300	500	700	900	1100
<i>Pinus silvestris</i>			*			
<i>Quercus pubescens</i>						
Total biomass			*			
Total number	***	***	***	***	***	**
LAI		*	**			

Significance levels: ◦:  $P < 0.1$ ; \*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ; \*\*\*:  $P < 0.001$ .

yse. The last 20 years have seen a steady proliferation of ever more sophisticated forest gap models, and they have heuristically proven to be useful for many purposes. Yet, to understand their underlying assumptions and limitations, we believe that they should be analysed carefully. Specifically, the statistical, systems theoretical and ecological basis of these complex models should be explored further. Then their range of applicability can be determined better, making it possible to plan appropriate simulation experiments, which then will produce optimally valid results.

The results from the analysis of model convergence emphasize the need to investigate the statistical properties of the time series produced by forest gap models (cf. Emanuel et al., 1978). For the FORECE model we found that it is necessary to sample some 200 runs to compute species composition reliably, and we surmise that a similar sample size is required also for many other gap models. However, in most studies published to

date only 10 to 50 simulation runs have been performed (Table 1). We suggest that other forest gap models should also be checked for their convergence properties. This would enable to test whether the recommended sample size of about 200 runs is generally valid for gap models. Although such an analysis may be painstaking, we suggest that the more complex the model, the more important it is. An appropriate sample size is especially crucial if several model versions are to be compared, e.g. during model development, in sensitivity analyses, and when the models are applied to study the effects of, for example, air pollution and climatic change.

The implementation of a consistent update mechanism of the state variables in the FORECE model did not lead to dramatic changes of model behaviour, although the correct updating is fundamentally different from a systems theoretical point of view. This appears to confirm the finding of Shugart (1984) that no single part of a forest gap model is very sensitive to its exact formulation. However, the update mechanism influenced the distribution of tree numbers significantly, which may be essential in studies that compare and validate gap models (e.g. Leemans, 1992). Therefore we recommend to revise forest gap models so that they include a consistent update mechanism for their state variables. This may even lead to an improvement in the efficiency of the simulation model: in the case of FORECE, the version with a correct updating is even approximately 25% faster. Although published a long time ago, the systems theoretical foundations of ecological modelling (Wymore, 1976, 1984; Zeigler, 1976, 1979) are still neither fully recognized

Table 5

Summary of results from the Mann–Whitney U-test for the sites with larger numbers of significant differences due to a changed state vector updating mechanism in the FORECE model

Site	No. cases analysed	Number of cases significant at			% of cases at $P < 0.05$
		$0.05 > P \geq 0.01$	$0.01 > P \geq 0.001$	$P < 0.001$	
Locarno	78	8	2	1	14.1
Sion	30	3	2	5	33.3
Zermatt	48	4	1	0	10.4

nor applied in practice (cf. Fischlin, 1991). We conclude that complex simulation models of ecological systems need to be implemented in formal ways adhering to systems theoretical foundations.

The complexity of current gap models also gives rise to the question whether the essence of the original ecological hypothesis of forest dynamics underlying these models (Botkin et al., 1972) is responsible for the quite realistic behaviour of the models (Shugart, 1984), or whether their behaviour is simply due to additional details cluttering the core structure of the models. Recent studies suggest that simpler models could provide equally valid descriptions of forest dynamics (cf. Bugmann and Martin, 1995). Such models would be easier to interpret ecologically and would allow for a more detailed analysis of their behaviour, taking advantage of the user interface of modern personal computers and workstations instead of batch-oriented host computers.

Not only would these developments enable detailed analyses of the sensitivity and stability of forest gap models, but their large-scale application in the context of, for example, landscape ecology would also become feasible. We are convinced that analyses of this promising class of ecological models bear the potential to considerably increase our quantitative understanding of forest dynamics.

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