

REGENERATION IN GAP MODELS: PRIORITY ISSUES FOR STUDYING FOREST RESPONSES TO CLIMATE CHANGE

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Abstract. Recruitment algorithms in forest gap models are examined with particular regard to their suitability for simulating forest ecosystem responses to a changing climate. The traditional formulation of recruitment is found limiting in three areas. First, the aggregation of different regeneration stages (seed production, dispersal, storage, germination and seedling establishment) is likely to result in less accurate predictions of responses as compared to treating each stage separately. Second, the related assumptions that seeds of all species are uniformly available and that environmental conditions are homogeneous, are likely to cause overestimates of future species diversity and forest migration rates. Third, interactions between herbivores (ungulates and insect pests) and forest vegetation are a big unknown with potentially serious impacts in many regions. Possible strategies for developing better gap model representations for the climate-sensitive aspects of each of these key areas are discussed. A working example of a relatively new model that addresses some of these limitations is also presented for each case. We conclude that better models of regeneration processes are desirable for predicting effects of climate change, but that it is presently impossible to determine what improvements can be expected without carrying out rigorous tests for each new formulation.

1. Introduction

Studies of the climate record and simulations with General Circulation Models (GCM) suggest that both temperature and precipitation patterns are likely to change



Climatic Change **51**: 475–508, 2001.

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within the next 50–100 ys, due to increases in atmospheric concentrations of greenhouse gases (e.g., Houghton et al., 1996). These variables are the primary underlying climatic drivers for forest gap models, as they are for many ecosystem models. The physiological effects of changes in climate and CO₂ levels on mature trees and seedlings are being investigated (e.g., Jarvis, 1998), but are far from fully understood. Even less is known about possible impacts of change on regeneration processes such as pollination and seed development. In the case of seed germination, critical temperature and moisture requirements for some species are known, but sensitivities to extremes and variability, both within and between species, are only beginning to be investigated.

In general, the processes by which juvenile trees (saplings) are produced and established within a forest stand are represented very simplistically in traditional forest gap models. The term *regeneration* is often used to refer to these processes, which include the production, dispersal and germination of tree seeds and the subsequent establishment of seedlings, as well as vegetative regrowth following mortality of aboveground portions of mature trees. Regeneration involves both the physiological and developmental (autecological) mechanisms inherent in plant biology as well as external ecological factors, including interactions with other biota, climate and disturbances. For example, seed production is presumably related to species, age, size and vigor of the parent tree, whereas dispersal and germination of seeds are largely stochastic rather than deterministic processes – at least when considered at the spatial and structural scales normally represented in gap models. The successful establishment of seedlings (i.e., the survival and growth processes that transform them into saplings) is possibly even more complex, because plant ecophysiology, environment and random events all play important roles. Regeneration processes contribute both to the maintenance of species composition in forests, and, because they allow species to invade new regions, to changes in species composition and hence, the migration of tree species across landscapes.

This paper focuses on the relationships between forest regeneration processes and environmental factors, and considers whether the current representation of regeneration in gap models is adequate to allow these models to be used to provide accurate estimates of the effects of global climate change on forest ecosystems. Specific issues to be addressed include: (1) what current uncertainties concerning regeneration processes in gap models limit their usefulness for predicting forest responses to climate change? (2) how are these uncertainties handled in current gap models? (3) how should they be addressed in the next generation of models? and (4) will improved representation of regeneration processes enable better predictions of how forest species composition will respond to climate change?

First we consider the limitations of existing gap models: What aspects of regeneration should be captured if gap models are to be used for simulating responses of forest dynamics under a changing climate? Which of these are feasible to implement? For each of the important limitations identified we first review the ‘traditional’ gap model treatments, and the problems resulting from them. We then

discuss possible alternative formulations, based on observations from reality and our assessment of the feasibility of implementing them in models, or citing examples from existing models where appropriate. In some cases, of course, these formulations might still be inadequate, in which case we try to determine what is still lacking and whether this is important in the context of global climate change. Finally, we present a ‘working example’ of a model which features routines that go some way to addressing these limitations in more traditional formulations, but focusing on those aspects sensitive to climatic change. Readers are referred also to the companion paper by Wullschleger et al. (2001), which discusses aspects of regeneration dependent upon soil conditions (germination and seedling establishment).

As part of our treatment of regeneration, we will be discussing dispersal and migration, but we are not going to delve into the topic of forest migration over long distances in response to climatic change. Rather, this discussion will focus at the scale of the patch and forest stand, and on whether the current representation of dispersal processes may lead to demonstrably incorrect predictions of stand development under a changing climate. The development of spatially-explicit landscape models to track disturbances, succession and long-distance migration is critically important, but it was not the focus of the workshop from which this paper is derived (Pitelka et al., 2001).

2. Limitations of Traditional Gap Models

In traditional gap models (*sensu* Botkin et al., 1972a,b; Shugart and West, 1977; Shugart, 1984), regeneration of individual tree species is not simulated explicitly, but instead is typically represented by one or more species-specific sapling recruitment parameters (Bugmann, 2001). Two distinct algorithms have been used widely. Both Botkin and Shugart favored stochastic formulations where established saplings would appear spontaneously, on an annual timestep, in each gap model plot at a stem density consistent with field observations. In JABOWA (Botkin et al., 1972a, b) and FORET (Shugart, 1984), temperature (or growing degree days, GDD) and shading by other trees are the key environmental determinants of regeneration ‘thresholds’. The threshold algorithm proposes that it is not the number of saplings to be established which depends on environmental conditions but rather whether seedlings of a given species can or cannot survive in a given year. If they can, the recruitment parameter is used directly as input to a uniform random number generator (RNG) to obtain the numbers of saplings to be established (or ‘planted’) in the stand. In the original JABOWA model, regeneration of a particular species occurs when temperature is within a specified range and soil moisture above a specified minimum. Eligible species are classified into three distinct classes of light-tolerance and different stochastic functions are applied to determine the number of new recruits. In FORET, light tolerance is first applied as

a filter and new saplings established randomly from the list of eligible species – usually one to eight individuals per species per patch in each annual timestep.

In some recent gap models such as FORSKA (Prentice et al., 1993), the regeneration parameter is a *maximum* sapling recruitment rate, based on field observations of sites considered to provide optimal conditions for the regeneration of that species. The actual recruitment rate is then simulated as the product of the maximum rate and one or more environmental constraints represented as continuous multipliers between 0 and 1. This actual establishment rate is used as the input to the RNG to determine how many new individuals are established in the current time step. A similar approach was adopted in JABOWA II, where regeneration is assumed to vary with the same functions of environmental conditions as does growth (Botkin, 1993).

Shugart (1984) argued that it was reasonable to treat regeneration processes very simply because at that time detailed knowledge for most tree species was lacking, and because more rigorous representation of these processes would be too expensive in computing terms. In particular, while it might have been possible to model the more deterministic components such as seed production, the gains from doing this would be marginal, given that sapling establishment appeared to be a random process and was therefore difficult to simulate mechanistically (Shugart, 1984; A. Solomon, 1999, personal communication). A brief review of regeneration algorithms employed in traditional gap models suggests that, with a few recent exceptions, the formulation of regeneration processes has changed very little in the last 15 yr (Table I). This led us to identify three major limitations of particular concern in the context of global change: (1) the treatment of regeneration as a single aggregated process; (2) the assumption of homogeneity in site conditions; and (3) the lack of consideration of forest herbivore impacts.

2.1. TREATMENT AS A SINGLE AGGREGATED PROCESS

Traditional gap models typically represent stand regeneration as the spontaneous appearance in the patch of a number of established saplings each year. There is usually no separate mechanistic treatment of pollination, seed production, dispersal, germination and early seedling development, let alone consideration of the ecophysiology driving these different stages. To be fair, this approach has generally been acceptable for current environmental conditions. In those forests where gap phase dynamics dominate the mortality-regeneration cycle, a supply of shade-tolerant saplings is typically present, even though years or decades may pass while many individuals germinate, establish and eventually die. Conversely for ecosystems where large-scale (stand-replacing) disturbances are frequent (i.e., average return intervals are typically much shorter than the life-spans of the dominant tree species), it is common for prolific seed dispersal and establishment of shade-intolerant pioneers to occur relatively rapidly following disturbance.

Table I

Overview of regeneration processes included in gap-models; a distinction is made between processes at seedling population dynamics level and processes at the individual tree level (> 1.5 m tall) (- not considered; + is considered).

MODEL	Reference	Population dynamics of seedlings ^a				Seedling establishment and growth		Sapling recruitment	
		Seed production	Seed dispersal	Seed germination	Seedling establishment and growth	Recruitment of individual trees (> 1.5 m tall)	Vegetative reproduction		
4C	Bugmann et al., 1997	-	-	+	+	-	-		
FORANAK	Busing and Clebsch, 1987	-	-	-	-	+	+		
FORCLIM-P	Bugmann, 1996	-	-	-	-	+	-		
FORECE	Kienast, 1987;	-	-	-	-	+	-		
	Kienast and Kuhn, 1989								
FORET/	Shugart and West, 1977	-	-	-	-	+	-		
ZELIG	Smith and Urban, 1988								
FORGRA	Jorritsma et al., 1999	+	+	+	+	-	-		
FORSKA	Leemans and Prentice, 1987, 1989; Prentice et al., 1993	-	-	-	-	+	+		
FORSUM	Kräuchi and Kienast, 1993	-	-	-	-	+	-		
GUESS	Smith et al., 2000	-	-	-	-	+	-		
HYBRID	Friend et al., 1993	-	-	-	-	-	-		
JABOWA	Botkin et al., 1972a	-	-	-	-	+	-		
JABOWA-II ^b	Malanson and Armstrong, 1996	-	± ^{for trees}	-	-	-	-		
PICUS ^c	Lexer and Hönninger, 2000	+	+	+	+	+	-		
SPACE	Busing, 1991	-	-	-	-	+	+		

^a Seedlings are individuals < 1.5 m tall or < 1 cm dbh.

^b Patterns in seed-dispersal determine the spatial distribution of recruitment.

^c Regeneration processes are not explicitly modeled, but recruitment of individuals is a function of seed production, dispersal etc.

Table II

Possible responses to changes in some important external factors on forest population dynamics. Changes in external factors are assumed to be increases, based on current trends and projections from General Circulation Models. Hence decreases would be assumed to have opposite effects. Responses are indicated as increase (+), decrease (-), indifferent (0). ? indicates uncertainty

	Temperature	CO ₂	Precipitation	Storm frequency	Fire
Seed production	±	+	±	-	-?
Seed dispersal	0	0	+	+	+?
Seed germination	+	+	±	-	±?
Sprouting (vegetative reproduction)	0	+?	0	+	+?
Seedling establishment and growth	±	+	±	-	±?

In reality, however, the presence of saplings of many tree species in a stand will be determined by several interacting factors not explicitly considered in gap models, of which at least some are potentially sensitive to a changing climate (Figure 1, Table II). Indeed, the climatic variables generally considered to govern tree growth (light, temperature, rainfall) are usually the most critical factors affecting survival of seedlings during establishment. The most obvious example is higher temperatures that increase respiration and transpiration rates while reducing water availability in the surface layers of litter and soil. Climate change effects on other aspects of regeneration may be more subtle, e.g., availability of preferred food sources for browsing mammals may be altered, leading to changes in the grazing pressure exerted on the remaining trees. Consequent changes in habitat are also likely to affect wildlife populations, resulting in additional adjustments to forest composition as the grazing intensity changes. Warmer growing seasons could also trigger explosions in insect populations, leading to extensive defoliations with consequences for seed production. In managed forests, changes in climate may reduce the success of artificial regeneration techniques, and hence require changes to silvicultural practices.

Winter chilling provides a simple example of how the separation of germination and subsequent development could lead to more realistic modeling of regeneration under climate change. In traditional gap models there is no winter chilling requirement, and sapling establishment is generally prevented if a minimum growing-season temperature sum is not exceeded. Using this approach, higher winter temperatures (as projected by GCMs) would then lead to increased sapling establishment. In reality, however, we expect natural regeneration of some species to be significantly reduced because critical chilling requirements, both for seed production and germination, will be met less often. Thus a more sophisticated modeling approach, i.e., one that separates regeneration into distinct stages, should

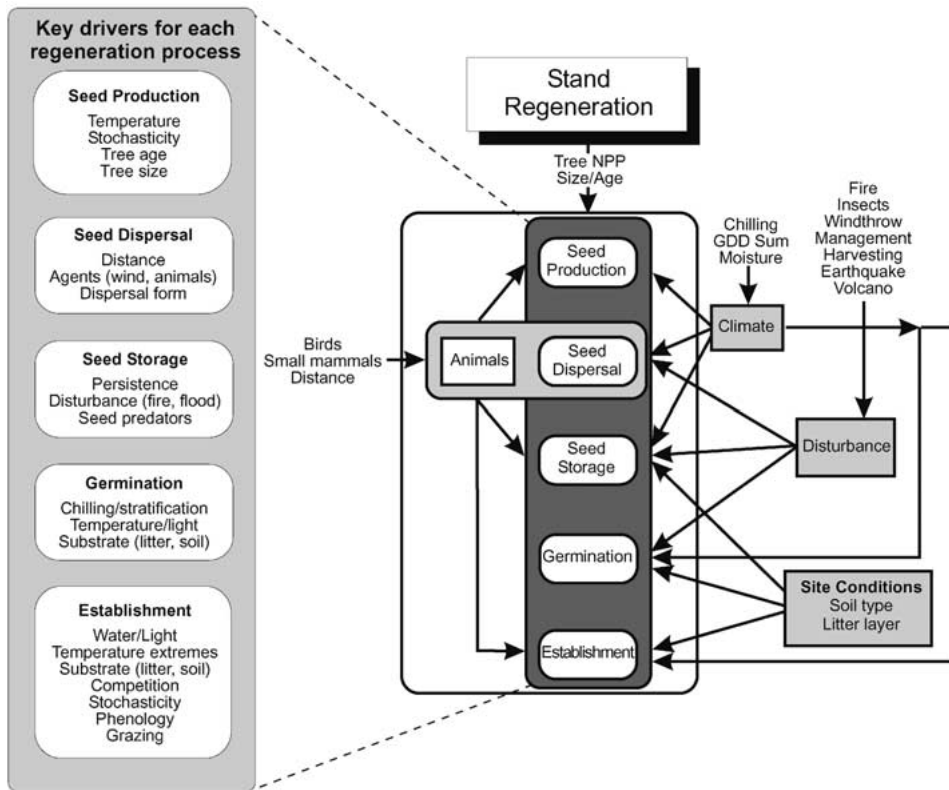


Figure 1. Diagram illustrating how stand regeneration can be disaggregated into component processes, each of which is dependent upon particular biotic and abiotic influences. Each of these separate processes may or may not be a candidate for more detailed representation within new gap model formulations. See text for further explanations. Note: vegetative reproduction is not considered here, but discussed in the text.

enable some of the interacting environmental effects on the component processes to be captured more successfully. The problem is to identify those particular aspects of regeneration that are both critical determinants of stand species composition, yet clearly sensitive to climatic change.

2.1.1. Seed Production

For sufficiently mature trees in temperate and boreal regions, flowering and pollination are generally considered dependent upon temperature or heat sums – although it is usually the thermal regime during a specific period of the year that determines the timing of these phenological stages rather than annual averages or totals. Chuine et al. (1999) showed that flowering of several European trees can be predicted by classical bud-burst models. Best results were obtained when chilling temperatures were coupled to forcing temperatures by a negative exponential relationship. This suggests that flowering may be delayed by warmer winter tem-

peratures, i.e., if the chilling requirement is not fully met. Cannell and Smith (1986) also suggested that warm winters delay flowering and/or cause misshapen flowers that reduce successful pollination. Delayed flowering or impeded pollination would decrease the time available for seed production. Conversely, some studies (Fitter et al., 1995; Maak and von Storch, 1997) suggest that flowering is better determined by the mean temperature of the month before flowering. Hence, increased spring temperatures would advance the time of flowering. Such findings are not necessarily contradictory; they indicate that flowering and seed formation can be correlated either to winter or spring thermal regimes and are therefore sensitive to climatic warming. While the exact nature of these relationships differs among species and requires further investigation, the important lesson is that warmer conditions may cause effects substantially different from those that would be predicted from gap models if the traditional representation of temperature effects on regeneration were employed.

Sykes et al. (1996) developed the first gap models to incorporate winter chilling requirements as a factor determining production of viable seed. Lexer and Hönninger (2000) followed this approach in the PICUS model, where seed production is considered also as a function of parent tree size, and absorbed light. A similar formulation was adopted by Bugmann and Solomon (2000) when modifying FORCLIM for application in the Pacific Northwest of the U.S.A. In the latter region, winter minimum temperatures are often too warm to induce dormancy and hence flowering could be greatly reduced by even slight increases in mean temperatures.

Although relatively little is known about the ecological requirements for most species, seed production is determined by a number of factors that have not traditionally been considered in gap models. These include the age, size and vigour of parent trees, genetic characteristics, and previous reproductive effort, as well as flowering phenology (see above). In general seed production is not directly related to primary production, although in many northern temperate tree species it appears well correlated to the climatic factors that also drive annual growth (see also Norby et al., 2001). Summer temperatures have a particularly marked effect on seed production and the frequency of mast years. For instance, Matthews (1955) found significant correlations between beech (*Fagus sylvatica* L.) masts and July temperature (and sunshine) in the previous year. In the Netherlands, 37 yr of observation provided evidence that seed production in beech, birch (*Betula pendula* Roth), pedunculate oak (*Quercus robur* L.) and Scots pine (*Pinus sylvestris* L.) was significantly affected by weather conditions (particularly temperature and radiation) during the two previous years (LaBastide and Vredenburg, 1970; P. J. van der Meer, unpublished data).

Mencuccini et al. (1995) found that the frequency of Norway spruce (*Picea excelsa* Link) mast years in the eastern Alps decreased with increasing altitude, but was higher on the more fertile north-facing slopes – indicating direct links between favorable environmental conditions and cone production. In Sweden, simple models based on seasonal heat sums have been used to estimate cone production in

Norway spruce and Scots pine. However, Sork et al. (1993) concluded that annual variations in seed production of several North American oak species are not simply a response to weather conditions but also a function of inherent mast-fruiting cycles.

There is also anecdotal evidence that the environmental stresses which lead to reduced productivity may enhance seed production in some species – perhaps as a survival mechanism – though published data in support of this are hard to find. Possibly, the warmer than average summer temperatures that trigger masting are an example of climatic stress. Koenig and Knops (1998) showed that masting involves switching of resources between growth and reproduction; i.e., seed production is often inversely correlated with tree-ring width, because it reduces allocation to stemwood. Such observations suggest that it would be more appropriate to model seed production directly as a function of climatic effects, and in those years when it is predicted, to simulate the consequent effects on annual stem diameter growth. Correlations observed in reality between annual ring width and seed production could be used to validate the modeled estimates of annual diameter increment. Possible drivers would include summer temperature or GDD, moisture availability, and biotic factors, such as abundance of pollinators. A minimum tree size might be specified as a switch for seed production, e.g., in PICUS (Lexer and Hönninger, 1998) seed production is treated as a function of parent tree size, species and leaf area.

2.1.2. *Seed Dispersal*

Seed dispersal in trees depends on the quantity of seeds produced, the adaptations for dispersal, the availability of appropriate dispersal agents (wind, animals) and the distances over which seeds must be transported to encounter new sites suitable for germination. At larger scales, these factors are major determinants of the success and speed of species ‘migration’ along environmental gradients.

Quantifying the potential colonization rates of individual species is crucial for predicting how forest ecosystems can respond to the rapid changes in climate that are forecast (Solomon and Kirilenko, 1997). The most likely outcomes are either invasion of new regions by species better adapted to the altered climate, or else a general impoverishment because these better adapted species cannot arrive at the site rapidly enough to replace those that are in decline. In extreme cases, forests may die back completely to be replaced by shrub or grassland species, e.g., as discussed for the continental climate of Valais by Bugmann (1997). Thus, the introduction of seed dispersal would be a significant conceptual improvement over the traditional assumption that at any given location in a simulated stand, seeds of all species are equally available (Finegan, 1984; see also discussion below). If patches are treated as spatially disconnected samples of a landscape, the effects of processes such as seed dispersal are lost and forest dynamics are removed from their spatial/temporal context (Urban et al., 1999).

There exists a wealth of data characterising anemochorous seed dispersal for North American species (K. R. Brown et al., 1988; Chambers and McMahon, 1994; Farmer, 1997; Green, 1980; Greene and Johnson, 1989, 1995; Matlack, 1987). For European species, such data are available, though less abundant (e.g., Matlack, 1987; Stoecklin and Baeumler, 1996). There are also considerable data indicating that seed predators (birds and small mammals) are important agents in the spread and proliferation of forest trees (e.g., Van der Wall and Balda, 1977; Hutchins and Lanner, 1982; Jensen, 1985; Johnson and Adkisson, 1985; Stapanian and Smith, 1986; Maurer and Heywood, 1993; Botkin, 1992).

Where seed dispersal is represented in gap models, it is most often parameterised using deterministic seed-rain curves. These describe local densities of available seed and germinants, as a function of distance from parent trees. In gap models they can be used to influence the patterns of forest composition emerging from forest dynamics (Pacala and Deutschman, 1995). Some studies indicate that little is known about the importance of the tails of seed rain-curves (Cain et al., 1998; Malanson and Armstrong, 1996; Portnoy and Willson, 1993); i.e., it is unclear which part of a seed rain curve contributes most to the speeds of migration observed at different spatial scales (Cain et al., 1998; Williamson, 1996, 1999). The initial portion of a seed rain curve characterises frequent occurrence of dispersal over short distances (typically within the dimensions of a gap model patch). Conversely, the tail of the distribution represents much rarer long distance seed transport.

2.1.3. *Seed Storage*

Many species store seeds within cones or capsules on the parent tree until released, e.g., in species with serotinous cones. This implies that there may be a lag between seed production and dispersal either for a fixed period, or until the occurrence of a specific disturbance event, such as a fire. Similarly, some hard-seeded tree species establish mainly from seed stored in the soil seed bank, for which germination is delayed possibly by several seasons, or induced by a climatic trigger or a perturbation event.

Serotiny is a mechanism that allows seeds to be stored over several years and then dispersed *en masse* in the period immediately following a fire. Thus maximum dispersal and germination of seeds are automatically timed to coincide with maximum availability of suitable microsites. Such fire-adapted species are important in temperate and boreal landscapes where extensive fires are frequent (e.g., Gauthier et al., 1992, 1996), although interestingly, the only example of a model where serotiny is specifically simulated is the BRIND model applied to ecosystems in Australia (H. H. Shugart, 2000, personal communication). To represent effects of serotiny in jack pine (*P. banksiana* Lamb) in the North American boreal forest, Price et al. (1999) increased the sapling establishment rate of this species by a factor of 10, but only in the first year following a simulated patch disturbance.

Changes in climate are themselves likely to affect the incidence of ecosystem disturbance, a topic reviewed recently by Dale et al. (2001), who highlight a number of impacts on forest regeneration. Disturbances can promote or prevent seed dispersal and hence trigger alterations in the successional pathway, particularly when they are also responding to changes in environmental conditions. Gap models recognise the role of disturbance as a key factor influencing succession but generally treat it as a simple stochastic phenomenon, neglecting climatic influences on the frequency, timing and intensity of events such as wildfires, storm winds and insect outbreaks (Ojima et al., 1991; Turner et al., 1998).

2.1.4. *Seed Germination*

Even though seeds of many species require winter chilling (vernalization) to germinate successfully (e.g., Wareing and Saunders, 1971; Vegis, 1964, 1973), low spring temperatures often delay germination, and short growing seasons can have major impacts on seed production and viability. Black and Bliss (1980) performed comprehensive studies of regeneration in black spruce (*Picea mariana* (Mill.) B.S.P.) along a transect across the northern limits of the Canadian boreal zone, and concluded that "initial germination was the major determinant of stand reproduction". In this extreme environment, they found that germination was impossible where maximum temperatures were normally below 15 C, and that even relatively short periods of below-average temperatures could prevent post-fire germination, hence suggesting a possible mechanism for relatively rapid retreats of the northern boreal tree line in response to periods of colder climate.

The climatic and edaphic factors controlling seed germination are well known for many common species, and are already incorporated in some models as general constraints on sapling recruitment. Possible germination triggers include threshold soil moisture or light levels, chilling or stratification periods, and events such as fires.

Other potential constraints for modeling germination include litter depth and soil type. Heat sums needed for seed germination have been studied extensively by seed physiologists as well as ecologists, although it is only comparatively recently that the variability between and within forest tree species has begun to be explored (e.g., Mohan et al, 1984; Chikono and Choinski, 1992; El Kassaby et al., 1993; Salomao et al., 1996; Hobbie and Chapin, 1998).

2.1.5. *Sprouting (Vegetative Reproduction)*

We estimate that approximately one third of temperate and boreal tree species are able to reproduce vegetatively. Little research has been conducted on either the climate-sensitivity of vegetative regeneration or on its importance in forest succession, but it is clearly an important mechanism by which site occupancy can be achieved rapidly, particularly when climatic conditions such as drought impede seedling establishment (see also Bond and Midgley, 2001a). Vegetative reproduction in forests may be an important issue under climate change, because some

species may survive through continual resprouting in regions where conditions have become too inhospitable for seedling establishment, or disturbances such as fire have become too frequent to allow seed production.

Sprouting of new stems takes advantage of the already established root system of the parent tree, after some portion of the aboveground parts have been killed. In Central Europe, practical experience with coppice management systems has shown that under severe drought conditions, coppiced trees have a competitive advantage (Kasrajan et al., 1974). This would suggest that under a warmer drier climate, shifts could occur in forest composition, towards domination by species with vegetative reproduction. At the southern boundary of the North American boreal zone, aspen (*Populus tremuloides* Michx.) dies back during periods of drought, but is able to regrow in wetter years, allowing it to survive in regions where no other boreal tree species regenerate naturally (Hogg, 1994).

Some traditional gap models allow for vegetative reproduction, based on the relatively simple assumption that production of suckers or other vegetative structures is related to stem dimensions at the time of death (i.e., of the aboveground portions of the tree), as well as to climatic conditions. Typically, these models assume that stems can sprout from 'dead' stumps indefinitely (i.e., assuming that true mortality occurs for other reasons). In reality the potential for sprouting may increase with tree size (Bond and Midgley, 2001a), or it may decrease with increasing age, based on evidence from management of coppice systems in Central Europe (Krissl and Müller, 1989). More detailed field research on this topic is needed. Based on observations for forage plants, sprouting capacity is presumably related to the availability of carbohydrate reserves in the root system, and there is some published evidence for this in trees (Kobe, 1997; Sakai et al., 1997). If climate change affects these reserves, then there could be profound impacts on the success of vegetative reproduction. In particular, elevated CO₂ may increase root storage of non-structural carbohydrates, or average stem diameter growth (assuming other factors are non-limiting) – either of which could increase sprouting success and thus provide a competitive advantage over non-sprouting species (Hoffman et al., 2000; Bond and Midgley, 2001b).

In the VAFS/STANDSIM model of Roberts (1996), sprouting is related to accumulated carbohydrate storage. After the aboveground portion is killed, carbohydrate storage in the root system is assumed to decrease with every time step. For species known to produce suckers (e.g., aspen), simulated sprouting occurs if there is sufficient light to enable growth of the young plant. Carbohydrate storage in the roots is further decreased until the tree reaches maturity, but is then allowed to increase again to a species-specific maximum, as a function of annual stem growth.

2.1.6. *Seedling Establishment and Growth*

It is generally thought that low light intensity at ground level is the primary factor preventing seedling establishment in mature forests (but see Wullschleger et al., 2001). Several shade-tolerant species germinate profusely and subsequently

create a dense mat of small seedlings under the closed forest canopy (e.g., *Tsuga canadensis* (L.) Carr in North America; *Fagus sylvatica* and *Abies alba* Mill. in Europe). Such seedlings may experience virtually no height growth for several years, but can resume rapid growth when released by creation of a canopy gap. Apparently they are able to survive more-or-less indefinitely under conditions in which carbon assimilation through photosynthesis barely meets demand – conditions under which established trees might be expected to undergo stress-induced mortality. Alternatively, it is possible that the seedlings actually die off after a few years, but are replaced periodically in mast years. The former of these explanations would be adequately represented by the traditional gap model assumption of an unlimited supply of saplings, but the latter would require modifications to ensure that parent trees are both within dispersal distance and capable of producing viable seeds (see Section 2.2 below).

For recently disturbed forests (or large gaps in the canopy) where light is not limiting, the top layer of the soil or surface organic layer is subjected to the greatest diurnal temperature extremes, and the greatest depletion in moisture content (e.g., Livingston and Black, 1986). Seedlings and saplings are generally more susceptible than mature trees to drought stress because leaf area and carbohydrate storage capacity are lower and roots smaller and shallower. Limited root development in young seedlings implies that even short-term water deficits in upper soil layers may threaten survival, in contrast to larger saplings, which often survive extended periods of drought. Seedlings are often subject to intense competition from faster growing herbaceous species, as well as being highly vulnerable to damage or mortality due to browsing, whereas survival and growth of mature trees are generally unaffected.

The traditional gap model formulation assumes that seedlings are always available, but regeneration is reduced or prevented when calculated average annual light intensity at the ground falls below a threshold value due to shading by mature trees on the patch. Only the survivors are recruited directly into the stand. Sensitivity to low light conditions is parameterized according to the shade tolerance of the species (e.g., Ellenberg, 1996). This approach greatly simplifies the simulation of competition between seedlings – not only for light but also for nutrients and water. Some gap models estimate seasonal heat sums (total GDD over some temperature threshold) as a climatic factor determining sapling survival, e.g., FORSKA (Prentice et al., 1993). Winter minimum temperature (monthly mean of the coldest month) below a species-specific threshold is also often used to prevent survival of less hardy species. A more mechanistic representation of seedling growth would presumably include separate treatments of assimilation, competition (including allelopathy), responses to water and nutrient stress, and mortality, to be implemented for each stage of plant development from germination to sapling recruitment.

2.1.7. Working Example: Sapling Establishment and Recruitment in 4C

The 4C model (Bugmann et al., 1997; Schaber et al., 1999; Mäkelä et al., 2000) is based on the traditional gap model approach but includes some more mechanistic formulations in its representation of stand development, e.g., for photosynthesis and allocation. The modelled stand is structured into tree cohorts, each comprising a specific number of identical trees growing on a patch of defined area. The regeneration submodel describes the processes of seed germination, growth and mortality of seedling cohorts, and their recruitment into the tree cohorts. A species-specific number of available seeds is first estimated using an approach initially developed in SIMSEED (Rogers and Johnson, 1998). Germination success of these seeds depends on light availability, temperature and moisture conditions in the litter layer. In the current version, however, only the light regime is actually used as a driver. Germination fails if the leaf area index of all seedlings previously established in the layer (0–50 cm height) is greater than 1.0, which indicates total coverage of the patch. Otherwise, the number of germinated seeds is derived from the fraction of the patch not shaded by leaves in the seedling layer.

A single seedling cohort is generated for each species that germinates successfully in a given year. Empirical functions of seed mass are used to estimate total seedling biomass, and the height of each seedling cohort is updated as a nonlinear regression function of shoot biomass (van Hees, 1997). Allocation to biomass in shoot, roots and foliage is based on the functional balance principle (Davidson, 1996; Johnson and Thornley, 1987), which employs allometric relationships derived from data in the literature (e.g., van Hees, 1997). Mortality of seedling cohorts from stress is then simulated as a consequence of an unfavourable carbon balance.

Growth of each seedling cohort is updated annually. Net primary production and phenology are estimated similarly to those of older tree cohorts, using radiation, temperature, CO₂ concentration, water and nutrient availability as inputs. When the simulated height of the seedlings exceeds an arbitrary threshold value, the entire cohort is transformed into a regular tree cohort.

A test of 4C applied to a dense beech (*Fagus sylvatica* L.) stand simulated over several decades verified that the simulated seedlings do not survive until a gap opens in the canopy following death of a large tree, after which classical gap phase dynamics are reproduced. In a second test, stand development was simulated from bare ground using a prescribed number of seedlings to resemble planting. The subsequent simulated trajectories of stem density and biomass compared favourably with yield table data, showing that the transition between the initial seedling development phase and established saplings was captured successfully.

It was also found that both seedling and stand development were reproduced more realistically when seedlings were initialized with different sizes, related to observed distributions of seed mass. This suggests that several cohorts could be introduced each year, in place of a single cohort of identical seedlings. Differences in physiological status among cohorts could then be used to simulate the processes of competition and mortality and the effects of climatic variations.

2.2. ASSUMPTION OF HOMOGENEITY IN SITE CONDITIONS

The second common criticism of regeneration routines in most gap models is that they assume stands are spatially homogeneous; i.e., seeds are dispersed uniformly within a stand, the suitability of the site for germination is uniform and short-term temporal variations in climate and stand structure (which may greatly affect germination success and seedling survival) are completely ignored (but see: Smith and Urban, 1988; and Pacala et al., 1993). A closely related concern is the assumption that each patch is independent of the surrounding landscape, i.e., there is no representation of the spatial connections between the patch being simulated and other patches around it. This unrealistic concept requires the assumption of uniform seed availability for the gap model to work. Together, these problems create major limitations in the model's ability to represent competitive replacement and the provision of regeneration niches (but see Urban and Smith (1989), for a possible solution). Moreover, changes in the trajectories of stand development, particularly those due to changes in climate and disturbance regimes, must affect seed production and dispersal, and hence alter seed availability (Figure 1).

2.2.1. *Effects of Spatial Heterogeneity*

The assumption of uniform regeneration may be acceptable for species that have broad regeneration niches and high dispersal distances, or where parent trees are abundant both within and among sites. In temperate forests, however, there is compelling evidence that most seedling establishment occurs close to parent trees, causing recruitment density to vary within and among gaps. Hence community structure is found to depend strongly on species-specific dispersal characteristics (Ribbens et al., 1994; Houle, 1998; Clark et al., 1999; Nathan and Muller-Landau, 2000). In addition, there is strong differentiation in regeneration niches for some tree species both within and among sites (Gray and Spies, 1997; Ne'eman and Izhaki, 1999; Kwit et al. 2000; Nathan and Muller-Landau, 2000; Van der Meer et al. 1998). This spatial heterogeneity is widely thought to enable the coexistence of two or more species at different microsites within a stand or at different sites in the landscape (Pickett and White, 1985; Wu and Levin, 1994).

A clear example of the importance of heterogeneity in controlling regeneration comes from a long term study in a beech-maple forest which showed that recruitment in 36 canopy gaps was correlated with seed source proximity and differences in site quality (Kupfer and Runkle, 1996). Such observations strongly suggest that forest diversity is partially explained by interactions between niche differentiation and dispersal limitations – occurring at spatial scales that could be classified in most gap models as the '*within-patch*' and '*between-patch*' scales.

The lack of representation of spatial heterogeneity in a gap model, within and among patches, could seriously hamper its capacity to predict correctly the effects of climate change on forest diversity. This would be particularly true if (1) dispersal mechanisms are affected by climatic change (see section 2.1.2), or (2) changes

in *average* environmental conditions caused by climate change do not adequately represent changes in the range and diversity of regeneration niches. For example, a patch (or group of patches) that is classified on average as having ‘optimal moisture’ for the establishment of a particular species might in reality contain a mixture of microsites (or patches) that are ‘too wet’, ‘optimal’ and ‘too dry’. A change in average conditions from ‘optimal’ to ‘too dry’ would then lead to the elimination of that species in most gap models – even though in reality a number of ‘optimal’ microsites (or patches) might remain (i.e., those that were shifted from ‘too wet’ to ‘optimal’ after climate change).

2.2.2. *Seed Availability and Competitive Dominance*

Gap dynamic models have proven successful in reproducing both the changes in species dominance observed during stand development, and the maintenance, in mature forests, of communities containing both early and late-successional species. Clark and Ji (1995) have argued, however, that this success may be due partly to two opposing sources of error in the simulation of regeneration processes – leading to the ‘right answer for the wrong reasons’. On the one hand, diversity tends to be exaggerated by the assumption of a uniform seed supply, which enables inferior competitors to maintain populations under conditions in which they would otherwise succumb to competitive exclusion (Pacala and Hurtt, 1993). In reality, establishment success within a plant community is affected by seed availability (Finegan, 1984; Loehle and LeBlanc, 1996), and seed pools are unlikely to be distributed uniformly among patches (e.g., Beatty, 1984; Houle, 1992; Shibata and Nakashizuka, 1995; Clark et al. 1998b). On the other hand, the absence of dispersal constraints would tend to increase dominance by species that are competitively superior, but happen to have poor seed dispersal ability. The latter effect would tend to compensate for the former by reducing net diversity.

If correct, Clark and Ji’s (1995) assertion tends to undermine confidence in the predictions made by present-day gap models when driven by climate data other than those for which they have been calibrated and tested. For example, Solomon and Kirilenko (1997) found that the assumption of uniform seed availability typically caused overestimation of migration rates in simulations of forest responses to climate change.

2.2.3. *Effects of Climate Change on Forest Migration*

It is generally accepted that changes in past climate have caused changes in species distribution, both geographically (Webb, 1981; Davis et al., 1986; Prentice, 1986; Ritchie, 1986), and with altitude, e.g., near the tree-line (Gear and Huntley, 1991; Kullman and Engelmark, 1991; Grabherr et al., 1994; Wick and Tinner, 1997; Lotter et al., 1998). Indeed, paleo-ecological studies have established that most modern species assemblages do not have long histories (Davis, 1983; Birks, 1993). There is general agreement that species migrated following changes in the Holocene climate and that each species did so individualistically (Prentice et al., 1991). Moreover,

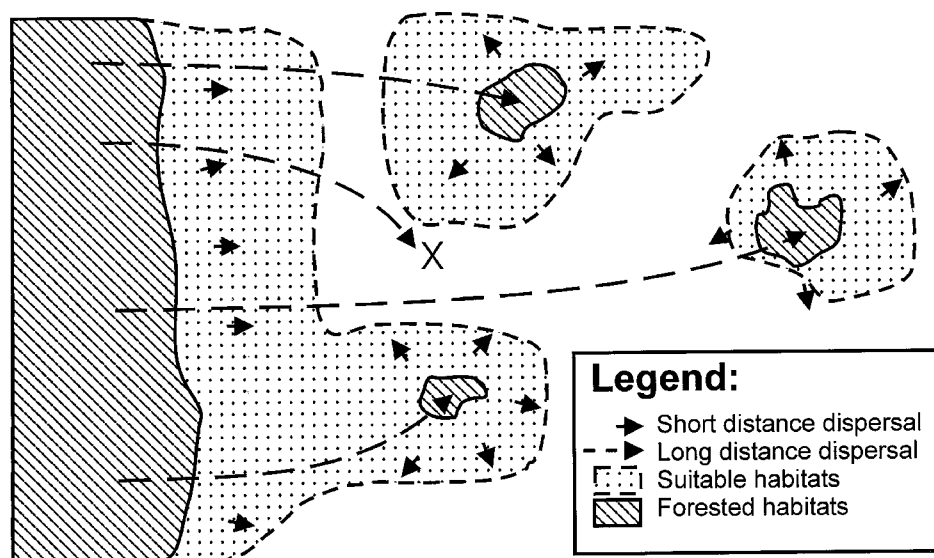


Figure 2. Diagram of conceptual model of seed dispersal: Dispersal can be viewed as operating at different scales, with each scale applicable to different processes.

it has been determined that species range expansions did not follow continuous population fronts, but instead occurred through establishment of advance colonies, with later occupation of the spaces in-between (Pielou, 1979; Hengeveld, 1989; Figure 2).

Controversy remains as to whether these population responses are an expression of dynamic equilibrium (Webb, 1986; Prentice et al., 1991), or instead show signs of lags in the readjustment of vegetation composition due to differences in migration rates (Bennet, 1983; Davis, 1989; Lotter et al., 2000). This has also led to speculation that differences in seed dispersal characteristics have limited tree migration in the past (i.e., causing the lags following the Holocene climate change (Prentice et al., 1991; Melillo et al., 1996; Pitelka et al., 1997). This problem is not easy to resolve due both to uncertainties in dating paleo-ecological records, and to the coarse spatial resolution of the paleo samples. Recent work suggests that some tree species migrated very fast to form advance colonies far from the moving front (Kullmann, 1996, 1998), thus indicating dynamic equilibrium, but that local disequilibrium with climate also occurred due to migrational lags when long-range dispersal was absent (Lotten et al., 2000).

Modern analyses of paleo-ecological data have shown that in some regions tree species have migrated at rates of up to 4 km yr^{-1} in eastern North America, regardless of their dispersal mechanism (King and Herstroem, 1997). To put this in perspective, some climatic zones are expected to shift polewards at average rates of $4\text{--}6 \text{ km yr}^{-1}$ as the global climate warms (Solomon et al., 1984), which is an order of magnitude greater than the average past migration rate of trees (Solomon,

1997), and even exceeds King and Herstroem's (1997) estimate. Such observations suggest that seed dispersal may well limit future migration, particularly in highly fragmented landscapes where successful colonization will be limited to relatively few suitable regeneration sites (Melillo et al., 1996; Iverson and Prasad, 1998).

2.2.4. *Possibilities for Remediating Spatial Limitations of Gap Models*

Modifications to a gap model to represent spatial heterogeneity must generally be accompanied by better representations of seed dispersal and seedling establishment. This implies the development of explicit linkages between seed sources (mature trees) and germination sites (i.e., newly created gaps, newly disturbed patches, or other suitable microsites). There is a serious risk, however, that such 'improvements' may cause over-sensitivity to parameterization – a common problem when adding complexity to models (e.g., see Reynolds et al., 1993). Furthermore, they will result inevitably in greater data needs and more tedious model validation.

Although such linkages are not usually present in existing gap models, spatially-configured vegetation simulators that represent seed dispersal as a distinct process have been developed. Dyer (1995) studied species migration for wind and animal dispersed species using cellular automata with landscape barriers, but neglected other forest processes. Kienast (1987) coupled seed availability to the presence of parent trees of the same species, thereby reducing (or eliminating) the probability of establishment of species not present in the simulated stand, but did not consider spatial heterogeneity in germination sites. Several forest succession models have since been developed to simulate spatially-explicit forest dynamics, of which a few include subroutines to represent seed dispersal and/or spatial heterogeneity effects on seed availability within a simulated stand (e.g., Lexer and Hönninger, 2000; Pastor et al., 1999).

The common approach employs an array of *contiguous* patches with 10–30 m node separation. ZELIG (Smith and Urban, 1988; Urban and Smith, 1989; Urban 1990) was probably the first gap model to be used in this way to create a grid-based forest simulator, where trees cast shade on adjacent cells. Modifications to ZELIG to include effects of spatial heterogeneity on seed dispersal have been explored, though not yet published (D. Urban, 2000, personal communication). The FORMIX-based models (Bossel and Krieger, 1991, 1994; Koehler and Huth, 1998; Huth and Ditzer, 2000) have been used to simulate dynamics in tropical dipterocarp forests using a 5 by 5 spatial grid where seeds, shade and falling trees affect neighbouring cells. Malanson and co-workers applied a spatially explicit extension of JABOWA-II (Botkin, 1993) called MOSEL, that includes seed dispersal, to a series of artificial landscapes (Hanson et al., 1989, 1990; Malanson et al., 1996). MOSEL has been used to analyse the effect of seed dispersal on diversity in different landscape fragmentation schemes (Malanson and Armstrong, 1996); to study the effect of seed diffusion and density-dependent mortality on species diversity (Malanson, 1996); to test effects of (positive) feedbacks and seed

rain on ecotone patterns (Malanson, 1997); and to simulate the effects of dispersal and fragmentation-related factors on migration rates of forest trees (Malanson and Cairns, 1997).

Pastor et al. (1999) used a spatially explicit version of the LINKAGES model (Pastor and Post, 1985; Post and Pastor, 1996) to investigate interactions between seed dispersal habits and nutrient cycling. In boreal forests, the litter from deciduous pioneer species such as birch and aspen decomposes quickly, whereas shade-tolerant conifers, such as spruces, which typically establish below the broadleaved species, produce more recalcitrant litter, and hence retard nitrogen (N) cycling. The pioneers also produce buoyant seeds that are easily dispersed into newly created openings (e.g., those caused by fires) whereas the conifers produce denser seed that are generally dispersed close to parent trees and hence form more clumped distributions. Pastor et al. (1999) analysed the effects of different seed dispersal distances on modelled distributions of biomass production and N cycling, and were thus able to demonstrate that these differences contribute to spatial patterning at larger scales.

Such models retain consistency with the original gap model concept, i.e., that within individual patches, competition among trees can be adequately represented without distance-dependent processes. Seed dispersal, however, is represented on the basis of distances between patches (e.g., patch centre to patch centre). Seed densities and microsites are considered uniform within each patch but may differ between patches. Mature parent trees must be present in at least one patch in order for seeds to be available, but within the array of patches, seeds can be dispersed from parent trees to germination sites across patch boundaries.

With such an approach, environmental factors could be derived from topographic information (altitude, slope, aspect, water flow routes, etc.) and other spatially explicit data (e.g., parent material, soil type, land use history) to define mean site quality for each patch. The assumption is that variability in the key site factors influencing regeneration and establishment of different species will be adequately represented by differences in mean conditions for each patch. Patch-level dynamics would then operate as in a traditional gap model, but would be influenced by the site conditions found in each patch, hence replacing some stochasticity by determinism. Note, however, that such representations of seed dispersal would not be applicable to the landscape-scale processes driving species migration (i.e., with dispersal distances of the order of 1 km or greater).

2.2.5. Working Example: Seed Dispersal and Occupation of Microsites in PICUS
The PICUS model (Lexer and Hönninger, 1998, 2000) is one of a few gap models to incorporate simultaneous treatment of seed dispersal and spatial heterogeneity. In PICUS, mature parent trees must be present for seed production to occur. For each parent tree, seed production is estimated as a function of tree size, species and light interception (based on leaf area), and a notional maximum seed production potential estimated for an open-grown tree. Seed production is also dependent upon

whether winter chilling requirements have been met (following Sykes et al., 1996). Observations of seed production in mast years (e.g., as reported by Rohmeder, 1972) are used to calibrate this maximum, and to determine appropriate random seed year intervals for each species. Seed dispersal is represented as a true conical distribution centred around each parent tree. Each cone is defined by the tree's height and the maximum dispersal range determined for each species, based on typical seed buoyancy and an assumed mean wind speed in the stand of 2.5 m s^{-1} (Rohmeder, 1972; Landsberg, 1986). Total seed availability for each species per patch is then calculated from the integrals of all the distribution cones overlapping within that patch. For those species where dispersal by animals is known to be important, a maximum dispersal range from each parent tree is assumed. A fixed percentage of each tree's seed production is assumed to be evenly distributed by animals based on observations. The number of potential seedlings per species and patch is given by the seed potential in each patch, but reduced by a species-specific germination rate. This number is then modified by the environmental response of each species to current microsite conditions (including temperature, available light below the canopy, and soil moisture and nutrients).

As with traditional gap models, established saplings enter the stand at an initial size of approximately 1 cm DBH, subject to an imposed maximum density of one individual per m^2 of stockable area (following Shugart, 1984). The proportion of patch area available for stocking is an externally imposed patch-specific attribute; e.g., soil moisture and nutrient status may vary among patches. The proportion of tree positions open for establishment of saplings in a given year is a function of how well the prevailing site conditions meet the requirements of each species represented in the seed supply, thus allowing slow regeneration at extreme sites to be simulated. With this approach, the time needed for successful regeneration of a given area depends partly on the physiological suitability of available species and not entirely on seed availability. For each patch, a uniform RNG is used to determine which species (of those with seeds available) will regenerate in each unoccupied microsite.

Although PICUS has been applied in several experiments (Lexer and Hönninger, 1998; Lexer, 2001; Jäger et al., 2000), tests are still in progress to assess the simulation of spatially-explicit seed production and dispersal on heterogeneous sites.

2.3. LACK OF HERBIVORE IMPACTS

Herbivores have substantial effects on plant growth (e.g. Crawley, 1983), but this has only rarely been addressed in forest gap models. Vertebrate herbivores (primarily rodents, ungulates and birds) affect forest ecosystems mainly by direct browsing of leaves and predation of seeds (Jensen, 1985; Hutchins and Lanner, 1982; Johnson and Adkisson, 1985; McInnes et al., 1992; Stapanian and Smith, 1986). Selective feeding on seedlings and saplings by large herbivores can change species

composition and consequently the availability of their present-day food sources (e.g., Van Wieren, 1996). This feedback mechanism has important consequences for population dynamics of both herbivores and plants.

Invertebrate herbivores (mainly insects) generally have most impact on adult trees, rather than on seedlings, but given that some forest pest insects are able to develop faster under warmer conditions (e.g., Fleming and Volney, 1995; Régnière and Sharov, 1999), their capacity to affect forest regeneration could be significant. Insect herbivores such as bark beetles may affect tree and seedling survival mainly through the spread of pathogens, although many are efficient defoliators that in large numbers can cause widespread mortality and stand replacement. Some defoliators, such as spruce budworm (*Choristoneura fumiferana* Clemens), may also attack cones and hence destroy seeds directly (Turgeon and de Groot, 1992). Insect herbivory is characterised by periodic outbreaks showing a more or less random frequency (Brown et al., 1988), but often appears correlated to extreme weather events (Fleming and Volney, 1995).

To include effects of animals on regeneration and growth in gap models, two approaches are possible: (1) a mechanistic herbivory module such as that used in FORGRA (Jorritsma et al., 1999) or (2) a more empirical model of herbivory. Empirical approaches may be easier to develop accurately but are generally more site-specific, and therefore less suitable for simulating new systems, such as those resulting from climate change scenarios. The mechanistic approach requires detailed knowledge of the grazing process and may have greater levels of uncertainty (Sharpe, 1990). Here we provide examples of both approaches for both vertebrate and invertebrate grazers.

FORET (Shugart and West, 1977) and its derivatives (eg., FORENA, Solomon, 1986; ZELIG, Urban and Smith, 1989; and others) treat grazing superficially by decreasing in random years, the regeneration success of species identified as vulnerable to wildlife. Pastor and Naiman (1992) simulated vertebrate (beaver and moose) herbivory by simply removing fixed percentages of newly formed twigs. The adjusted FORECE model (Kienast et al., 1999) simulates grazing by ungulates as a function of site-specific browsing intensity (using empirical field data), and species-specific sensitivity of growth reduction due to browsing stress (Kienast, 1987). Pastor et al. (1999) explored a mechanistic approach to simulating effects of browsing preferences of moose on boreal forest spatial heterogeneity, although this was not linked to a gap model. FORGRA (Jorritsma et al., 1999) is one of the few gap models in which ungulate grazing has been considered more mechanistically: diet choice of large herbivores is not fixed, but depends on the best food available (Table III).

When simulating the impacts of insect herbivory, the key processes are generally treated as random events. In Dyer and Shugart (1992), an insect population outbreak is simulated using a random number generator. Lexer and Hönninger (1998) included mortality due to bark beetles (*Ips typographus*) in the PICUS model (see also Keane et al., 2001). The BOREALIS model of Clark et al. (D.

Table III
Examples of forest models simulating animal impacts on forest dynamics and stand structure

Model	Approach	Herbivores included	Foliage consumption algorithm	Impacts
FORGRA (Jorritsma et al., 1999)	Mechanistic	Ungulates (four species)	Function of herbivore biomass; tree species are consumed according to palatability (diet choice)	Reduces growth and increases mortality
FORECE (Kienast, 1987; Kienast and Kuhn, 1989; Kienast et al., 1999)	Quantitative	Ungulates (three species)	Site-specific, empirically derived browsing intensities are used against a species-specific growth sensitivity to browsing (see Kienast, 1987)	Reduces growth and increases mortality of seedlings; changes species composition and stand structure
FORCLIM (Bugmann, 1996)	Quantitative	Not specific	Assumes 'normal' rate of herbivory, and year-to-year deviations on a scale of 1–9 (5 = normal rate)	Increases mortality
BOREALIS (Clark et al., pers. comm)	Mechanistic	Insects capable of killing trees	Affected species are defoliated and die	Reduces growth and increases mortality
PICUS (Lexer and Hönninger, 1998)	Quantitative	<i>Ips typographus</i> , <i>Pityogenes</i> <i>chalcographus</i>	Probability of attack is estimated from stand and climatic variables; damage intensity is estimated from stand variables	Distribution of killed trees is modelled in a spatially explicit manner

F. Clark, 2000, personal communication) simulates outbreaks of spruce budworm observed in eastern Canadian boreal forests (Bergeron et al., 1995; Bergeron and Leduc, 1998; Gray et al., 1999). In all cases, the simulation approaches are empirical, and therefore largely overlook the detailed interactions between pest populations and forest dynamics; we are not aware of a single mechanistic approach used to model insect grazing in forests at the patch level. The integration of patch-level simulators into landscape scale models of insect population dynamics (such as Holling's (1992) conceptual framework for simulating insect outbreaks and forest responses in boreal landscapes), would appear necessary to properly account for these interactions, under both present-day and possible future climates.

2.3.1. Working Example: Herbivore Impacts on Regeneration in FORGRA

In FORGRA (Jorritsma et al., 1999), establishment of new individuals in a patch results from a number of interacting processes and factors, including: seed pro-

duction, dispersal, predation, viability and germination, followed by seedling competition and ungulate grazing. In comparison to the random herbivory in the FORET type models, herbivory in FORGRA is modelled more mechanistically and affects both seed availability and seedling mortality. In the model, seed consumption of certain species (e.g., *Quercus robur* L. and *Fagus sylvatica* L.) is considered dependent upon the population densities and species of herbivores, as well as on other food sources available to them. The total number of seeds available for regeneration in each patch is then the sum of seed production in the patch plus seeds entering from adjacent patches and surrounding stands, minus seeds which are either consumed or dispersed to other patches.

Mortality of seedlings depends on competition for light and space, and on the presence of herbivores. Competition for light is translated into a mortality rate related to light availability. Competition for space is calculated from total seedling biomass in a plot, using the self-thinning rule (Begon et al., 1996). Mortality from herbivory is determined by the biomass of seedlings consumed by the herbivores, which is then translated into an equivalent number of whole plants.

The detailed mechanistic approach as applied in the FORGRA model provides us with a useful tool to study the role and impacts of ungulate grazing in forests. Results show that ungulate grazing can have a significant effect on forest regeneration success, and that inter-specific differences in palatability affect the long-term development of forests (Jorritsma et al., 1999). This emphasizes the need to include ungulate grazing and other forms of herbivory in forest gap models.

3. Concluding Remarks

We have discussed whether gap models can be useful for examining ecosystem responses to climatic change, by exploring the typical limitations of these models in capturing the climate-sensitive aspects of regeneration. While there is little to be gained by including more detailed representations of the processes underlying regeneration without reason, we have been able to identify several specific instances where this could prove justified. It may be possible to assess the case for additional processes more objectively than has been done here, e.g., by a more theoretical analysis. For the most part, these assessments are based on the observation that gap models fail to account for key mechanisms in regeneration that could be strongly influenced by climate change and, therefore, that more mechanistic simulations should improve things.

Forest regeneration is usually studied at small scales, but the primary application for gap models (as with most models) is to make predictions at the stand level or larger scales. Hence, further improvements to the representation of regeneration processes in gap models will depend on the evaluation of simulated results compared to patterns of regeneration observed at the scale at which the models

are applied. If this is not done, then the assumption that adding more detail will improve model performance and credibility will not have been adequately tested.

This concern is particularly true of the trend towards models that consider spatial issues such as site heterogeneity, seed dispersal and disturbances. Even though such models may appear to work, comprehensive validation of the effects of spatial connectedness on successional dynamics and species composition is still largely missing. Modeling spatial aspects seems to be crucial for simulating migration and changes in species composition under climate change. Although current models such as ZELIG and PICUS can be used successfully to simulate seed dispersal at smaller scales (i.e., over the domain of a spatially-explicit gap model, say 20 ha or less), a fully dynamic simulator of forest migration (at scales > 1.0 km) in natural landscapes remains to be tackled (e.g., see Mladenoff and Baker, 1999).

The major limitations in using traditional gap models to assess climate change impacts on forest regeneration seem fairly clear:

- (1) processes are aggregated in such a way that simulated changes in climate are likely to produce appreciably different results from those obtained if these processes are treated separately;
- (2) assumption of uniformity in site conditions and seed availability could lead to underestimation of species impoverishment and overestimation of forest migration rates; and
- (3) effects of insect and vertebrate herbivores, though largely unknown and rarely considered in gap models, could prove extremely important.

For each of these limitations we attempted to highlight the critical problems, and then suggested possible approaches for solving them. Clearly not all aspects of simulated regeneration in gap models need to be developed further in order to improve performance. Of the problems we identified, the most crucial appear to be the following, although no particular priority is intended because their relative importance will vary in different regions of the globe:

- *Seed production*: effects of climate change on winter chilling requirements for breaking dormancy, and successful flowering (scales: local to subcontinental).
- *Seed production*: effects of climate on the occurrence of mast seeding at the patch level, recognizing that the physiological controls are as yet poorly understood. This would enable consequences at larger scales to be investigated (scales: local to subcontinental).
- *Seed dispersal and availability*: interactions between seed dispersal mechanisms and spatial variability in site conditions as determinants of succession and migration in a changing global climate (scales: local to subcontinental).
- *Establishment*: occurrence of drought as a factor influencing seedling survival, and affecting vegetative regrowth (scale: local).
- *Sprouting*: the role of vegetative reproduction as an alternative strategy for recolonization following disturbance; and the effects of environmental change,

including increasing atmospheric CO₂, on the success of this strategy (scales: local to regional).

- *Animal effects*: investigation of potential responses of insect pest populations to climate change and effects on forest vegetation as food sources for all herbivores through habitat shifts (scales: local to subcontinental for ungulates; regional to global for insects).

Many of these crucial problems result from a lack of knowledge of the effects of climate on some aspects of forest regeneration, suggesting specific areas for further field research (and an opportunity for greater collaboration between modellers and experimentalists!). These include:

- Investigation of the effects of winter and spring thermal regimes on flower development and seed production (see 2.1.1). Depending on species, it appears that warmer conditions may cause serious harm or could be beneficial. Such differences need to be classified, not least because they could result in rapid shifts in relative dominance in communities where species in both classes presently co-exist.
- Information on potential colonization rates for dominant (or economically important) species in the major forest biomes (see 2.1.2). In particular, what are the characteristics of seed rain curves that determine colonization rates for individual species, and are these likely to be affected by changes in climate?
- Detailed ecophysiological studies of seed production and seedling establishment in a range of environments are required to validate process models of seedling growth and mortality, such as those being implemented in 4C (see 2.1.7). Particular questions include: what are the effects of climate on seed mass and the consequences of this for germination success and seedling survival (section 2.1.7)?; and how do the heat sums required for germination vary within and among species (section 2.1.4)?
- Similarly, stand-level studies of the processes of seed dispersal, storage and germination are needed to support further development of regeneration algorithms in spatially explicit models, e.g., PICUS (section 2.2.5).
- Finally, there is great uncertainty concerning the sensitivity to climate and elevated CO₂ of species that reproduce vegetatively (section 2.1.5). What are the ecological advantages and disadvantages of asexual regeneration under climate change, as compared to seeding? In particular, are species that reproduce primarily by sprouting at a major disadvantage when faced with the need for rapid migration?

The key recommendation to modelers concerned with investigating and overcoming any of these limitations (either in algorithms or available data) is to test more detailed model formulations and to assess, as rigorously as possible, what improvement (or degradation) in performance is achieved. In essence we conclude that gap models are likely to be useful for investigating climate change effects on

forest ecosystems, but we cannot determine what level of improvement will be achieved in their predictive power if more detailed representations of regeneration are included. It is doubtful whether the gains from such modifications can be quantified at present because very few experiments have been carried out to assess them objectively. State-of-the-art models like 4C, PICUS and FORGRA already have routines which go some way to addressing many of the important concerns (albeit using mostly empirical approaches), and which should be tested as widely as possible. Other existing models contain additional ecophysiological details that could presumably be adapted to improve simulation of seedling survival and early growth if needed.

Acknowledgements

We are grateful to Lou Pitelka, Harald Bugmann, and Jim Reynolds, and to John Pastor and an anonymous reviewer for their many helpful and constructive suggestions regarding the development and improvement of this article. This paper arose from a workshop on forest gap models held at Pingree Park, Colorado, in July 1999. The workshop was a joint activity of the Ecosystem Structure (Focus 2) and Ecosystem Physiology (Focus 1) elements of the Global Change and Terrestrial Ecosystems (GCTE) project of the International Geosphere-Biosphere Program (IGBP) and was sponsored by grants from the National Science Foundation (DEB-98-12440), the U.S. Department of Energy (DE-FG02-98ER62694) and the U.S. Forest Service.

References

- Beatty, S. W.: 1984, 'Influence of Microtopography and Canopy Species on Spatial Patterns of Forest Understorey Plants', *Ecology* **65**, 1406–1419.
- Begon, M., Harper, J. L., and Townsend, C. R.: 1996, *Ecology: Individuals, Populations and Communities, Third Edition*, Blackwell Science, Oxford, p. 1068.
- Bennet, K. D.: 1983, 'Postglacial Population Expansion of Forest Trees in Norfolk, U.K.', *Nature* **303**, 164–167.
- Bergeron, Y. and Leduc, A.: 1998, 'Relationships between Change in Fire Frequency and Spruce Budworm Outbreak Severity in the South-Eastern Canadian Boreal Forest', *Journal of Vegetation Science* **9**, 492–500.
- Bergeron, Y., Morin, H., Leduc, A., and Joyal, C.: 1995, 'Balsam Fir Mortality following the Last Spruce Budworm Outbreak in Northwestern Quebec', *Can. J. Forest Res.* **25**, 1375–1384.
- Birks, H. J. B.: 1993, 'Quaternary Paleoecology and Vegetation Science – Current Contributions and Possible Future Developments', *Reviews in Palaeobotany and Palynology* **79**, 153–177.
- Black, R. A. and Bliss, L. C.: 1980, 'Reproductive Ecology of *Picea mariana* (Mill.) B.S.P., at Tree Line near Inuvik, Northwest Territories, Canada', *Ecol. Monogr.* **50**, 331–354.
- Bond, W. J. and Midgley, J. J.: 2001a, 'Ecology of Sprouting in Woody Plants: the Persistence Niche', *Trends in Ecology and Evolution*, **10**, 45–51.
- Bond, W. J. and Midgley, G. F. A.: 2001b, 'A Proposed CO₂-Controlled Mechanism of Woody Plant Invasion in Grasslands and Savannas', *Global Change Biology*, in press.
- Bossel, H. and Krieger, H.: 1991, 'Simulation Model of Natural Tropical Forest Dynamics', *Ecol. Modelling* **59**, 37–71.

- Bossel, H. and Krieger, H.: 1994, 'Simulation of Multi-Species Tropical Forest Dynamics using a Vertically and Horizontally Structured Model', *Forest Ecol. Manage.* **69** (1–3), 123–144.
- Botkin, D. B.: 1992, 'Global Warming and Forests of the Great Lake States, an Example of the Use of Quantitative Projections in Policy Analysis', in Schmandt, J. and Clarkson, J. (eds.), *The Regions and Global Warming, Impacts and Response Strategies*, Oxford University Press, New York, pp. 154–161.
- Botkin, D. B.: 1993, *Forest Dynamics, an Ecological Model*, Oxford University Press, Oxford.
- Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1972a, 'Some Ecological Consequences of a Computer Model of Forest Growth', *J. Ecol.* **60**, 849–872.
- Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1972b, 'Rationale, Limitations and Assumptions of a Northeastern Forest Growth Simulator', *IBM Journal of Research and Development* **16**, 101–116.
- Brown, K. R., Zobel, D. B., and Zasada, J. C.: 1988, 'Seed Dispersal, Seedling Emergence, and Early Survival of *Larix laricina* (DuRoi) K. Koch in the Tanana Valley, Alaska', *Can. J. Forest Res.* **18**, 306–314.
- Brown, V. K., Gange A. C., and Gibson, C. W. D.: 1988, 'Insect Herbivory and Vegetational Structure', in Werger, M. J. A., van der Aart, P. J. M., During, H. J., and Verhoeven, J. T. A. (eds.), *Plant Form and Vegetation Structure*, Academic Publishing BV, The Hague, pp. 263–279.
- Bugmann, H.: 1996, 'A Simplified Forest Model to Study Species Composition along Climate Gradients', *Ecology* **77**, 2055–2074.
- Bugmann, H.: 1997, 'Sensitivity of Forests in the European Alps to Future Climatic Change', *Clim. Res.* **8**, 35–44.
- Bugmann, H.: 2001, 'A Review of Forest Gap Models', *Clim. Change* **51**, 259–305.
- Bugmann, H., R. Grote, R., Lasch, P., Lindner, M., and Suckow, F.: 1997, 'A New Forest Gap Model to Study The Effects of Environmental Change on Forest Structure and Functioning', in Mohren, G. M. J., Kramer, K., and Sabaté, S. (eds.), *Impacts of Global Change on Tree Physiology and Forest Ecosystems*, Kluwer Academic Publishers, Dordrecht, pp. 255–261.
- Bugmann, H. K. M. and Solomon, A. M.: 2000, 'Explaining Forest Composition and Biomass across Multiple Biogeographical Regions', *Ecol. Appl.* **10**, 95–114.
- Busing, R. T.: 1991, 'A Spatial Model of Forest Dynamics', *Vegetatio* **92**, 167–191.
- Busing, R. T. and Clebsch, E. E. C.: 1987, 'Application of a Spruce-Fir Forest Canopy Gap Model', *Forest Ecol. Manage.* **20**, 151–169.
- Cain, M. L., Damman, H., and Muir, A.: 1998, 'Seed Dispersal and The Holocene Migration of Woodland Herbs', *Ecol. Monogr.* **68**, 325–347.
- Cannell, M. G. R. and Smith, R. I.: 1986, 'Climatic Warming, Spring Budburst and Frost Damage on Trees', *J. Appl. Ecol.* **23**, 177–191.
- Chambers, J. C. and MacMahon, J. A.: 1994, 'A Day in the Life of a Seed: Movements and Fates of Seeds and their Implications for Natural and Managed Systems', *Ann. Rev. Ecol. Syst.* **25**, 263–292.
- Chikono, C. and Choinski, J. S. Jr.: 1992, 'Thermotolerance Characteristics of Seeds from Geographically Isolated Populations of the African Tree *Combretum apiculatum* Sonder', *African J. Ecol.* **30**, 65–73.
- Chuine, I., Cour, P., and Rousseau, D. D.: 1999, 'Selecting a Model to Predict the Timing of Flowering of Temperate Trees: Implications for Tree Phenology Modelling', *Plant, Cell Environ.* **22**, 1–13.
- Clark, J. S. and Ji, Y.: 1995, 'Fecundity and Dispersal in Plant-Populations – Implications for Structure and Diversity', *Amer. Nat.* **146**, 72–111.
- Clark, J. S., Fastie, C., Hurr, G., Jackson, S. T., Johnson, C., King, G. A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E. W., Webb III, T., and Wyckoff, P.: 1998a, 'Reid's Paradox of Rapid Plant Migration – Dispersal Theory and Interpretation of Paleoeological Records', *BioScience* **48**, 13–24.
- Clark, J. S., Macklin, E., and Wood, L.: 1998b, 'Stages and Spatial Scales of Recruitment Limitation in Southern Appalachian Forests', *Ecol. Monogr.* **68**, 213–235.

- Clark, J. S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J.: 1999, 'Seed Dispersal Near and Far, Patterns Across Temperate and Tropical Forests', *Ecology* **80**, 1475–1494.
- Crawley, M. J.: 1983, *The Dynamics of Animal-Plant Interactions*, Blackwell Scientific Publications, Oxford, U.K.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., and Wotton, B. M.: 2001, 'Disturbances, Agents of Forest Transformation under a Changing Climate', *BioScience* **51**, 723–734.
- Davidson, R. L.: 1996, 'Effect of Root/Leaf Temperature Differentials on Root/Shoot Ratios in Some Pasture Grasses and Clover', *Ann. Botany* **33**, 561–569.
- Davis, M. B.: 1983, 'Holocene Vegetational History of The Eastern United States', in Wright, H.E. (ed.), *Late-Quaternary Environments of the United States*, University of Minnesota, Minneapolis, pp. 166–181.
- Davis, M. B.: 1989, 'Lags in Vegetation Response to Greenhouse Warming', *Clim. Change* **15**, 75–82.
- Davis, M. B., Woods, K. D., Webb, S. L., and Futyma, R. P.: 1986, 'Dispersal versus Climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes', *Vegetatio* **67**, 93–103.
- Dyer, J. M.: 1995, 'Assessment of Climatic Warming Using a Model of Forest Species Migration', *Ecol. Modelling* **79**, 199–219.
- Dyer, M. I. and Shugart, H. H.: 1992, 'Multi-level Interactions Arising from Herbivory: A Simulation Analysis of Deciduous Forests Utilizing FORET', *Ecol. Appl.* **2**, 376–386.
- El Kassaby, Y. A., Chaisurisri, K., Edwards, D. G. W., and Taylor, D. W.: 1993, 'Genetic Control of Germination Parameters of Douglas-Fir, Sitka Spruce, Western Redcedar, and Yellow-Cedar and its Impact on Container Nursery Production', in Edwards, D. G. W. (ed.), *Dormancy and Barriers to Germination*, Proceedings of International Symposium of IUFRO Project Group P2.04-00, Victoria, B.C., pp. 37–42.
- Ellenberg, H.: 1996, *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht [Vegetation of Central Europe including the Alps, in Ecological, Dynamic and Historical Context]*, 5th edn., Verlag Eugen Ulmer, p. 1095, in German.
- Farmer, R. E. J.: 1997, *Seed Ecophysiology of Temperate and Boreal Zone Forest Trees*, St. Lucie Press, Delray Beach.
- Finegan, B.: 1984, 'Forest Succession', *Nature* **312**, 109–114.
- Fitter A. H., Fitter R. S. R., Harris I. T. B., and Williamson M. H.: 1995, 'Relationship between First Flowering Date and Temperature in The Flora of a Locality in Central England', *Func. Ecol.* **9**, 55–60.
- Fleming, R. A. and Volney, W. J. A.: 1995, 'Effects of Climate Change on Insect Defoliator Population Processes in Canada's Boreal Forest: Some Plausible Scenarios', *Water Air Soil Pollut.* **82**, 445–454.
- Friend, A. D., Shugart, H. H., and Running, S. W.: 1993, 'A Physiology-Based Gap Model of Forest Dynamics', *Ecology* **74**, 792–797.
- Gauthier, S., Bergeron, Y., and Simon, J.-P.: 1996, 'Effects of Fire Regime on the Serotiny Level of Jack Pine', *J. Ecol.* **84**, 539–548.
- Gauthier, S., Simon, J.-P., and Bergeron, Y.: 1992, 'Genetic Structure and Variability in Jack Pine (*Pinus banksiana* Lamb.) Populations: Effect of Insularity', *Can. J. Forest Res.* **22**, 1958–1965.
- Gear, A. J. and Huntley, B.: 1991, 'Rapid Changes in The Range Limits of Scots Pine 4000 Years Ago', *Science* **251**, 544–547.
- Grabherr, G., Gottfried, M., and Pauli, H.: 1994. 'Climate Effects on Mountain Plants', *Nature* **369**, 448.
- Gray, A. N. and Spies T. A.: 1997, 'Microsite Controls on Tree Seedling Establishment in Conifer Forest Canopy Gaps', *Ecology* **78**, 2458–2473.

- Gray, D. R., Régnière, J., and Boulet, B.: 1999, *Forecasting Defoliation by Spruce Budworm in Québec*, Research Note No. 7, Nat. Resour. Can., Can. For. Serv., Laurentian For. Cent., Sainte-Foy, QC, p. 8.
- Green, D. S.: 1980, 'The Terminal Velocity and Dispersal of Spinning Samaras', *American Journal of Botany* **67**, 1218–1224.
- Greene, D. F. and Johnson, E. A.: 1989, 'A Model of Wind Dispersal of Winged or Plumed Seeds', *Ecology* **70**, 339–347.
- Hanson, J. S., Malanson, G. P., and Armstrong, M. P.: 1989, 'Spatial Constraints on the Response of Forest Communities to Climate Change', in Malanson, G. P. (ed.), *Natural Areas Facing Climatic Change*, SPB Academic, The Hague, The Netherlands, pp. 1–23.
- Hanson, J. S., Malanson, G. P., and Armstrong, M. P.: 1990, 'Landscape Fragmentation and Dispersal in a Model of Riparian Forest Dynamics', *Ecol. Modelling* **49**, 277–296.
- Hengeveld, R.: 1989, *Dynamics of Biological Invasions*, Chapman and Hall, London.
- Hobbie, S. E. and Chapin, F. S., III: 1998, 'An Experimental Test of Limits to Tree Establishment in Arctic Tundra', *J. Ecol.* **86**, 449–461.
- Hoffman, W. A. et al.: 2000, 'Elevated CO₂ Enhances Resprouting of a Tropical Savanna Tree', *Oecologia* **123**, 312–317.
- Hogg, E. H.: 1994, 'Climate and the Southern Limit of the Western Canadian Boreal Forest', *Can. J. For. Res.*, **24**, 1835–1845.
- Holling, C. S.: 1992, 'The Role of Forest Insects in Structuring the Boreal Landscape', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge University Press, NY, pp. 170–195.
- Houghton, J. T., Meira Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., and Maskell, K. (eds.): 1996, *Climate Change, 1995 – The Science of Climate Change*, Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, U.K., and New York, U.S.A., 572 pp.
- Houle, G.: 1992, 'Spatial Relationship between Seed and Seedling Abundance and Mortality in a Deciduous Forest of North-eastern North America', *J. Ecol.* **80**, 99–108.
- Houle, G.: 1998, 'Seed Dispersal and Seedling Recruitment of *Betula alleghaniensis*: Spatial Inconsistency in Time', *Ecology* **79**, 807–818.
- Huntley, B. and Birks, H. J. B.: 1983, *An Atlas of Past and Present Pollen Maps for Europe, 0–13000 Yr Ago*, Cambridge University Press, Cambridge, U.K.
- Hutchins, H. E. and Lanner, R. M.: 1982, 'The Central Role of Clark's Nutcracker in the Dispersal and Establishment of Whitebark Pine', *Oecologia* **55**, 192–201.
- Huth, A. and Ditzer, T.: 2000, 'Simulation of the Growth of a Lowland Dipterocarp Rain Forest with FORMIX3', *Ecol. Modelling* **134**, 1–25.
- Iverson, L. R. and Prasad, A. M.: 1998, 'Predicting Abundance of 80 Tree Species Following Climate Change in the Eastern United States', *Ecol. Monogr.* **68**, 465–485.
- Jäger, D., Lexer, M. J., Hönninger, K., Neubauer, Ch., Katzensteiner, K., and Blab, A.: 2000, 'Simulated Effects of Ecosystem Restoration Measures: The Potential Natural Vegetation Approach Revisited', in Hasenauer, H. (ed.), *Ecological and Economical Impacts of Restoration Processes in Secondary Coniferous Forests*. Proceedings of the International Conference on Ecosystem Restoration, Universität für Bodenkultur, Vienna, pp. 137–142.
- Jarvis, P. G. (ed.): 1998, *European Forests and Global Change: The Likely Impacts of Rising CO₂ and Temperature*, Cambridge University Press, Cambridge, U.K., p. 380.
- Jensen, T. S.: 1985, 'Seed-Seed Predator Interactions of European Beech, *Fagus SilvatICA*, and Forest Rodents', *Oikos* **44**, 149–156.
- Johnson, I. R. and Thornley, J. H. M.: 1987, 'A Model of Shoot:Root Partitioning with Optimal Growth', *Ann. Botany* **60**, 133–142.
- Johnson, W. C. and Adkisson, C. S.: 1985, 'Dispersal of Beech Nuts by Blue Jays in Fragmented Landscapes', *American Midland Naturalist* **113**, 319–324.

- Jorritsma, I. T. M., Van Hees, A. F. M., and Mohren G. M. J.: 1999, 'Forest Development in Relation to Ungulate Grazing: A Modeling Approach', *For. Ecol. Manage.* **120**, 23–34.
- Kasrajan, V. O., Churschudjan, P. A., and Gabrieljan, V. G.: 1974, *On the Physiology of Aging in Trees from Stump Sprouting* [translation from Russian by Krapfenbauer, A.], Tiflis Forest Research Station, Report No. XXI.
- Keane, R. E., Austin, M., Field, C., Huth, A., Lexer, M. J., Peters, D., Solomon, A., and Wyckoff, P.: 2001, 'Tree Mortality in Gap Models: Application to Climate Change', *Clim. Change* **51**, 509–540.
- Kienast, F.: 1987, *FORECE – a Forest Succession Model for Southern Central Europe*, ORNL/TM-10575, Environmental Sciences Division Publication No. 2989, Oak Ridge National Laboratory, Oak Ridge, TN, p. 73.
- Kienast, F. and Kuhn, N.: 1989, 'Simulating Forest Succession Along Ecological Gradients in Southern Central Europe', *Vegetatio* **79**, 7–20.
- Kienast, F., Fritschi, J., Bisseger, M., and Abderhalden, W.: 1999, 'Modeling Successional Patterns of High-Elevation Forests under Changing Herbivore Pressure - Responses at The Landscape Level', *Forest Ecol. Manage.* **120**, 35–46.
- King, G. A. and Herstrom, A. A.: 1997, 'Holocene Tree Migration Rates Objectively Determined from Fossil Pollen Data', in Huntley, B., Cramer, W., Morgan, A. V., Prentice, H. C., and Allen, J. R. M. (eds.), *Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*, Springer Verlag, Berlin, **47**, pp. 91–101.
- Kobe, R. K.: 1997, 'Carbohydrate Allocation to Storage as a Basis of Interspecific Variation in Sapling Survivorship and Growth', *Oikos* **80**, 226–233.
- Koehler, P. and Huth, A.: 1998, 'The Effects of Tree Species Grouping in Tropical Rainforest Modelling: Simulations with the Individual-Based Model FORMIND', *Ecol. Modelling* **109**, 301–321.
- Koenig, W. D. and Knops, J. M. H.: 1998, 'Scale of Mast-Seeding and Tree-Ring Growth', *Nature* **396**, 225–226.
- Kräuchi, N. and Kienast, F.: 1993, 'Modelling Subalpine Forest Dynamics as Influenced by a Changing Environment', *Water Air Soil Pollut.* **68**, 185–197.
- Krissl, W. and Müller, F.: 1989, *Waldbauliche Bewirtschaftungsrichtlinien für das Eichenmischwaldgebiet in Österreich* [Silvicultural Guidelines for Oak Forests in Austria], Federal Forest Research Station, Vienna, FBVA-Report No. 40, p. 134, in German.
- Kullman, L.: 1996, 'Norway Spruce Present in the Scandes Mountains, Sweden at 8000 BP: New Light on Holocene Tree Spread', *Global Ecology and Biogeography Letters* **5**, 94–101.
- Kullman, L.: 1998, 'Palaeoecological, Biogeographical and Palaeoclimatological Implications of Early Holocene Immigration of *Larix sibirica* Ledeb. into the Scandes Mountains, Sweden', *Global Ecol. Biogeog. Lett.* **7**, 181–188.
- Kullman, L. and Engelmark, O.: 1991, 'Historical Biogeography of *Picea abies* (L.) Karst. at its Subarctic Limit in Northern Sweden', *J. Biogeogr.* **18**, 63–70.
- Kupfer J. A. and Runkle J. R.: 1996, 'Early Gap Successional Pathways in a *Fagus-Acer* Forest Preserve: Pattern and Determinants', *Journal of Vegetation Science* **7**, 247–256.
- Kwit, C., Platt W. J., and Slater H. H.: 2000, 'Post-Hurricane Regeneration of Pioneer Plant Species in South Florida Subtropical Hardwood Hammocks', *Biotropica* **32**, 244–251.
- LaBastide, J. G. A. and Vredenburg, C. L. H.: 1970, *The Influence of Weather Conditions on the Seed Production of Some Forest Trees in the Netherlands*, Report 102, Forest Research Institute 'De Dorschkamp', Wageningen, The Netherlands.
- Landsberg, J. J.: 1986, *Physiological Ecology of Forest Production*, Academic Press, London, p. 198.
- Leemans, R. and Prentice, I. C.: 1987, 'Description and Simulation of Tree-Layer Composition and Size Distribution in a Primaeval *Picea-Pinus* Forest', *Vegetatio* **69**, 147–156.
- Leemans, R. and Prentice, I. C.: 1989, *FORSKA, a General Forest Succession Model*, Institute of Ecological Botany, Uppsala, p. 70.

- Lexer, M. J.: 2001, 'Simulation der potentiellen natürlichen Vegetation für Österreichs Wald. Vergleich von statischen und dynamischen Modellkonzepten' [Simulating potential natural vegetation in the Eastern Alps: Comparison of dynamic and static modeling approaches] Forstliche Schriftenreihe, Universität für Bodenkultur, Vienna, in German, in press.
- Lexer, M. J. and Hönninger, K.: 1998, 'Simulated Effects of Bark Beetle Infestations on Stand Dynamics in *Picea Abies* Stands: Coupling a Patch Model and a Stand Risk Model', in Beniston, M. and Innes, J. L. (eds.), *The Impacts of Climate Variability on Forests, Lecture Notes in Earth Sciences* **74**, Springer-Verlag, p. 329.
- Lexer M. J. and Hönninger, K.: 2000, 'A Modified 3D-Patch Model for Spatially Explicit Simulation of Vegetation Composition in Heterogeneous Landscapes', *For. Ecol. Manage.* **144**, 43–65.
- Livingston, N. J. and Black, T. A.: 1986, 'Water Stress and Survival of Three Species of Conifer Seedlings Planted on a High South-Facing Clear-Cut', *Can. J. Forest Res.* **17**, 1115–1123.
- Loehle, C. and LeBlanc, D.: 1996, 'Model-Based Assessments of Climate Change Effects on Forests: A Critical Review', *Ecol. Modelling* **90**, 1–31.
- Lotter, A. F., Birks, H. J. B., Eicher, U., Hofmann, W., Schwander, J., and Wick, L.: 2000, 'Younger Dryas and Allerod Summer Temperatures at Gerzensee (Switzerland) Inferred from Fossil Pollen and Cladoceran Assemblages', *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **159** (3–4), 349–361.
- Lotter, A. F., Birks, H. J. B., Hofmann, W., and Marchetto, A.: 1998, 'Modern Diatom, Cladocera, Chironomid, and Chrysophyte Cyst Assemblages as Quantitative Indicators for The Reconstruction of Past Environmental Conditions in the Alps. II. Nutrients', *J. Paleolim.*, **19**, 443–463.
- Maak, K. and von Storch, H.: 1997, 'Statistical Downscaling of Monthly Mean Air Temperature to the Beginning of Flowering of *Galanthus nivalis* L. in Northern Germany', *Int. J. of Biometeorol.* **41**, 5–12.
- Mäkelä, A., Sievänen, R., Lindner, M., and Lasch, P.: 2000, 'Application of Volume Growth and Survival Graphs in the Evaluation of Four Process-Based Forest Growth Models', *Tree Physiology* **20** (5–6), 347–355.
- Malanson, G. P.: 1996, 'Effects of Dispersal and Mortality on Diversity in a Forest Stand Model', *Ecol. Modelling* **87**, 103–110.
- Malanson, G. P.: 1997, 'Effects of Feedbacks and Seed Rain on Ecotone Patterns', *Landscape Ecology* **12**, 27–38.
- Malanson, G. P. and Armstrong, M. P.: 1996, 'Dispersal Probability and Forest Diversity in a Fragmented Landscape', *Ecol. Modelling* **87** (1–3), 91–102.
- Malanson, G. P., Armstrong, M. P., and Bennett, D. A.: 1996, 'Fragmented Forest Response to Climatic Warming and Disturbance', in Goodchild, M. F., Steyaert, L. T., Parks, B. O., Crane, M. P., Johnston, C. A., Maidment, D. R., and Glendinning, S. J. (eds.), *GIS and Environmental Modelling: Progress and Research Issues*, Fort Collins, CO, GIS World, pp. 243–247.
- Malanson, G. P. and Cairns, D. M.: 1997, 'Effects of Dispersal, Population Delays, and Forest Fragmentation on Tree Migration Rates', *Plant Ecol.* **131**, 67–79.
- Matlack, G. R.: 1987, 'Diaspore Size, Shape, and Fall Behavior in Wind-Dispersed Plant Species', *American Journal of Botany* **74**, 1150–1160.
- Matthews, J. D.: 1955, 'The Influence of Weather on the Frequency of Beech Mast Years in England', *Forestry* **28**, 107–116.
- Maurer, B. A. and Heywood, S. G.: 1993, 'Geographical Range Fragmentation and Abundance in Neotropical Migratory Birds', *Conservation Biology* **7**, 501–509.
- McInnes, P. F., Naiman, R. J., Pastor, J., and Cohen, Y.: 1992, 'Effects of Moose Browsing on Vegetation and Litter of Boreal Forest, Isle Royale, Michigan, U.S.A.', *Ecology* **73**, 2059–2075.
- Mencuccini, M., Piussi, P., and Zanzi Sulli, A.: 1995, 'Thirty Years of Seed Production in a Subalpine Norway Spruce Forest: Patterns of Temporal and Spatial Variation', *Forest Ecol. Manage.*, **76**, 109–125.

- Melillo, J. M., Prentice, I. C., Farquhar, G. D., Schulze, E. D., and Sala, O. E.: 1996, 'Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate', in Houghton, J. T., Meira Filho, L. G., Callander, B.A., et al. (eds.), *Climate Change, 1995: The Science of Climate Change*, Cambridge University Press, Cambridge, U.K., pp. 445–481.
- Mladenoff, D. J. and Baker, W. L.: 1999, *Spatial Modeling of Forest Landscape Change: Approaches and Applications*, Cambridge University Press, Cambridge, U.K.
- Mohan, E., Mitchell, N., and Lovell, P.: 1984, 'Environmental Factors Controlling Germination of *Leptospermum scoparium* (Manuka)', *New Zealand Journal of Botany* **22**, 95–101.
- Ne'eman, G. and Izhaki, I.: 1999, 'The Effect of Stand Age and Microhabitat on Soil Seed Banks in Mediterranean Aleppo Pine Forests after Fire', *Plant Ecol.* **144**, 115–125.
- Nathan, R. and Muller-Landau, H. C.: 2000, 'Spatial Patterns of Seed Dispersal, their Determinants and Consequences for Recruitment', *Trends in Ecology and Evolution* **15**, 279–285.
- Norby, R. J., Ogle, K., Curtis, P. S., Badeck, F.-W., Huth, A., Hurtt, G. C., Kohyama, T., and Peñuelas, J.: 2001, 'Aboveground Growth and Competition in Forest Gap Models: An Analysis for Studies of Climate Change', *Clim. Change* **51**, 415–447.
- Ojima, D. S., Kittel, T. G. F., Rosswall, T., and Walker, B. H.: 1991, 'Critical Issues for Understanding Global Change Effects on Terrestrial Ecosystems', *Ecol. Appl.* **1**, 316–325.
- Pacala, S. W., Canham, C. D., and Silander, J. A. Jr.: 1993, 'Forest Models Defined by Field Measurements: I. The Design of a Northeastern Forest Simulator', *Can. J. Forest Res.* **23**, 1980–1988.
- Pacala, S. W. and Deutschman, D. H.: 1995, 'Details that Matter – The Spatial Distribution of Individual Trees Maintains Forest Ecosystem Function', *Oikos* **74**, 357–365.
- Pacala, S. W. and Hurtt, G. C.: 1993, 'Terrestrial Vegetation and Climate Change: Integrating Models and Experiments', in Kareiva, P., Kingsolver, J. G., and Huey, R. B. (eds.), *Biotic Interactions and Global Change*, Sinauer, Sunderland, Mass., pp. 57–74.
- Pastor, J., Cohen, Y., and Moen, R.: 1999, 'Generation of Spatial Patterns in Boreal Forest Landscapes', *Ecosystems* **2**, 439–450.
- Pastor, J. and Naiman, R. J.: 1992, 'Selective Foraging and Ecosystem Processes in Boreal Forests', *The American Naturalist* **139**, 690–705.
- Pastor, J. and Post, W. M.: 1985, 'Development of a Linked Forest Productivity–Soil Process Model', ORNL/TM-9519, Oak Ridge National Laboratory, Oak Ridge, TN.
- Pickett, S. T. A. and White, P. S. (eds.): 1985, *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, Orlando.
- Pielou, E. C.: 1979, *Biogeography*, John Wiley and Sons, New York.
- Pitelka, L. F., Bugmann, H., and Reynolds, J. F.: 2001, 'How Much Physiology is Needed in Forest Gap Models for Simulating Long-Term Vegetation Response to Global Change? Introduction', *Clim. Change* **51**, 251–257.
- Pitelka, L. and the Plant Migration Workshop Group: 1997, 'Plant Migration and Climate Change', *American Scientist* **85**, 464–473.
- Portnoy, S. and Willson, M. F.: 1993, 'Seed Dispersal Curves, Behavior of the Tail of the Distribution', *Evolut. Ecol.* **7**, 25–44.
- Post, W. M. and Pastor, J.: 1996, 'LINKAGES – an Individual-Based Forest Ecosystem Model', *Clim. Change* **34**, 253–261.
- Prentice, I. C.: 1986, 'Vegetation Response to Past Climatic Variation', *Vegetatio* **67**, 131–141.
- Prentice, I. C., Bartlein, P. J., and Webb III, T. W.: 1991, 'Vegetation and Climate Change in Eastern North America since the Last Glacial Maximum', *Ecology* **72**, 2038–2056.
- Prentice, I. C., Sykes, M. T., and Cramer, W.: 1993, 'A Simulation Model for the Transient Effects of Climate Change on Forest Landscapes', *Ecol. Modelling* **65**, 51–70.
- Price, D. T., Halliwell, D. H. Apps, M. J., and Peng, C. H.: 1999, 'Adapting a Patch Model to Simulate the Sensitivity of Central-Canadian Boreal Ecosystems to Climate Variability', *J. Biogeogr.* **26**, 1101–1113.

- Régnière, J. and Sharov, A.: 1999, 'Simulating Temperature-Dependent Ecological Processes at the Sub-Continental Scale: Male Gypsy Moth Flight Phenology as an Example', *Int. J. Biometeorol.* **42**, 146–152.
- Reynolds, J. F., Hilbert, D. W., and Kemp, P. R.: 1993, 'Scaling Ecophysiology from the Plant to the Ecosystem: A Conceptual Framework', in Ehleringer, J. R. and Field, C. B. (eds.), *Scaling Physiological Processes: Leaf to Globe*, Academic Press, San Diego, pp. 127–140.
- Ribbens E., Silander, J., and Pacala, S.: 1994, 'Seedling Recruitment in Forests: Calibrating Models to Predict Patterns of Tree Seedling Dispersion', *Ecology* **75**, 1794–1806.
- Ritchie, J. C.: 1986, 'Climate Change and Vegetation Response', *Vegetatio* **67**, 65–74.
- Roberts, D. W.: 1996, 'Modelling Forest Dynamics with Vital Attributes and Fuzzy Systems Theory', *Ecol. Modelling* **90**, 161–173.
- Rogers, R. and Johnson, P. S.: 1998, 'Approaches to Modeling Natural Regeneration in Oak-Dominated Forests', *Forest Ecol. Manage.* **106**, 45–54.
- Rohmeder, E.: 1972, *Das Saatgut in der Forstwirtschaft*, [Seed in Forestry Practice], Paul Parey, p. 273, in German.
- Sakai, A., Sakai, S., and Akiyama, F.: 1997, 'Do Sprouting Tree Species on Erosion-Prone Sites Carry Large Reserves of Resources?', *Ann. Botany* **79**, 625–630.
- Salomao, A. N., Da Eira, M. T. S., and Da Cunha, R.: 1996, 'The Effect of Temperature on Seed Germination of Four *Dalbergia nigra* Fr. Allem. Leguminosae Trees', *Revista Arvore*, **19**, 588–594.
- Schaber, J., Badeck, F.-W., and Lasch, P.: 1999, 'Ein Modell der Sukzessionsdynamik europäischer Wälder [A model of successional dynamics in European forests] – Forest Ecosystems in a Changing Environment (4C)', in Pelz, D. R., Rau, O., and Saborowski, J. (eds.), *Deutscher Verband forstlicher Versuchsanstalten, Sektion forstliche Biometrie und Informatik, 11. Jahrestagung und Internationale biometrische Gesellschaft, Deutsche Region, Arbeitsgruppe Ökologie, Herbstkolloquium, Freiburg*, pp. 212–217, in German.
- Sharpe, P. J. H.: 1990, 'Forest Modeling Approaches: Compromises between Generality, and Precision', in Dixon, R. K., Meldahl, R. S., Ruark, G. A., and Warren, W. G. (eds.), *Process Modeling of Forest Growth Responses to Environmental Stress*, Timber Press, pp. 180–190.
- Shibata, M. and Nakashizuka, T.: 1995, 'Seed and Seedling Demography of Four Co-occurring *Carpinus* Species in a Temperate Forest', *Ecology* **76**, 1099–1108.
- Shugart, H. H.: 1984, *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*, Springer-Verlag, New York, p. 278.
- Shugart, H. H. and West, D. C.: 1977, 'Development of an Appalachian Deciduous Forest Succession Model and its Application to Assessment of the Impact of the Chestnut Blight', *J. Environ. Manage.* **5**, 161–179.
- Smith, B., Prentice, I. C., and Sykes, M. T.: 2001, 'Representation of Vegetation Dynamics in Modelling of Terrestrial Ecosystems: Comparing Two Contrasting Approaches within European Climate Space', *Global Ecol. Biogeogr.* **10**, 621–638.
- Smith, T. M. and Urban, D. L.: 1988, 'Scale and Resolution of Forest Structural Pattern', *Vegetatio* **74**, 143–150.
- Solomon, A. M.: 1986, 'Transient Responses of Forests to CO₂-Induced Climate Change: Simulation Modeling Experiments in Eastern North America', *Oecologia* **68**, 567–579.
- Solomon, A. M.: 1997, 'Natural Migration Rates of Trees: Global Terrestrial Carbon Cycle Implications', in Huntley, B., Cramer, W., Morgan, A. V., Prentice, H. C., and Allen, J. R. M. (eds.), *Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*, Springer-Verlag, Berlin, **47**, pp. 455–468.
- Solomon, A. M. and Kirilenko, A. P.: 1997, 'Climate Change and Terrestrial Biomass: What If Trees Do Not Migrate!', *Global Ecol. Biogeogr. Lett.* **6**, 139–148.
- Solomon, A. M., Sharp, M. L., West, D. C., Taylor, G. E., Webb, J. W., and Trimble, J. L.: 1984, *Response of Unmanaged Forests to Carbon Dioxide-Induced Climate Change: Available Information, Initial Tests, and Data Requirements*, TR-009, United States Department of Energy, Washington, D.C.

- Sork, V. L., Bramble, J., and Sexton, O.: 1993, 'Ecology of Mast-Fruiting in Three Species of North American Deciduous Oaks', *Ecology* **74**, 528–541.
- Stapanian, M. A. and Smith, C. C.: 1986, 'How Fox Squirrels Influence the Invasion of Prairies by Nut-Bearing Trees', *J. Mammol.* **67**, 326–332.
- Stoecklin, J. and Baeumler, E.: 1996, 'Seed Rain, Seedling Establishment and Clonal Growth Strategies on a Glacier Foreland', *J. Veg. Sci.* **7**, 45–56.
- Sykes, M. T., Prentice, I. C., and Cramer, W.: 1996, 'A Bioclimatic Model for the Potential Distribution of North European Tree Species under Present and Future Climates', *J. Biogeogr.* **23**, 203–233.
- Turgeon, J. J. and de Groot, P.: 1992, *Management of Insect Pests of Cones in Seed Orchards in Eastern Canada*, Field Guide, Ontario Ministry of Natural Resources and Forestry Canada, Sault Ste. Marie, ON, p. 98.
- Turner, M. G., Baker, W. L., Peterson, C. J., and Peet, R. K.: 1998, 'Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances', *Ecosystems* **1**, 511–523.
- Urban, D. L.: 1990, *A Versatile Model to Simulate Forest Pattern: A User's Guide to ZELIG Version 1.0*, University of Virginia, Charlottesville, VA.
- Urban, D. L., Acevedo, M. F., and Garman, S. L.: 1999, 'Scaling Fine-Scale Processes to Large-Scale Patterns Using Models Derived from Models: Metamodels', in Mladenoff, D. and Baker, W. L. (eds.), *Spatial Modeling of Forest Landscape Change*, Cambridge University Press, Cambridge, U.K., pp. 70–98.
- Urban, D. L. and Smith, T. M.: 1989, 'Extending Individual-Based Forest Models to Simulate Large-Scale Environmental Pattern', *Bull. Ecol. Soc. Amer.* **70**, Suppl., 284–285.
- Van der Meer, P. J., Sterck, F. J., and Bongers, F.: 1998, 'Tree Seedling Performance in Canopy Gaps in a Tropical Rain Forest at Nouragues, French Guiana', *J. Tropical Ecol.* **2**, 119–137.
- Van der Wall, S. B. and Balda, R. P.: 1977, 'Coadaptations of the Clark's Nutcracker and the Pinon Pine for Efficient Seed Harvest and Dispersal', *Ecol. Monogr.* **47**, 89–111.
- Van Hees, A. F. M.: 1997, 'Growth and Morphology of Pedunculate Oak (*Quercus robur* L.) and Beech (*Fagus sylvatica* L.) Seedlings in Relation to Shading and Drought.' *Annales des Sciences Forestières* **54**, 9–18.
- Van Wieren, S. E.: 1996, 'Do Large Herbivores Select a Diet That Maximises Short-Term Energy Intake Rates?', *Forest Ecol. Manage.* **88**, 149–156.
- Vegis, A.: 1964, 'Dormancy in Higher Plants', *Ann. Rev. Plant Physiol.* **15**, 185–224.
- Vegis, A.: 1973, 'Dependence of Growth Processes on Temperature', in Precht, C. J., Hensel, H., and Larcher, W., *Temperature and Life*, Springer-Verlag, Berlin, pp. 145–169.
- Wareing, P. F. and Saunders, P. F.: 1971, 'Hormones and Dormancy', *Ann. Rev. Plant Physiol.* **22**, 261–288.
- Webb III, T.: 1981, 'The Past 11,000 Years of Vegetational Change in Eastern North America', *BioScience* **31**, 501–506.
- Webb III, T.: 1986, 'Is Vegetation in Equilibrium with Climate? How to Interpret Late-Quaternary Pollen Data', *Vegetatio* **67**, 75–91.
- Wick, L. and Tinner, W.: 1997, 'Vegetation Changes and Timberline Fluctuations in the Central Alps as Indicators of Holocene Climatic Oscillations', *Arctic and Alpine Research* **29**, 445–458.
- Williamson, M.: 1996, *Biological Invasions*, Chapman and Hall, London.
- Williamson, M.: 1999, 'Invasions', *Ecography* **22**, 5–12.
- Wu, J. and Levin, S. A.: 1994, 'A Spatial Patch Dynamic Modeling Approach to Pattern and Process in an Annual Grassland', *Ecol. Monogr.* **64**, 447–464.
- Wullschleger, S. D., Jackson, R. B., Currie, W. S., Friend, A. D., Luo, Y., Mouillot, F., and Shao, G.: 2001, 'Below-Ground Processes in Gap Models for Simulating Forest Response to Global Change', *Clim. Change* **51**, 449–473.

(Received 24 May 2000; in revised form 15 May 2001)