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Modeling the competitive dynamics and distribution of tree species along moisture gradients

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Introduction

Ecology seeks to elucidate the mechanisms underlying patterns in the distribution and abundance of species. Models play an increasingly important role in examining the relationship between pattern and process because the broadest patterns in nature are not amenable to direct experimental study. This trend is particularly evident in the proliferation of landscape models (Baker, 1989).

Landscape ecology is increasingly reliant on models because they provide the means to explore how large-scale patterns emerge from complex dynamics at smaller scales. Yet, landscape models must be empirically grounded in order to yield true understanding of the mechanisms that govern landscape patterns. In this chapter both the design and field calibration of an individual-based model of forest landscape dynamics are described. The model was developed to address how landscape-scale variation in soil moisture influences the competitive dynamics and distribution of tree species.

Variation in species composition along soil moisture gradients is one of the most striking and well-studied patterns of forest landscapes (Whittaker, 1967; Oliver and Larson, 1996). A long tradition of gradient analysis has employed moisture gradients to demonstrate that environmental heterogeneity is one of the primary determinants of landscape pattern. Yet the underlying processes that give rise to gradient patterns have rarely been examined. Smith and Huston (1989) were among the first to examine the relationship between pattern and process using an individual-based model to simulate how landscape variation in soil moisture influences the dynamics and distribution of tree species. This chapter seeks to demonstrate how calibrating such a model with field data yields new insights into the underlying causes of landscape patterns and dynamics. The development of gradient models is first reviewed to illustrate how these models have led to the development of the model presented in this chapter.

Gradient models

Gradient analysis and niche models

Gradient analysis was developed in the 1950s and 1960s to characterize community assembly patterns by correlating the distribution and abundance of species with environmental factors that vary across landscape gradients (Curtis and McIntosh, 1951; Whittaker, 1956, 1967). Early gradient studies revealed continuous variation in species composition along all but the steepest environmental gradients, confirming Gleason's individualistic hypothesis of community assembly (Curtis and McIntosh, 1951; Whittaker, 1956). Gradient analysis was later refined to fit explicit functions to species' distribution patterns and evaluate whether they conform to patterns predicted by niche models of resource partitioning (Gauch and Whittaker, 1972).

Niche theory posits that species exhibit symmetric or Gaussian distribution patterns and that species are regularly segregated along environmental gradients (Gauch and Whittaker, 1972). However, gradient analyses conducted in a wide variety of environments revealed that a majority of species distribution patterns did not conform to the regularly spaced, symmetric curves predicted by resource partitioning (Austin, 1985). Rather, the distributions of most species are skewed toward suboptimal conditions, suggesting that competitive displacement, rather than resource partitioning, is the dominant process governing the distribution and abundance of species along gradients.

Resource competition models

Before the widespread use of gradient analysis, the experimental studies of Ellenberg (1954) had demonstrated that the resource requirements of species cannot necessarily be inferred from their observed distribution patterns. Ellenberg showed that grass species generally exhibit peak abundance under mesic conditions when grown in monoculture, but that peak abundance was skewed toward extreme conditions when grown in competition (Ellenberg, 1954). In the quarter century following the publication of Ellenberg's pioneering competition experiments, plant community ecologists invested considerable effort in measuring species responses to environmental gradients and relating species resource requirements to the results of competition experiments (Parrish and Bazzaz, 1976; Pickett and Bazzaz, 1978*a*, *b*). However, few attempts were made to elucidate the mechanisms by which plants compete for resources.

In the 1980s, Tilman developed and tested non-spatial models of resource competition to examine whether the outcome of competition is determined by the ability of species to deplete limiting resources (Tilman, 1982). His studies demonstrated that variation in the supply rate of limiting resources can give rise to species replacement patterns because constraints on the acquisition of multiple limiting resources impose trade-offs on species' ability to compete along resource supply gradients (Tilman, 1987). Tilman has forcefully argued that such competitive trade-offs cause a broad range of vegetation patterns and that mechanistic (resource-based) models of competition must be developed to understand vegetation patterns (Tilman, 1990).

While non-spatial competition models have been extremely useful in understanding resource competition, they omit important processes that govern the interplay of population dynamics and resource availability. Non-spatial models assume that the spatial scale of competition and dispersal is large enough to prevent disturbance and demographic stochasticity from generating spatial heterogeneity in plant density and resource availability. Yet, studies have shown that biotic heterogeneity has a significant effect on the dynamics and composition of plant communities (Reynolds *et al.*, 1997). Theorists have only just begun to develop models that are both spatial and analytically tractable, in order to study the consequences of biotically generated spatial structure (Tilman and Kareiva, 1998).

Individual-based models

Forest ecologists have long recognized the importance of the biotic heterogeneity generated by disturbance (Watt, 1925, 1947). Indeed, gap dynamics has been an organizing concept in forest ecology since Watt first articulated the importance of disturbance and regeneration in plant communities (Pickett and White, 1985). Thus, forest ecologists were among the first to develop spatially explicit computer models to simulate the competitive interactions among individual plants (Botkin *et al.*, 1972*a*, *b*; Shugart *et al.*, 1973; Botkin, 1993).

Individual-based models have typically been designed to simulate the dynamics of succession in a homogeneous environment. However, individual-based models have also been employed to examine how species competitive interactions vary across environmental gradients (Botkin *et al.*, 1972; Pastor and Post, 1986; Solomon, 1986; Tilman, 1988; Smith and Huston, 1989). Like non-spatial competition models, some of these models have been used to examine how constraints on the acquisition and use of multiple limiting resources impose trade-offs on species' ability to compete along resource gradients (Tilman, 1988; Smith and Huston, 1989). Smith and Huston (1989) simulated species zonation along soil moisture gradients with an individual-based model in which species performance was governed by a trade-off between the ability to grow in low light and the ability to grow in low soil moisture conditions. This trade-off between shade tolerance and drought tolerance is premised on leaf-level constraints on balancing carbon gain and water loss, and whole-plant allocation constraints on balancing carbon gain and water supply.

In this chapter an individual-based model is presented that was calibrated with field data to address whether such a trade-off between shade tolerance and drought tolerance governs the distribution and abundance of species along landscape soil moisture gradients. The analysis presented employs the same conceptual framework developed by Smith and Huston (1989) to simulate the competitive dynamics and distribution of species along landscape moisture gradients. However, an attempt will be made to evaluate whether landscape patterns can be traced to aspects of whole-plant performance that can be measured in the field.

Model design and calibration

The model presented in this chapter is a simple extension of the SORTIE model of forest stand dynamics (Pacala *et al.*, 1996). In order to model landscape dynamics using SORTIE, species responses to landscape-scale variation in soil moisture have been incorporated. Nevertheless, the structure of the landscape model remains largely the same as in the original version of SORTIE. Thus, for the sake of clarity, SORTIE is first described as originally designed and calibrated and the changes required to incorporate landscape-scale variation in soil moisture are subsequently described. The data and methods are then briefly described for assessing how species performance varies with soil moisture. A full description of the structure, dynamics, parameter estimation and error analysis of SORTIE can be found in Pacala *et al.* (1996).

The SORTIE algorithm is written in C and various versions run on UNIX workstations and personal computers. The model contains a record of every individual tree's diameter, species identity, and x- and y-coordinates. SORTIE simulates the dynamics of succession by predicting the fate of each individual using submodels of tree growth, mortality, recruitment and resource depletion (Fig. 2.1). The submodels were designed simultaneously with the field methods and maximum likelihood estimators necessary to estimate their parameters directly from field measurements. Each of the submodels was calibrated in the transition oak-northern hardwood forests of northeastern Connecticut.

Resource and performance submodels of SORTIE

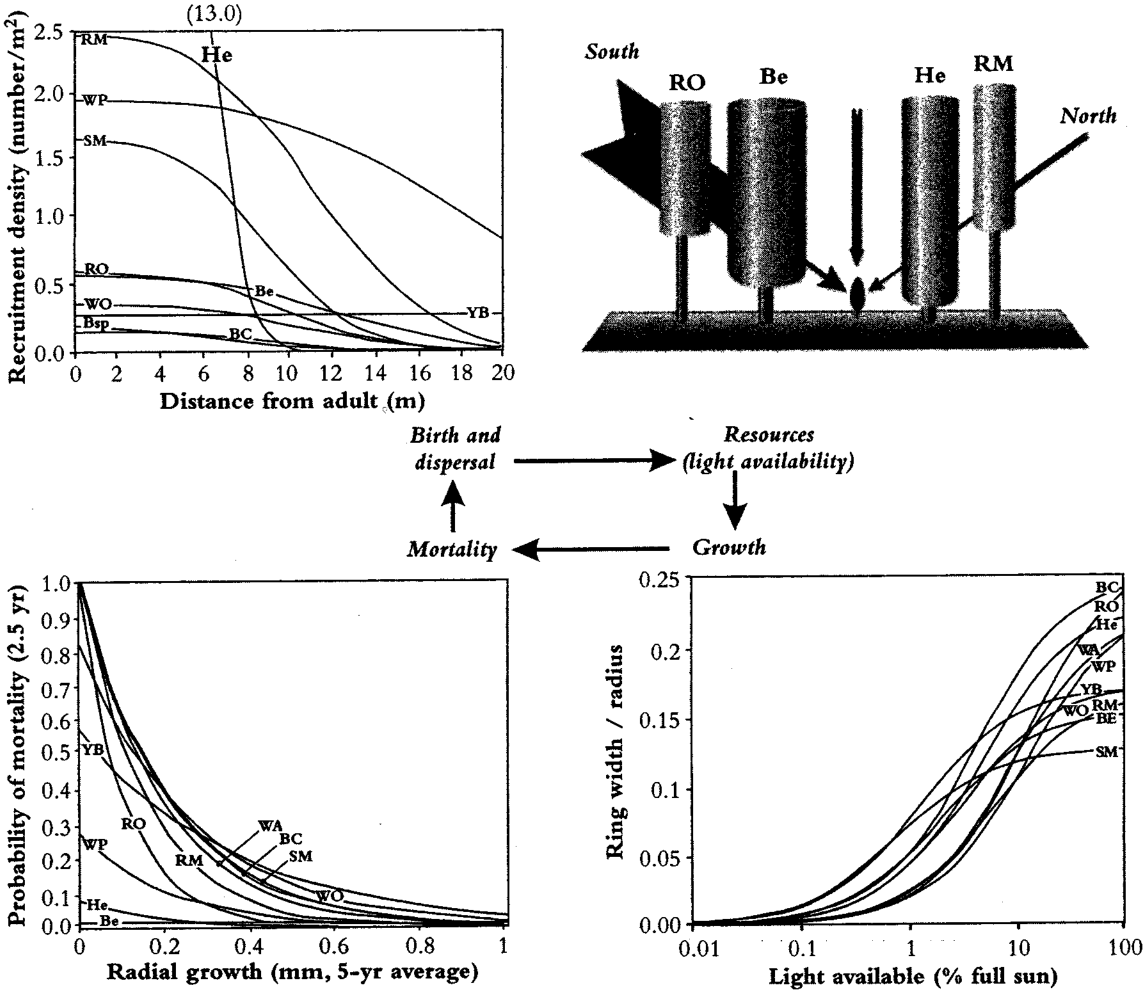
Light submodel

The light submodel calculates the light available to an individual as a function of the species identity and location of neighboring trees as well as the diurnal and seasonal movement of the sun. The model is defined by four attributes of the neighborhood and radiation regime: (i) species-specific equations relating tree height, crown diameter, and crown depth to stem diameter, (ii) species-specific light extinction coefficients, (iii) the diurnal and seasonal movements of the sun and (iv) the mix of diffuse and beam radiation. These attributes are used to compute the distribution of canopy openness above any given individual as a function of the density and species identity of neighboring trees:

$$\text{Openness} = e^{-\Sigma E_i (\#\text{ crowns of species } i \text{ intercepted})} \qquad (1)$$

where E_i is the light extinction coefficient for species i. Canopy openness is then combined with the distribution of sky brightness (from attributes (iii) and (iv)) to

Fig. 2.1. Species-specific sub-models of SORTIE (Equations 1–4 in the text). Clockwise from upper right: light extinction as a function of solar zenith and azimuth, crown geometry and light attenuation; radial growth as a function of light availability; mortality as a function of growth; recruitment as a function of distance and adult size. Species codes: red maple (RM), sugar maple (SM), American beech (Be), white ash (WA), white pine (WP), red oak (RO), eastern hemlock (He), yellow birch (YB), black cherry (BC).



compute the Gap Light Index (GLI), a measure of whole-season photosynthetically active radiation in units of percent of full sun (Canham *et al.*, 1993).

Growth submodel

The growth submodel consists of species-specific equations that predict radial growth of saplings from stem radius and GLI:

$$\text{Annual radial increment} = \text{Radius}\,[(G_1 \times \text{GLI}) \,/\, ((G_1/G_2) + \text{GLI})] \qquad (2)$$

where G_1 is the asymptotic growth rate at high light and G_2 is the slope at zero light. In accordance with the Constant Area Increment Law (Phipps, 1967), the basal area increment of canopy trees cannot exceed a constant maximum rate, G_3.

Mortality submodel

The sapling mortality submodel consists of species-specific equations that predict the individual's probability of mortality as a function of recent growth:

$$\text{Probability of mortality} = M_1\, e^{-M_2 g} \tag{3}$$

where g is radial growth, M_1 is the probability of mortality at zero growth and M_2 is the rate at which the probability of mortality decays with growth (Kobe *et al.*, 1995). This model specifies the probability of mortality over a $2\frac{1}{2}$-year-period as a function of average annual growth during the previous 5 years. The mortality submodel also includes purely random disturbance whereby all individuals, including adults, have a constant probability of dying from density independent factors. For model runs described here, this background annual mortality rate was set to 0.01. This yields an average gap-to-gap interval of 100 years that is representative of gap-phase disturbance regimes in late-successional stands (Runkle, 1985).

Recruitment submodel

The recruitment submodel consists of species-specific equations that predict the number and spatial locations of seedlings produced by maternal trees as a function of the location and diameter of maternal trees (Ribbens *et al.*, 1994). The number of seedling recruits per unit area is a function of the number of recruits produced by maternal trees and the proportion of those recruits that disperse to a given distance from the maternal tree:

$$\text{Seedling density} = R_2\, (\text{diameter}/100)^2 \times [\exp(-R_1 \times \text{distance}^3)/n] \tag{4}$$

where R_2 is the number of 5-year-old recruits produced by an adult of 100 cm in diameter. The spatial dispersal of recruits is determined by the function in brackets, a radially symmetric probability density centered on the maternal tree. R_1 is the species-specific decay parameter and n is a normalizer that ensures the area of the density function equals one.

A run of the stand-level model is initiated with a random distribution of individuals of specified number, size, and species identity. At the beginning of each 5-year iteration, SORTIE uses the light model to calculate a GLI for each sapling and then computes growth rate from GLI and diameter. Competition occurs whenever individuals are shaded by taller neighbors. SORTIE then uses the estimated growth rate to calculate the probability of mortality using the mortality models and pseudo-random coin tosses. Finally, SORTIE uses the recruitment submodels to determine the number and spatial positions of all recruits produced by every tree. By repeated iterations of the model, SORTIE forecasts the long-term changes in the abundance and spatial distribution of all tree species populations in a stand.

The importance of spatial processes

SORTIE simulations have shown that the relative scale of dispersal and competition has profound effects on both the structure and function of forest ecosystems. First, short dispersal combined with demographic stochasticity causes significant clustering and species segregation to develop at scales of 25 m after 500 years of succession. As a consequence, a mosaic of monodominant stands develops late in the course of succession even though the environment is homogeneous and the spatial distribution distributions are initially random.

Second, the relative scale of clustering and competition is also a critical determinant of the total biomass accumulation and rate of turnover in community composition during the course of succession. Pacala and Deutschman (1995) developed a non-spatial version of SORTIE which omits spatial structure by assuming that the density in each plant's neighborhood equals the mean density of the stand as a whole. This non-spatial version of SORTIE predicts a two-fold reduction in basal area and a two-fold increase in species turnover as compared to the spatial version of SORTIE. The basal area is predicted to be higher in the spatial version of the model because clustering serves to decrease the intensity of competition in the stand as a whole. Species turnover occurs at half the rate in the spatial version of the model because clustering allows shade-intolerant species to persist in low density areas later into the course of succession.

Implementation at the landscape scale

In order to implement SORTIE at the landscape scale, topographic variation in soil moisture has been focused on because it is one of the principal determinant of landscape variation in forest community composition in the region (Damman and Kershner, 1977; Whitney, 1991). Many other factors are likely to affect species performance at landscape scales, but topographic variation in soil moisture has been chosen to focus on because the purpose of our model is to determine whether a simple suite of mechanisms is sufficient to produce patterns observed in natural landscapes. Moreover, competition for water is not included in the model because field studies demonstrate that the tree species in our study sites do not differ in their ability to deplete soil moisture (C. Canham, unpublished data). Thus, implementing the model at the landscape scale simply requires specifying how soil moisture varies as a function of landscape (topographic) position and how species performance varies as a function of water as well as light availability. First, the changes required to specify soil moisture as a function of landscape (topographic) position and the resulting spatial structure of the model are discussed. The field calibration and form of the submodels quantifying species performance as a function of water as well as light availability are subsequently described.

In the landscape version of SORTIE, variation in soil moisture is specified as a continuous function of the *x*- and *y*-coordinates of a simulated landscape. Just as each tree occupies a spatial position defined by its *x*- and *y*-coordinates, each tree experiences a soil moisture defined as a function of its *x*- and *y*-coordinates. Introducing abiotic heterogeneity introduces fixed spatial structure that influences the performance and competitive interactions of species. As a consequence, the trajectory of succession can vary with soil moisture across a heterogeneous landscape.

For the purposes of this chapter, landscape variation in soil moisture is specified as a linear gradient. It has been decided to collapse landscape variation in soil moisture onto a single dimension because it is easier to visualize species distribution and abundance patterns in one dimension as they have been traditionally illustrated in niche models and gradient analyses: the results can be readily generalized to a landscape in which soil moisture varies in two dimensions. Thus, the soil moisture experienced by an individual tree is simply defined as a linear function of its *x*-coordinate and expressed in percent volumetric content.

The range of variation in soil moisture and the distance over which it varies are chosen to be consistent with scale and magnitude of landscape variation in soil moisture observed in the field. The scale of topographic variation in soil moisture varies considerably in the uplands of northwestern Connecticut where SORTIE was calibrated. Both extremes of saturated soil and shallow ridgetop soil can be observed along slopes as short as a three to four hundred meters and a small watershed encompassing those extremes covers as little as 50 hectares or 0.5 km^2. A long hillslope slope gradient, however, may extend up to a few thousand meters. The landscape-level simulations presented in this chapter span a gradient that varies from 15–42% volumetric content over a distance of 1 km, the scale of a small watershed gradient in Connecticut. The plot size is 1000 meters by 1000 meters, or 1 km^2. Runs covering 1 km^2 and 500 years average approximately 5 hours on a UNIX workstation.

Field calibration

The primary study sites used to calibrate SORTIE are located in the gneiss and schist uplands in the vicinity of Great Mountain Forest (GMF) in northwestern Connecticut. The upland landscape in the vicinity of GMF is topographically heterogeneous, with elevations ranging from 250–700 m, encompassing a wide range of soil moisture conditions. Associated with landscape variation in soil moisture is variation in forest community composition (Damman and Kershner, 1977): xeric ridgetops are dominated by oak forests, mesic midslopes and valley bottoms above 250 m by transition oak – northern hardwood forests, and hydric wetland sites by stands of *Acer rubrum* and *Tsuga canadensis*. *Tsuga canadensis* also forms isolated stands on xeric ridgetops and steep slopes which gives rise to a bimodal distribution that is observed throughout much of its range, particularly in New England (Kessel, 1979). Forests in the vicinity of GMF are predominantly 80–120 years old.

To examine how landscape variation in soil moisture influences species distribution patterns, field studies were conducted to assess how the growth and mortality of the major tree species vary across landscape gradients of water availability. The seven species studied include *Tsuga canadensis* (eastern hemlock, He), *Fagus grandifolia* (beech, Be), *Acer saccharum* (sugar maple, SM), *Acer rubrum* (red maple, RM), *Quercus rubra* (red oak, RO), *Fraxinus americana* (white ash, WA), and *Pinus strobus* (eastern white pine, WP).

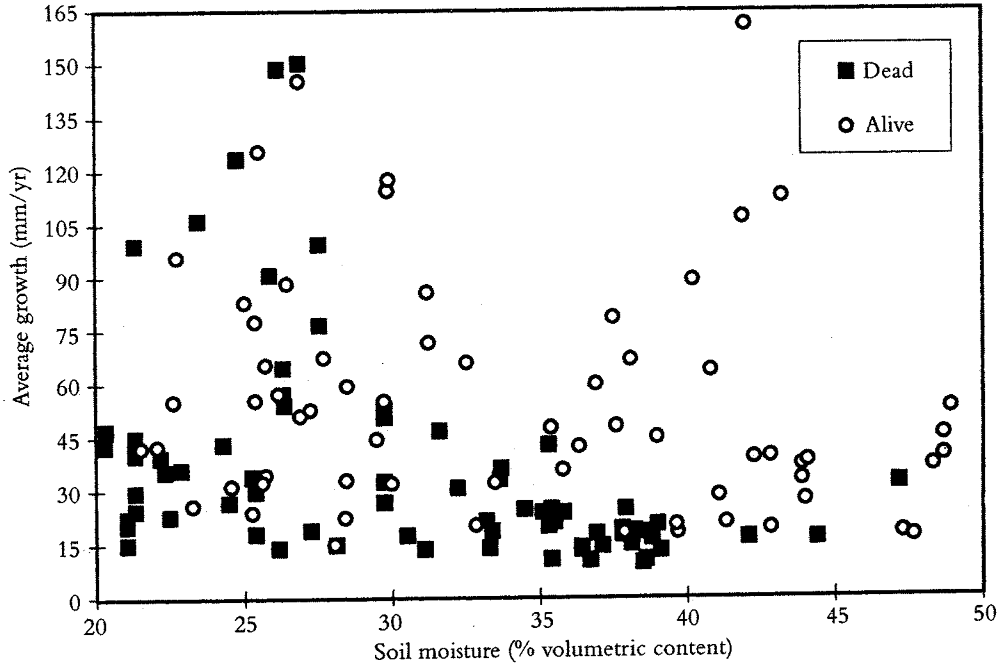
In the summer of 1996 several sites per species were located that encompassed a wide and continuous range of variation in soil moisture, excluding wetland or hydric soils. For the focal species at each site a random sample of the stems of live and recently dead saplings was collected and the proportion of live and recently dead saplings in the site estimated. Recently dead saplings included individuals whose leaf and bud retention and twig suppleness indicated that they had died within 2.5 years (Kobe *et al.*, 1995). To ensure that the growth of live saplings was examined across a full range of orthogonal variation in light and water availability, several additional sites were located for each species that encompassed an even broader range of conditions, including full sun and seasonally saturated soils.

Using a digital ring analyzer the annual radial growth rate of the live saplings was measured in each of the previous 5 years. For the recently dead saplings the annual radial growth rate was measured in each of the 5 years preceding death. After harvesting each sapling light and water availability were also measured. To measure light availability, hemispherical photographs of the canopy above each sapling were taken and an index computed of whole season light availability from the digitized photograph. Soil moisture (% volumetric content) was measured to a depth of 15 cm at the base of live and dead sapling on two dates in July and August 1996 using time domain reflectometry (TDR). For some saplings soil moisture was measured on only a single date. While soil moisture is temporally variable, the range of variation along landscape gradients is large enough that even a single measurement is sufficient to quantify landscape-scale variation. In general, even simple topographic indices are adequate to accurately capture the range of variation in soil moisture in heterogeneous landscapes (Barling *et al.*, 1994).

Despite the wide range of variation in soil moisture, regression analysis of growth in relation to both light and soil moisture reveals that the radial growth of saplings is not significantly correlated with soil moisture for any of the seven species (J. P. Caspersen and R. K. Kobe, unpublished data). Figure 2.2 illustrates that the 5-year average growth rate of live sugar maple saplings (circles) is uncorrelated with soil moisture, as is annual growth in any of the 5 years preceding harvest. In contrast, the probability of mortality increases dramatically with decreasing water availability. Under mesic conditions only those saplings that suffer suppressed growth are subject to mortality (squares), while saplings die at increasingly higher growth rates as soil moisture decreases (Fig. 2.2). Insofar as growth may vary with soil moisture, one would expect growth to vary in concert with mortality across the range of conditions sampled. Yet, Fig. 2.2 clearly illustrates that the effect of soil moisture on sapling growth is negligible relative to its effect on mortality.

To quantify the relationship between sapling mortality and soil moisture we modified the maximum likelihood methods used to estimate the probability of mortality as a function of growth (Eq. 3 in Kobe *et al.*, 1995). The modified

Fig. 2.2. 5-year average radial growth rate and soil moisture of live and dead sugar maple saplings.



maximum likelihood estimator is based on the conditional probability distribution governing the distribution of growth rates and soil moisture among the live and dead individuals (Fig. 2.3) and the binomial distribution of live and dead individuals at each site. The method works by estimating the mortality function that best reshapes the bivariate distribution of growth and soil moisture prior to mortality into the distribution of growth and soil moisture among dead individuals (Fig. 2.2).

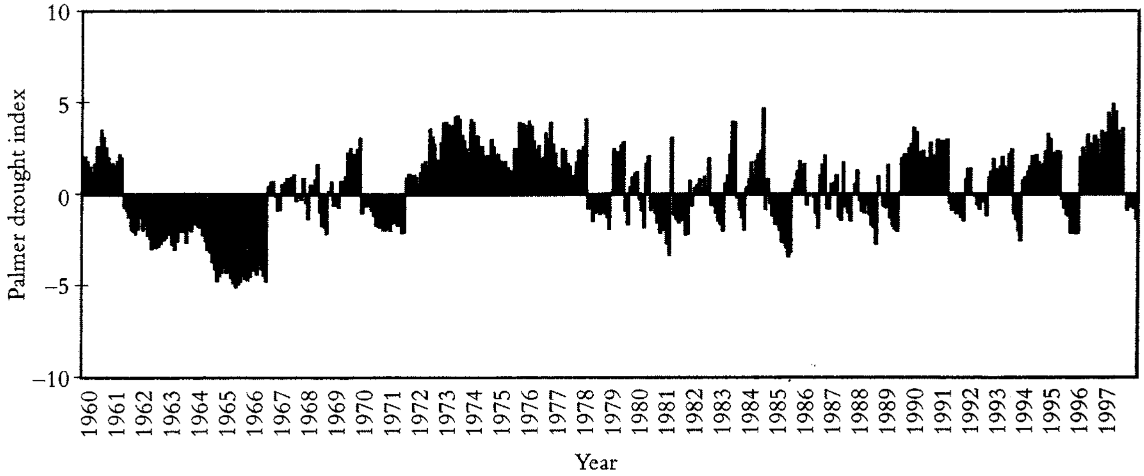
The modified mortality function specifies the probability of mortality over a 2.5-year period as a function of the average soil moisture as well as the average recent growth:

$$m(g) = e^{-M_1 g - M_2 g w} \qquad (5)$$

where g is the average growth in the previous 5 years, w is the average percent volumetric water content as measured by time domain reflectometry and M_1 and M_2 are species-specific parameters that define the rate of decay of the probability of sapling mortality with increasing growth and soil moisture.

As with any short-term field study, our sampling protocol provides only a snapshot of sapling mortality rates because it includes only those saplings that had died in the 2.5 years preceding harvest. Given that drought stress varies from year to year, mortality rates during any given 2.5-year-period may not be representative of long-term average mortality rates. However, the 1994–1996 period was neither

Fig. 2.3. Drought history of northwestern Connecticut. The Palmer drought severity index is derived from state climatic division monthly average temperature and precipitation (National Climatic Data Center). Mild drought = −1.0 to −2.0, moderate drought = −2.0 to −3.0, severe drought = −3.0 to −4.0, extreme drought < −4.0.

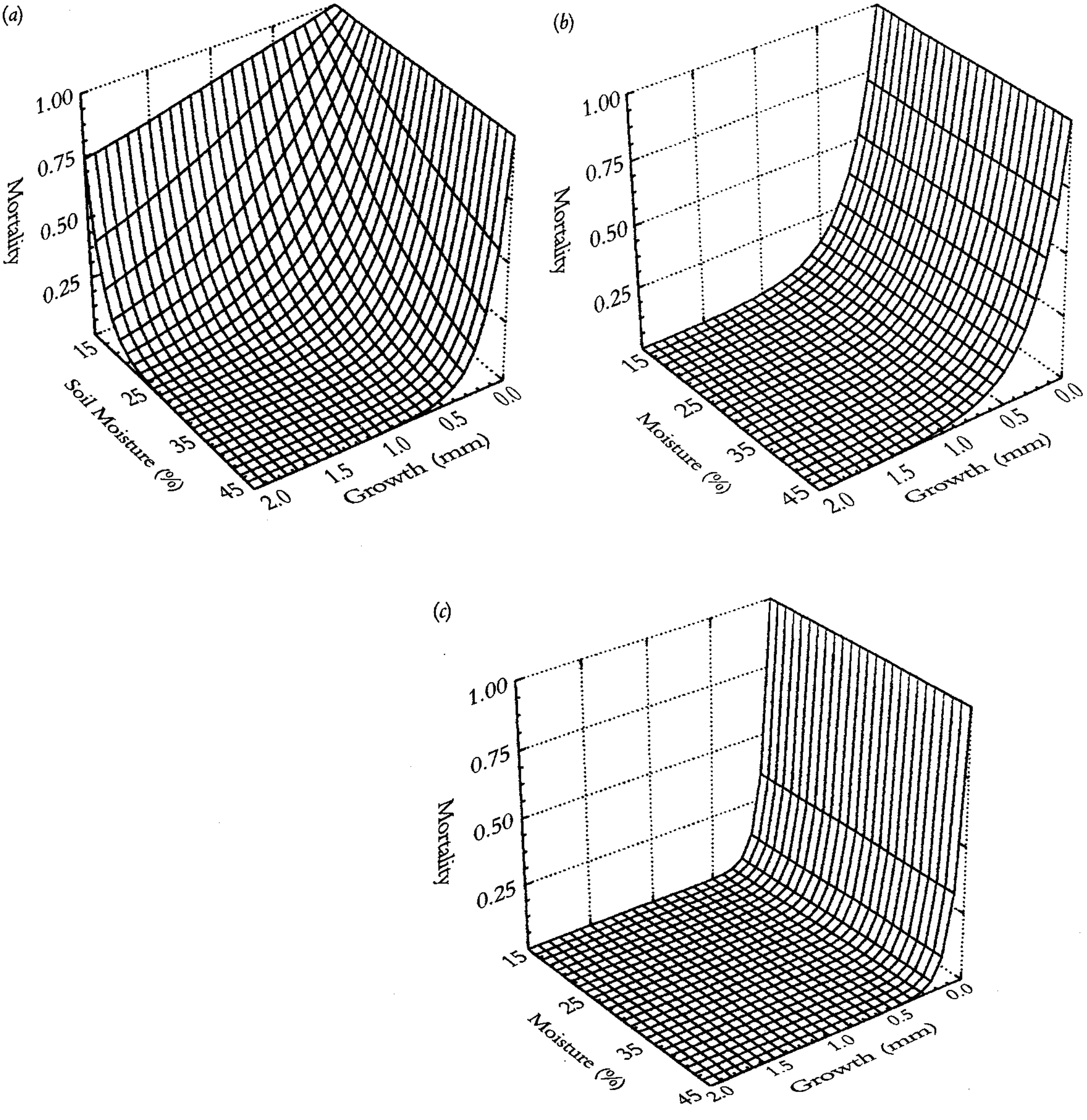


unusually dry or wet compared to the entire climate record for northwestern Connecticut, although it did include a moderate drought in 1995 (Fig. 2.3). Thus, the mean mortality rate during the 1994–1996 period represents as reasonable an estimate of mortality as could be obtained without employing long-term census data.

The estimated mortality functions reveal striking interspecific variation in the probability of sapling mortality with respect to both growth and soil moisture (Fig 2.4). Recall that growth itself varies as function of light but not water availability. Thus, the relationship between the probability of mortality and growth in part defines a species' shade tolerance: steeper slopes reflect greater shade tolerance. Both sugar maple and hemlock are shade tolerant under mesic conditions while red oak is not. For sugar maple, however, the slope of the relationship between growth and mortality flattens with decreasing soil moisture, indicating a trade-off between shade tolerance and drought tolerance. For hemlock, on the other hand, the probability of mortality does not vary with soil moisture. Thus, hemlock does not conform to the trade-off between shade- and drought-tolerance proposed by Smith and Huston (1989). Moreover, species differences in drought tolerance are determined largely by interspecific variation in mortality rather than growth.

The disparity between the mortality and growth responses suggests that water is only limiting to saplings during episodic drought. In a humid climate such as Connecticut's, the annual growth rate of saplings that survive episodic drought on xeric sites may not be measurably reduced because whole-season water balance remains favorable. Thus, the episodic nature of drought in humid climates likely explains why there was no significant relationship between soil moisture and growth across the range of conditions we studied. Because our results indicate that

Fig. 2.4. Probability of mortality as a function of growth and soil moisture (Eq. 5 in text) for (a) *sugar maple,* (b) *hemlock and* (c) *red oak.*



variation in annual radial growth is negligible relative to variation in mortality across the range of conditions sampled, only the effect of soil moisture on sapling mortality are included in the landscape model.

Hydric conditions

Assessing performance near the limit of a species distribution is hindered by the rarity of naturally occurring individuals. Under extreme conditions, mortality during establishment may be sufficiently high that few saplings naturally occur. In such cases, transplant experiments provide a means to assess how the limits of physiological tolerance affect species performance and distribution. A transplant experiment was conducted to assess the risk of mortality on seasonally saturated soils where considerable mortality occurs during establishment. Seasonally saturated soils are periodically inundated soils where the volumetric water content generally exceeds 60% and seedlings and saplings are occasionally subject to anoxia and frost heave. There is dramatic interspecific variation in mortality during establishment on saturated soils, with all species except white ash, red maple, and hemlock suffering more than 90% mortality on saturated soils. White ash exhibited the lowest mortality, 40%, and red maple and hemlock intermediate mortality rates, 56% and 73%, respectively. The probability of mortality during establishment on saturated soils is specified in the model as a species-specific constant M_4 (Table 2.1).

Performance metrics

During the course of succession, interspecific variation in performance is determined by the suite of parameters that define the various submodels. Thus, it is difficult to evaluate how a species will perform solely by examining individual parameter estimates. To clarify the competitive strategies of species we present measures of six aspects of species performance that, in addition to the probability of establishment on saturated soils (M_4), determine competitive dynamics under various conditions: the total amount of shade cast by a 30 cm diameter tree, time required to grow 3 m in full sun and at 1% full sun, mean dispersal distance, and 5-yr survivorship at low-light in mesic and xeric conditions (Table 2.1). Total shade was calculated as the absolute value of the difference between the spatial integral of ln(GLI) over the individual's shadow and the corresponding integral for full sun (GLI = 100).

Model dynamics and landscape pattern

Two sets of runs are presented to illustrate the dynamics of the model. First, stand-level runs are presented depicting the course of succession under mesic and xeric conditions. Second, landscape-level runs are presented depicting species' distribution and abundance along a continuous soil moisture gradient. Finally, the estimated establishment probabilities obtained from the transplant study are used to examine how species differences in establishment in seasonally saturated soils influence community dynamics.

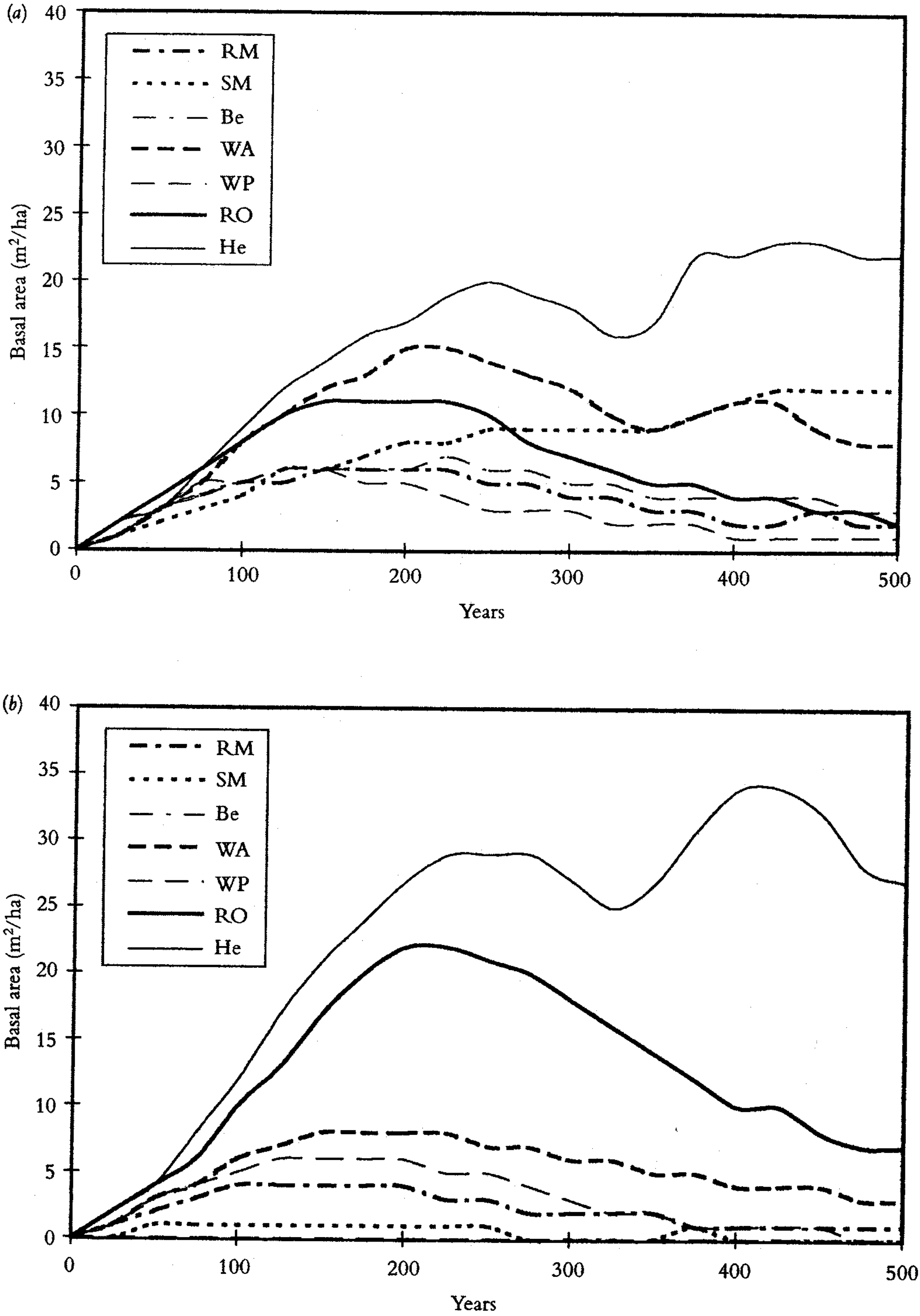
Simulations

With the exception of the mortality parameters (Eq. 5), each set of runs was initiated with the same estimated parameter values used in the original version of SORTIE (Pacala *et al.*, 1996). Unestimated parameters, R_2, G_3 and initial diameter, were assigned based on extensive sensitivity analyses (Pacala *et al.*, 1996). Fecundity,

Table 2.1 *Metrics summarizing interspecific variation in life-history traits (see explanation in text)*

Species	Probability of establishment on saturated soils	Shade cast by 30 cm diameter tree	Time to 3 m height in full sun (yr)	Time to 3 m height in 1% sun (yr)	Mean dispersal distance (m)	5-yr survivorship of a 2 cm diameter sapling in 1% sun and 40% soil moisture	5-yr survivorship of a 2 cm diameter sapling in 5% sun and 20% soil moisture
RM	0.56	25.7	14.6	92.8	10.6	0.30	0.64
SM	0.90	27.0	15.5	75.3	4.1	0.96	0.50
Be	0.84	78.5	19.4	55.0	5.9	0.96	0.00
WA	0.40	19.5	11.9	100.6	16.3	0.39	0.77
WP	0.84	16.6	14.7	158.0	15.8	0.00	0.36
RO	0.91	19.5	11.9	125.4	8.7	0.10	0.89
He	0.73	46.0	15.5	55.0	5.9	0.99	1.00

Fig. 2.5. Species basal area during the 500 years of succession in (a) *mesic and* (b) *xeric conditions.*



R_2, was set to 5 for all species, and individuals of dioeceous white ash were assigned a gender at random when born. The constant area increment of canopy trees, G_3, was assigned a value that corresponds to an annual radial increment of 1.5 mm for a tree 100 cm in diameter. New recruits were initiated with a diameter of 2 mm. Finally, each run was initiated with a random spatial distribution of 25 1 cm diameter saplings of each species per hectare.

Stand-level runs

The first set of runs described are stand-level runs that depict the course of succession under mesic and xeric conditions, 20% volumetric content and 35% volumetric content, respectively (Fig. 2.5). During the course of succession in mesic conditions, shade intolerant species increase in abundance initially then decline after reaching peak abundance between 100 and 200 years. Shade-tolerant species, including hemlock and sugar maple, continue to increase in abundance for 500 years (Fig. 2.5(*a*)). In xeric conditions, drought-intolerant species such as sugar maple, beech, red maple, and white ash suffer higher mortality. As a consequence, hemlock and red oak are dominant early in the course of succession until red oak declines and hemlock alone persists as the late-successional dominant (Fig. 2.5(*b*)).

Landscape-level runs

The landscape-level runs illustrate the distribution and abundance of species along a soil moisture gradient that varies from 15 to 42% volumetric content (Fig. 2.6). During the first 100 years of succession hemlock and red oak begin to dominate at the xeric end of the gradient because drought-intolerant species suffer higher mortality (Fig.2.6(*a*)). In contrast, the relative abundance of species remains relatively even in mesic conditions during the first 100 years of succession. By 250 years, the shade-intolerant species begin to decline under mesic conditions as well (Fig. 2.6(*b*)). As a result, the species that remain abundant exhibit skewed distribution patterns that reflect interspecific differences in shade tolerance and drought tolerance. By 500 years, hemlock alone is dominant across most of the gradient, except under mesic conditions where sugar maple continues to steadily increase (Fig 2.6(*c*)).

Seasonally saturated soils

The establishment probabilities obtained from the transplant experiment are incorporated into the model to examine how species differences in establishment influence community dynamics on seasonally saturated soils. White ash is predicted to be the dominant under hydric conditions, while hemlock and red maple are predicted to be subdominant (Fig. 2.7). Each of these three species are also predicted to dominate hydric soils in the absence of the other two (results not shown).

Causes of stand- and landscape-level predictions

The spatial and temporal patterns predicted by the model are governed by the suite of life-history traits summarized in Table 2.1. Several life-history traits, however,

Fig. 2.6. Species basal area across a soil moisture gradient at (a) *150 years,* (b) *250 years, and* (c) *500 years.*

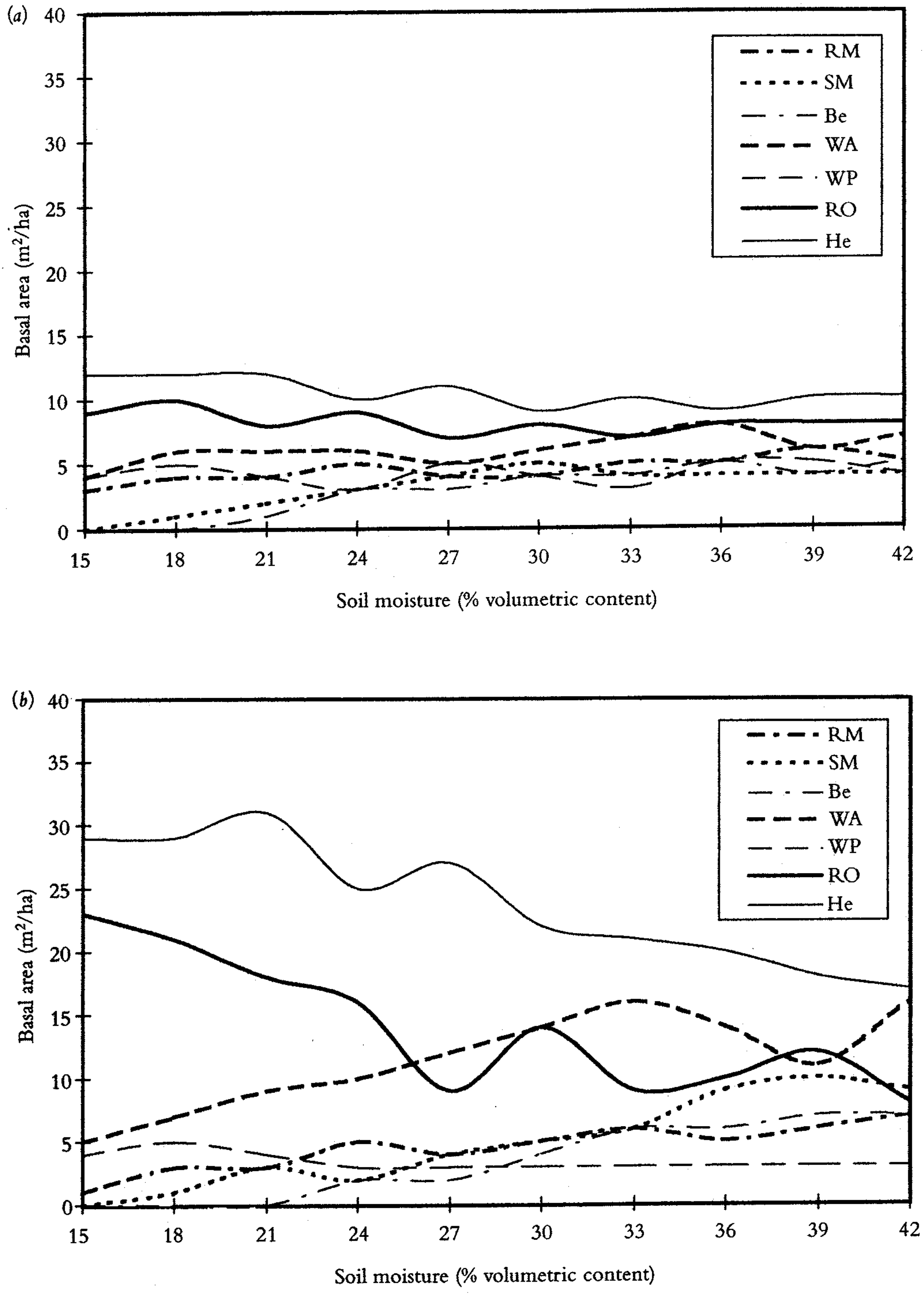


Fig. 2.6 (cont.)

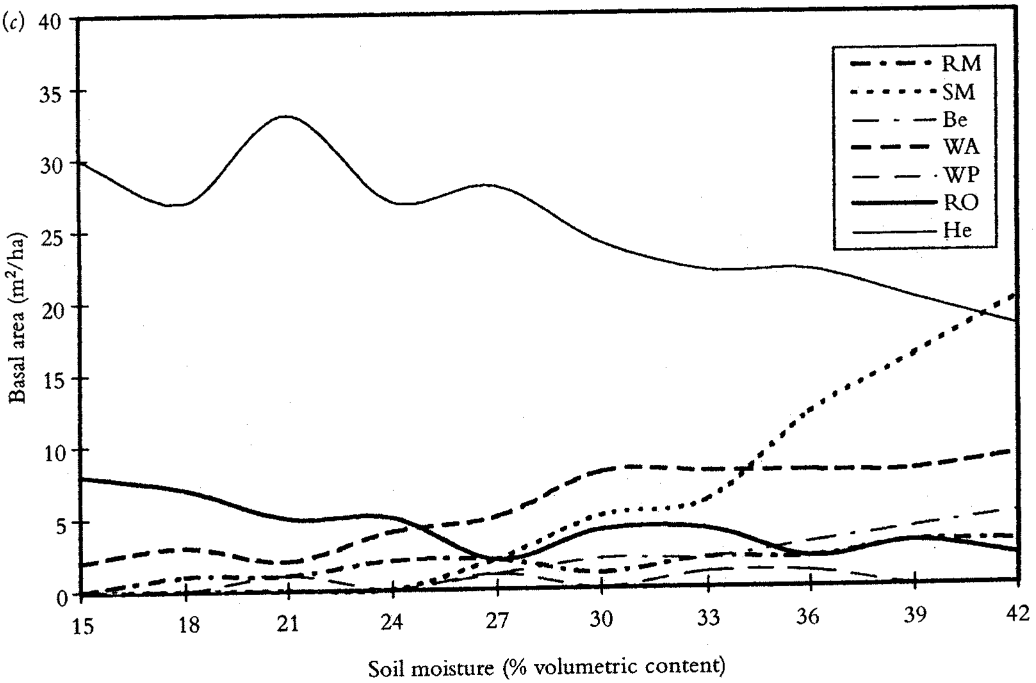
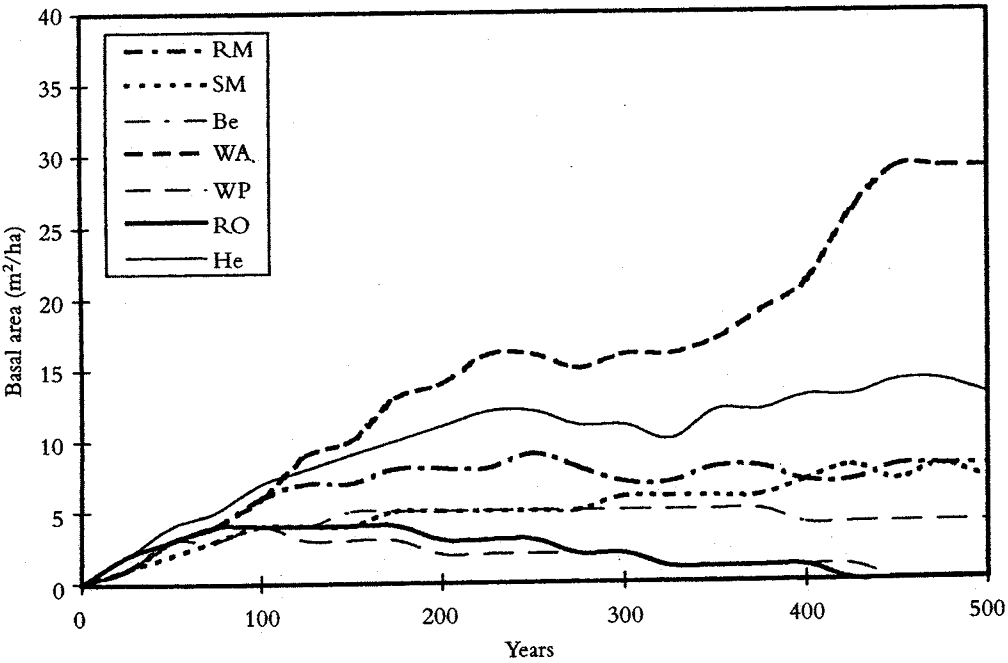


Fig. 2.7. Species basal area during the 500 years of succession in hydric conditions.



stand out as the critical determinants of the competitive dynamics and distribution of tree species along moisture gradients.

Under mesic conditions there is a prolonged trajectory of species turnover during the course of succession because there is a trade-off between high-light growth and low-light survivorship (Pacala *et al.*, 1996). Thus, species which grow rapidly in high light increase initially, then are replaced by species that survive better in low light. In contrast, large interspecific differences in mortality cause an autosuccessional trajectory in xeric conditions. There is no appreciable turnover is species composition because species intolerant of the combined effect of drought and shade are suppressed early on by competition from hemlock and red oak.

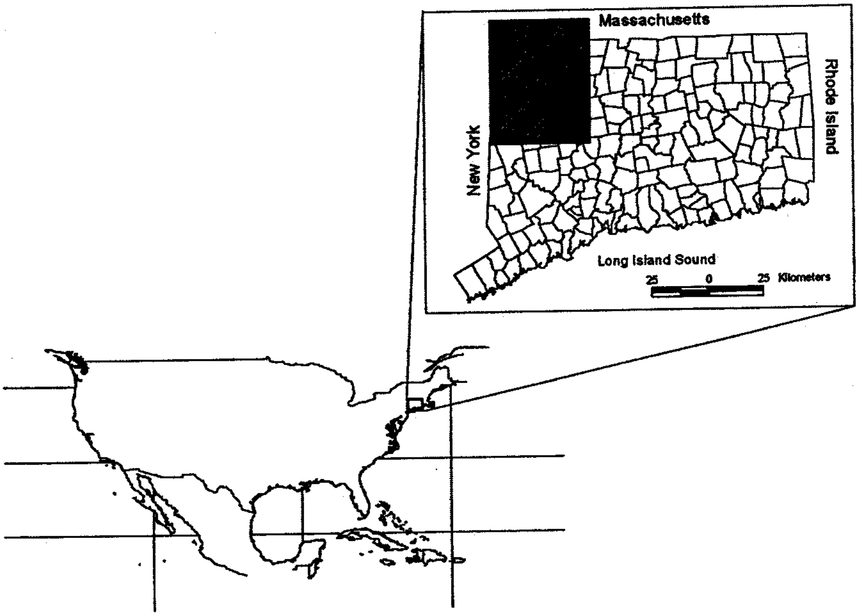
The distribution of species along the soil moisture gradient reflects the interplay of competition and environmental heterogeneity. In the absence of competition, all of the species are able to survive and grow in all but the most xeric and hydric conditions (results not shown). Thus, species distribution patterns unfold during the course of succession as species respond differentially to joint limitation by light and water (Fig. 2.6(*b*)). The distribution of the drought intolerant species, particularly sugar maple and beech, are skewed towards mesic conditions where they suffer less drought-induced mortality. The distribution of the drought-tolerant species, red oak and hemlock, are skewed towards xeric conditions where they experience less competition. Hemlock, however, is abundant in both mesic and xeric conditions because it is both shade tolerant and drought tolerant.

Comparing predictions with observed patterns

To assess the landscape-level predictions of the model a GIS data set was assembled composed of a forest classification map and digitized soil survey maps. The forest classification map was derived from three merged Landsat TM images of northwestern Connecticut and adjacent states (Mickelson *et al.*, 1998). The classification includes 20 forest classes (Fig. 2.8: for Fig. 2.8(*b*), see color section), most of which correspond to dominance or co-dominance by one or more of the seven species examined in the landscape model. The soil coverage was derived from digitized, geo-corrected soil polygon maps containing 74 soil types (Gonick and Shearin, 1970). The 74 soils types were aggregated into seven composite classes based on their associated soil moisture attributes: wetland (peat and muck soils), wet (poorly and very poorly drained soils), moist (somewhat poorly drained), intermediate (well and moderately well drained), dry (somewhat excessively well drained), dry and thin (thin well-drained and somewhat excessively well-drained soils with exposed bedrock), and very dry (excessively well drained). Of these, only acidic (non-calcareous) soils, typically above 250 m were considered.

To examine the association between forest cover and soil moisture, the frequency of occurrence of each of the forest classes on each soil class was calculated. The observed pixel distribution was then compared with what would be expected if a given forest cover class had been distributed at random across soil moisture classes. Goodness of fit *G*-tests on observed minus expected pixel frequencies were

Fig. 2.8. (a) *Location of study sites, GIS data coverages, and forest classification map (shown as cross-hatched area) in northwestern Connecticut and adjacent areas in New York and Massachusetts.* (b: see colour section). *Forest classification map (corresponding to cross-hatched region in* (a)) *derived from Landsat TM imagery. Legend shows the set of coverages, color coded, that were resolved in the image classification analysis (see Mickelson* et al. *in press for further details): RO – red oak (*Quercus rubra*) dominated stands; RO/Mx – red oak dominated, but with mixed hardwoods sub-dominant; RO/RM – red oak co-dominant with red maple (*Acer rubrum*); RM–red maple dominated stands; SM – sugar maple (*Acer saccharum*) dominated stands; SM/RO/Mx – mixed sugar maple, red oak stands; WA/RM/Mx – mixed white ash (*Fraxinus americana*) and red maple stands; Bc/SM/Mx – black cherry (*Prunus serotina*) with sugar maple and mixed hardwoods; Be – american beech (*Fagus grandifolia*) dominated stands; NHd/Be/SM – northern hardwoods, dominated by beech and sugar maple; NHd/YB/RM/HE – mixed northern hardwoods dominated by yellow birch (*Betula alleghaniensis*), red maple and eastern hemlock (*Tsuga canadensis*); MxHd – mixed hardwoods with no specific dominant; Mx/Hd/WP – mixed hardwoods with eastern white pine (*Pinus strobus*) co-dominant; WP – white pine dominated stands; P/MxConif – red pine (*Pinus resinosa*) dominated stands; He/RM – hemlock and red maple dominated stands; He/MxHd – mixed hemlock and hardwood stands; He – hemlock dominated stands; Sp–spruce dominated stands, primarily* Picea mariana *or* P. rubens. *The designation of LU or HU after some of the forest stand types indicates either mountain laurel (*Kalmia latifolia*) dominated understory forest sub-type (LU) or a hemlock dominated understory sub-type (HU). Other landcover types indicated: PFO/PSS – palustrine forested or scrub shrub wetlands; open water (lakes, ponds, rivers, etc.); Ag – all agricultural lands (including croplands, pastures, etc.), undifferentiated; Urban/Imperv – urban areas and paved surfaces; Barren/Soil/Quarry – all surfaces with exposed soil or rock; Cloud/shadow – areas obscured by cloud and associated shadows in one or more TM scene; Non-classified – landcover was not classified for these sites.*



used to determine whether observed patterns in the distribution of forest cover types deviated significantly from random. Values of G were compared with critical values of the chi-square distribution (Sokal and Rohlf, 1995). To facilitate graphical comparisons, results are shown on a standardized percent basis of observed minus expected number of pixels for forest cover type (Fig. 2.9). All results were significant at the 0.005 level.

Most of the forest classes dominated by the species included in the landscape model exhibit skewed distribution patterns (Fig. 2.9(*a*)–(*g*)). The sugar maple, northern hardwoods (including beech and sugar maple), white ash, and red maple classes occurred more frequently than expected at random on intermediate to wet soils and less frequently than expected on dry soils. Red oak, on the other hand, occurred more frequently than expected on dry soils and less frequently than expected on intermediate to wet soils. Thus, the observed distribution of these species is consistent with the skewed distributions predicted by the model.

Hemlock exhibited a bimodal distribution, with a pronounced affinity for hydric soils and a less pronounced but significant affinity for xeric soils (Fig. 2.9(*c*)). This pattern agrees with the bimodal distribution pattern reported in a previous study of ecotypic variation in Hemlock (Kessel, 1979). The bimodal distribution is also consistent with our finding that hemlock is both shade tolerant and drought tolerant. However, hemlock was predicted to be dominant in mesic and xeric conditions alike, but only subdominant in hydric conditions. As is argued in the discussion, the abundance of hemlock in mesic and xeric conditions likely reflects the role of disturbance and land-use history. The abundance of hemlock in wetland soils, on the other hand, may be due to factors which could not be evaluated with the transplant experiment.

Several forest classes were observed to be abundant on wet and wetland soils, including hemlock, red maple, and white ash. These are the same species that were observed to have the lowest mortality during establishment in seasonally saturated soils, 73%, 56%, and 40% mortality, respectively. Each of these three species is predicted to dominate hydric soils in the absence of the other two. In competition, however, white ash is predicted to dominate in hydric conditions. This suggests that other processes govern the regeneration and persistence of hemlock and red maple in wetland soils. In particular, the regeneration of hemlock in wetland soils may be due to the establishment on nurse logs, a factor which was not considered in the transplant experiment.

Discussion

In models, simple explanations are sought for the patterns observed in nature. Gradient models have been widely used to evaluate whether landscape patterns result from simple physiological and morphological constraints on the acquisition and use of multiple limiting resources (Tilman, 1988; Smith and Huston, 1989). Our effort to calibrate and test such a model has yielded simple explanations for species distribution patterns while also revealing further complexity in the causes of landscape pattern. It has been found that interspecific variation in drought and shade tolerance can, in part, explain landscape patterns in the distribution and abundance of species. However, it is also found that the relationship between shade and drought tolerance is not governed solely by physiological and morphological constraints on carbon gain. Furthermore, it is found that some species' distribution patterns may reflect the legacy of disturbance and land-use history as much as the underlying heterogeneity in resource availability.

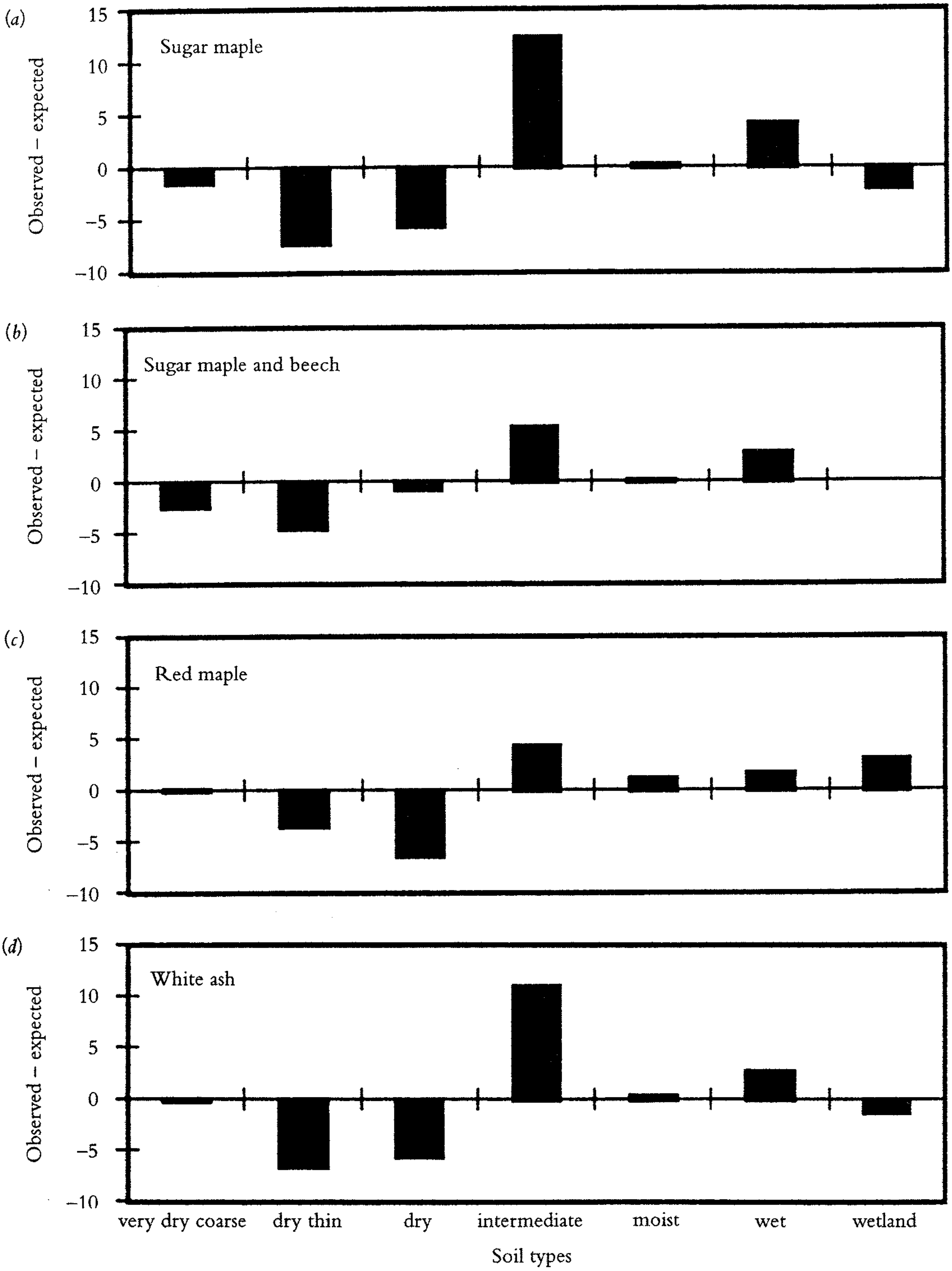
An emphasis on the physiology and allometry of carbon gain has eclipsed the role of survivorship in the development of vegetation models (Bazzaz, 1979; Kobe *et al.*, 1995). Previous landscape models have omitted a direct effect of water availability on mortality by assuming that the consequences of drought are expressed solely through chronic suppression of carbon gain (Smith and Huston, 1989; Huston, 1994). Thus, they assume that species differ in drought tolerance only insofar as they differ in growth. It has been found that differences in drought tolerance among the species studied are determined largely by interspecific variation in mortality rather than growth. These results have important consequences not only for the physiological underpinnings of drought tolerance but also for the relationship between drought tolerance and shade tolerance. The relationship between shade and drought tolerance may depend on the relative importance of growth and mortality in determining a species' ability to tolerate limiting resources.

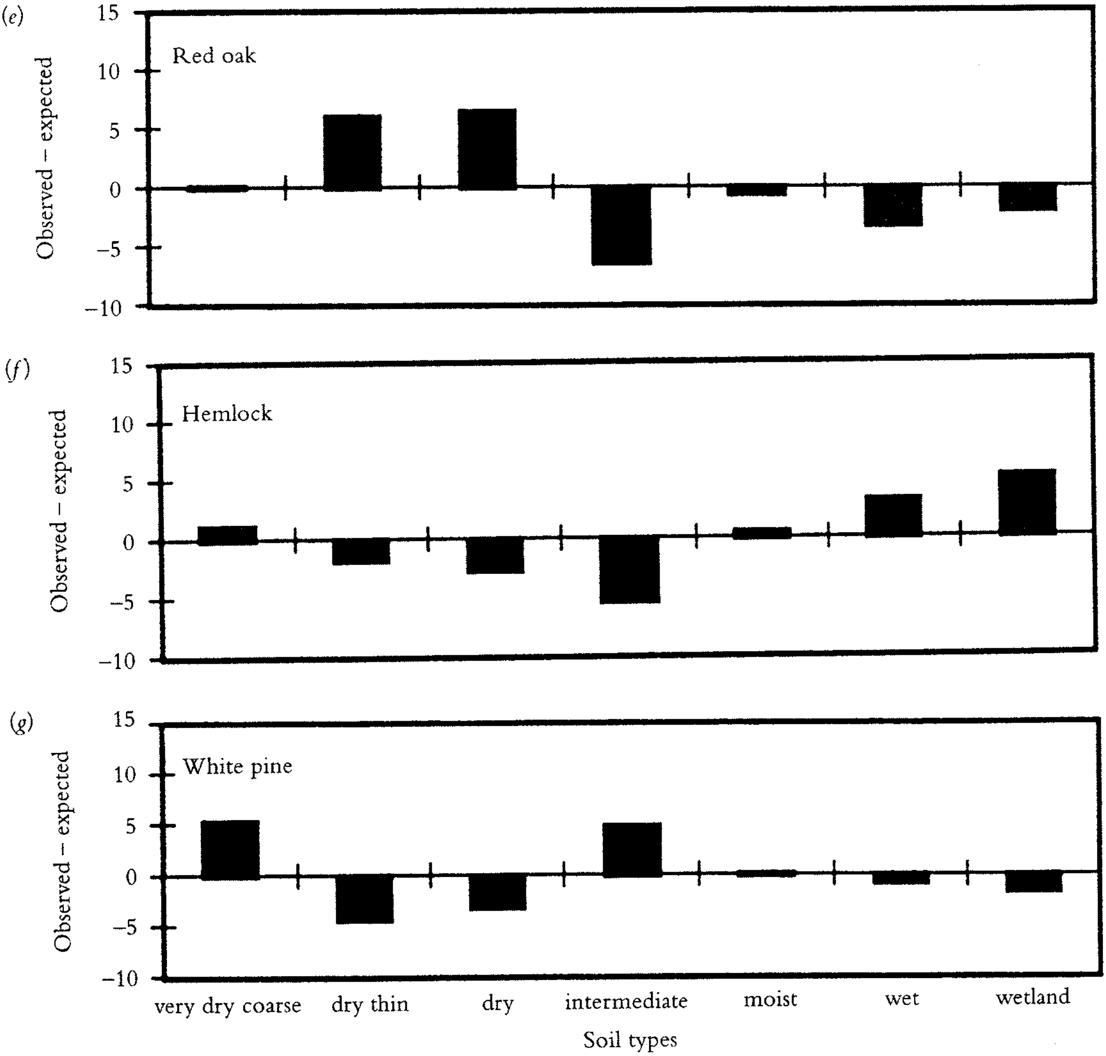
Many studies have shown that the ability to grow and survive in the shade are associated with distinct resource utilization strategies. The ability to grow in the shade is associated with a strategy for maximizing carbon gain, including allocation patterns that maximize leaf area and leaf traits that maximize photosynthetic efficiency (Walters and Reich, 1996), which may predispose saplings to drought stress. However, the ability to survive in the shade is also associated with leaf traits and allocation patterns that minimize susceptibility to herbivores, pathogens, and various other sources of mortality (Kitajima, 1994; Kobe, 1997). These include thicker and tougher leaves and higher allocation to roots, storage, and defense; traits which do not necessarily preclude drought tolerance and may, in fact, promote drought tolerance. Thus, survival may be associated with a conservative resource utilization strategy that permits tolerance of multiple limiting resources, whereas traits that maximize carbon gain may predispose saplings to inevitable trade-offs. Consequently, the extent to which species conform to a trade-off between shade tolerance and drought tolerance may depend on the relative importance of growth and survival in determining the species ability to tolerate limiting resources.

Most of the species we studied conform to a trade-off between shade tolerance and drought tolerance, both in terms of performance measured in the field and in terms of their distribution across the landscape. Hemlock, however, is distinctly bimodal in its distribution and our field studies indicate that it is drought tolerant as well as shade tolerant. This exception may reflect differences in the relative importance of low-light carbon gain in the shade tolerance strategies of deciduous broadleaf and needleleaf evergreen species.

It is widely recognized that hemlock is most common in moist habitats. However,

Fig. 2.9. Observed–expected frequency (shown standardized to percentage of pixels) of seven forest classes on seven soil types. (a) *sugar maple,* (b) *northern hardwoods (sugar maple and beech),* (c) *red maple,* (d) *white ash,* (e) *red oak,* (f) *hemlock, and* (g) *white pine.*





it is not widely recognized that hemlock is also locally abundant across a wide range of conditions. Indeed, there are two morphologically distinct ecotypes of hemlock associated with mesic and xeric habitats (Kessel, 1979). Furthermore, old-growth hemlock stands have been located in both intermediate and xeric habitats throughout southern New England, including xeric sites on sandy soils in GMF and shallow soils on steep slopes and ridgetops in western and central Massachusetts (Nichols, 1913; Dunwiddie *et al.*, 1996; David Orwig, personal communication). The wide amplitude and local abundance of hemlock suggest that competitive ability is but one determinant of a species' prevalence in a landscape, and that the current distribution and abundance of hemlock may reflect disturbance and land-use history.

Several studies suggest that the distribution and abundance of hemlock may be influenced by fire (Rogers, 1977; Kelty, 1986; Foster, 1995). Hemlock is particularly fire sensitive because it has shallow roots, thin bark and a thick, persistent leaf litter layer (Rogers, 1977). Moreover, hemlock does not exhibit rapid height growth and retains a deep canopy with foliage close to the ground (Pacala *et al.*, 1995). Thus, the fact that hemlock is most abundant in moist habitats and only locally abundant in intermediate and xeric habitats may reflect the higher frequency of fire in intermediate and xeric habitats.

Finally, the bimodal distribution of hemlock may reflect the legacy of land-use history. Old-growth stand composition, historical records and palynological studies suggest that prior to European colonization hemlock was more abundant and more widely distributed in the upland portions of New England than it is today (Nichols, 1935; Foster, 1995). As a consequence of widespread agricultural clearing in the eighteenth and nineteenth centuries, trees were restricted to relict stands located on soils unsuitable for cultivation, particularly on excessively wet or dry soils. Following agricultural abandonment over the last 100 years, hemlock has not readily recolonized the portions of the landscape where it was formerly abundant (Kelty, 1986; Foster, 1995). This suggests that bimodal distribution of hemlock may in part reflect its limited dispersal ability (Ribbens *et al.*, 1994).

Conclusions

There are two principal advantages to modeling landscape dynamics at the level of the individual. First, individual-based models provide the means to examine how large-scale pattern emerge from complex dynamics at smaller scales. Second, model parameters correspond directly to whole-plant processes that can be directly measured in the field. Thus, it has been shown how landscape patterns in the distribution and abundance of species reflect interspecific variation in drought and shade tolerance. However, there are several disadvantages to modeling landscape dynamics at the level of the individual. First, because the model is not analytically tractable it is not possible to fully explore parameter space and evaluate all the underlying assumptions of the model. Second, the sampling error grows with the complexity of the model and the error of the various submodels may interact non-additively. Finally, individual-based models are computationally intensive.

For these reasons, it has been sought to balance the need for biological realism with the need to minimize complexity. To further this goal, analysis and simplification of the model is continuing to evaluate the consequences and necessity of the model's complexity. To evaluate the robustness of the model predictions an error analysis is being conducted that translates the statistical uncertainty associated with each parameter into statistical uncertainty in the model's predictions. To further simplify the model a set of partial differential equations has also been derived, which approximates the first moments of the stochastic processes modeled by individual-based simulators. The initial results presented in this chapter demonstrate that the model strikes a reasonable balance between simplicity and biological realism, providing landscape-level predictions that can be traced to aspects of individual performance measured in the field.

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