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Disturbance and the population dynamics of *Liriodendron tulipifera*: simulations with a spatial model of forest succession

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Summary

1 Population dynamics of *Liriodendron tulipifera* throughout the successional sere were investigated with a spatial simulator of forest community dynamics. The simulations were complemented by data from Appalachian cove forests at different stages of development. Gap size was a key consideration in simulation of *Liriodendron* recruitment; seed regeneration of this shade-intolerant species was unlikely except in large gaps (> 0.04 ha).

2 In simulations of long-term forest development (800 years) without exogenous disturbance, *Liriodendron* was a dominant species in early succession (50–150 years), but it was absent or present at low levels in stands > 500 years of age. The simulated basal area levels of *Liriodendron* approximated actual levels in cove forests having a disturbance regime characterized by a very low frequency of severe, large-scale events.

3 The idea that canopy gap size distributions change over the course of forest development was supported by the simulations. Given that intolerant species require large gaps for successful establishment, it was clear that temporal patterns of large gap formation affected the dynamics of such species. Intolerants were unable to regenerate during the stem exclusion phase, but they could regenerate during the subsequent understorey reinitiation and old-growth phases having large gaps.

4 Certain simulated disturbances imposed on old forests elevated *Liriodendron* basal area. Components of the disturbance regime included patch size, return interval, severity and spatial dispersion. The largest increases in *Liriodendron* basal area resulted from disturbance patches > 0.04 ha. Gaps, 0.1 ha in size, formed at intervals < 100 years by the mortality of c. 25% of the canopy trees in a stand, were sufficient to maintain the high levels of *Liriodendron* observed in some primeval forests of eastern North America.

Keywords: canopy gap, forest dynamics, patch dynamics, regeneration niche, temperate deciduous forest

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Introduction

Liriodendron tulipifera L. is often abundant during the first century of temperate deciduous forest succession in eastern North America (Daubenmire 1978; Beck 1990). In young forests on mesic, fertile sites this tree forms almost pure stands (Della-Bianca 1983; Beck 1990). Despite its shade intolerance, *Liriodendron* also occurs in forests older than its maximum life span of approximately 300 years. In some primeval forests it comprises as much as one third of the canopy by density (Braun 1950; Lorimer 1976). How an intolerant species can persist at such high levels in very old forests has been a focus of inquiry (Buckner

& McCracken 1978; Barden 1980, 1981; Skeen *et al.* 1980; Lorimer 1980; Runkle 1985). Some suggest that canopy gaps allow *Liriodendron* regeneration and that these natural disturbance patches are critical to its persistence in old forests. It is further suggested that the frequency and size of gap disturbances may affect the success of *Liriodendron* (Lorimer 1980; Runkle 1985).

A tenet of patch dynamics theory is that disturbance patch size affects species colonization (Pickett 1980; Pickett & White 1985). Empirical and simulation studies of forests world-wide suggest that canopy gap size influences tree regeneration (Platt & Strong 1989; Denslow & Spies 1990; Prentice &

Leemans 1990). In particular, intolerant species such as *Liriodendron* require large gaps for high regeneration success. The gap size threshold for intolerants is estimated to fall in the 0.04 to 0.1 ha range (Hartshorn 1978; Whitmore 1982, 1988, 1989; Pickett 1983), and a minimum gap size of about 0.04 ha is necessary for abundant regeneration of *Liriodendron* (Runkle 1985; Busing 1994).

Prentice & Leemans (1990) suggest that, under entirely endogenous processes, the characteristic crown size of a forest determines the characteristic gap size. For example, boreal forests, consisting of narrow-crowned trees, typically have a preponderance of single-tree gaps that are too small for the regeneration of intolerants. In temperate forests, canopy gaps are generally smaller in young stands than in old stands (Clebsch & Busing 1989; Spies *et al.* 1990; Bradshaw & Spies 1992). The difference in gap size between young and old stands can be attributed to the comparatively small crown size of trees comprising the young stands (Clebsch & Busing 1989). Like the narrow-crowned boreal forests, young temperate stands also exhibit poor regeneration of intolerants. The effects of changes in tree size (and canopy gap size) during forest succession have not been considered in most gap model investigations simply because gap size is held constant (Shugart 1984). By contrast, in the simulations presented here, gap size is variable and determined largely by canopy tree size.

In this paper, how the disturbance regime can affect forest composition is demonstrated. It is shown that disturbances need not be catastrophic to alter composition; the frequency and size of tree-fall gaps can affect the relative success of species. As an example, the response of *Liriodendron* to disturbances is explored. Whether the frequency of large gaps, which allow *Liriodendron* regeneration, increases in late forest succession with the development of large, broad-crowned trees is also examined. Because regeneration processes can be major determinants of vegetation composition and diversity (Grubb 1977; Veblen 1992), interplay among canopy tree size, gap size and regeneration during forest development may influence the dynamics of forest composition and diversity.

Given that long-term data sets on forest dynamics are incomplete, simulations of forest processes over long time scales, combined with empirical observations, facilitate the study of forest dynamics. Using a multispecies model capable of simulating a range of canopy gap sizes, implications of the relationship between disturbance regime and regeneration are investigated, and the population dynamics of *Liriodendron* throughout the successional sere are explored. This is accomplished by: (i) simulating long-term forest development without exogenous disturbance, and (ii) imposing various exogenous disturbance regimes on simulated old-growth forests. How endogenous processes such as changes in tree

size affect disturbance patch size and regeneration processes of *Liriodendron* over the course of forest succession is addressed with the first set of simulations. Empirical data from the southern Appalachian Mountains where extensive old-growth forests remain and stands of young *Liriodendron* forest occur on adjacent sites complement these simulations. The second set of simulations is aimed at determining what disturbance regime(s) could maintain high *Liriodendron* levels in old forests.

Methods

THE STUDY FOREST

The first step in this investigation was to simulate the patch dynamics of an eastern deciduous forest comparatively free of exogenous disturbance. Forests of southern Appalachian coves (small, mid-elevation valleys surrounded by high ridges) fall into this category. Cove forests typically consist of 20–30 mesophytic tree species, often with more than 10 species per hectare in the canopy of old stands (Braun 1950; Whittaker 1956; Golden 1981; Clebsch & Busing 1989). As a whole, shade-intolerant species occur at low levels (*c.* 3% by density; Barden 1980, 1981) in old-growth canopies, and *Liriodendron* occurs at low levels or is absent from such stands (Table 1, Fig. 1). *Liriodendron* levels in cove forests of the Great Smoky Mountains are among the lowest for primeval deciduous forests of eastern North America (Runkle 1985).

The disturbance regime of southern Appalachian cove forests is a major reason for the paucity of *Liriodendron* trees in primeval stands (Runkle 1985). Natural disturbance is primarily in the form of small tree-fall gaps (< 0.04 ha). Large-scale natural disturbances of high severity (*sensu* White & Pickett 1985) are rare. High rainfall throughout the year (Shanks 1954) prohibits fire, especially on north-facing cove sites (Harmon *et al.* 1983). Large-scale wind damage is rare because of the regional location and local topographic position of cove forests (Runkle 1985). For these reasons, southern Appalachian cove forests experi-

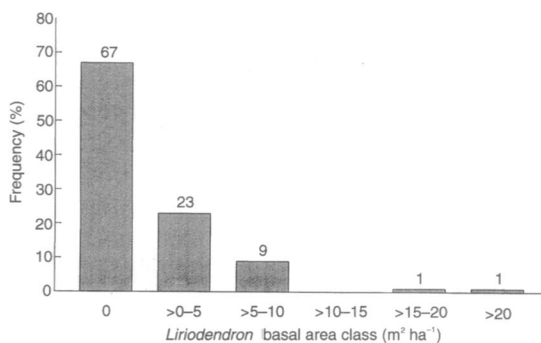


Fig. 1 *Liriodendron* basal area levels in a set of primeval cove forest plots from the Great Smoky Mountains. The percentage of plots in each *Liriodendron* basal area class is provided. The data are from ninety-three 0.08-ha plots.

Table 1 *Liriodendron* levels in young and old cove forest stands sampled with large plots (0.4–1.0 ha). Basal area is measured in $\text{m}^2 \text{ha}^{-1}$. Density refers to live trees $>2 \text{ cm DBH}$, and regeneration density refers to live trees $>2\text{--}10 \text{ cm DBH}$; both are measured in stems ha^{-1}

Site	Stand age (years)	<i>Liriodendron</i>			All species		
		Basal area	Density	Regeneration density	Basal area	Density	Regeneration density
Young stands							
Long Branch	42	33.8	483	48	39.4	1393	588
Long Branch	48	34.3	328	15	43.5	1299	603
Long Branch	63	43.0	305	0	47.8	1622	868
Long Branch	73	44.5	250	0	50.0	1368	965
Old stands							
Long Branch	> 400	1.4	5	0	44.9	577	243
Long Branch	> 400	0	0	0	38.8	727	395
Porters Creek	> 400	1.7	2	0	39.8	1075	522
Indian Camp							
Creek	> 400	6.1	13	0	52.7	600	207
Roaring Fork	> 400	< 0.1	1	1	47.8	898	535
Roaring Fork	> 400	2.9	6	2	55.3	972	501
Roaring Fork	> 400	0.2	1	0	54.2	763	428

ence a lower frequency of large-scale disturbances than other eastern deciduous forests. Cove forests of the Great Smoky Mountains lie at one end of the disturbance patch size continuum in that natural patch dynamics are driven almost exclusively by small canopy gaps $< 0.04 \text{ ha}$.

In young cove forest stands, however, *Liriodendron* is abundant and often occurs as the sole canopy dominant (Della-Bianca 1983; Clebsch & Busing 1989). Judging from the prolific colonization of artificially disturbed sites by *Liriodendron*, seed availability is not a limiting factor for this species in cove forests. *Liriodendron* regeneration is high in stands < 60 years of age, but very low in older successional stands. Thus, the regeneration process is a crucial step in the success of this species.

EMPIRICAL DATA

Long-term trends in cove forest composition, structure and patch dynamics were inferred from a 60-year study of forest development (Clebsch & Busing 1989) and from old-growth forest plot studies. The importance of *Liriodendron* in regeneration and overstorey classes at various stages of forest development was determined. All data were collected in the Great Smoky Mountains National Park ($35^{\circ}35'N$, $83^{\circ}30'W$).

The intensive study site where young and old stands occur in close proximity was located in Long Branch cove on the north slope of Mt. LeConte. Here two young stands of *Liriodendron* on former agricultural fields abandoned *c.* 1920 bordered an extensive primeval forest. One young stand and two old forest stands were first sampled at this site by S. A. Cain *c.* 1935 (Clebsch & Busing 1989; Busing 1989). The young forest was subsequently sampled in 1962,

1968, 1983, and 1993 by R. E. Shanks, E. E. C. Clebsch and R. T. Busing. Ages of the young stands ranged from 42 to 73 years (Table 1). The two old stands were subsequently sampled in 1988 by R. T. Busing.

Two sets of primeval cove forest data augmented the Long Branch succession study. The first set consisted of five 0.6–1.0-ha plots from the north-eastern slopes of the Great Smoky Mountains (Table 1). These were sampled by R. T. Busing *c.* 1990. The second set consisted of 93 plots extracted from a larger set of about 1375 0.08-ha plots sampled throughout the national park in the 1930s. F. H. Miller directed the 1930s project.

THE MODEL

The SPACE model (Busing 1991), a spatial adaptation of FORET (Shugart & West 1977), was employed in this study. Unlike earlier gap models, the new model tracks the locations of individual trees in a stand. Horizontal as well as vertical components of forest structure are simulated. This is noteworthy because the consideration of three-dimensional structure may yield ecological insight (Czaran & Bartha 1992; Kohyama 1993). Earlier models had fixed gap sizes of 0.01–0.1 ha (Botkin *et al.* 1972; Shugart 1984). By contrast, the new model simulates the dynamics of trees on a 0.4-ha tract of land, more than ten times the size of a typical gap in southern Appalachian cove forests (Runkle 1985). Endogenous, single-tree mortality processes produce gaps up to 0.03 ha in size. Large canopy trees produce gaps *c.* 0.03 ha, while smaller trees tend to produce smaller openings. Larger disturbance patches $> 0.03\text{--}0.4 \text{ ha}$ can be imposed on a modelled stand by the contemporaneous mortality of

adjacent canopy trees, simulating multiple-tree gap creation.

The model was parametrized for a 20-species assemblage representative of cove forests. Rates of diameter growth for each species were calibrated with growth measurements from trees in the Long Branch study stands. Following exploratory simulations and adjustment of regeneration parameters for each species to obtain reasonable population and community dynamics, parameters related to *Liriodendron* regeneration, growth and mortality were further adjusted for close agreement with empirical observations. Considerations in the final calibration of *Liriodendron* population processes were as follows.

SIMULATION OF *Liriodendron* POPULATION PROCESSES

Simulation of regeneration was enhanced from the initial version of SPACE (see Appendix for modifications). During model calibration, certain seed regeneration parameters for *Liriodendron* were held constant, while others were adjusted for agreement with empirical data. For example, dispersal probability (DISP) was set at 1.0 indicating no seed dispersal limitations, and the regeneration neighbourhood was set at 0.04 ha (Runkle 1985; Busing 1994). Two variables, characterizing maximum establishment rate (NSEDL, number/year) and canopy tolerance (CTOL), were adjusted to capture *Liriodendron* regeneration patterns in early forest development. A sharp decrease in *Liriodendron* regeneration by the 60th year of forest development was evident (Table 1) and simulation of this decrease was considered of utmost importance. NSEDL was set so that the observed number of *Liriodendron* trees (*c.* 200 at 42 years; Table 1) was present on the 0.4 ha simulation tract at year 42. Then the value of CTOL was decreased until *Liriodendron* stems < 10 cm DBH were rare or absent by year 60.

Vegetative regeneration was simulated to occur upon mortality of *Liriodendron* trees > 12 cm DBH. Five percent of the dying trees were randomly chosen to produce a vegetative stem *c.* 2 cm DBH.

Tree diameter growth was calculated annually as a function of shading leaf area and biomass of neighbours (Botkin *et al.* 1972). However, climatic effects were not included in the current simulations. The response of *Liriodendron* to light followed the shade intolerant growth curve relating relative growth rate to available light (Botkin *et al.* 1972). Diameter growth of *Liriodendron* was initially adjusted for agreement with field measurements by altering the growth scaling constant (G). Final calibration involved setting G so that 10-year diameter increments of the larger trees at simulation year 42 were within the 6–7-cm range measured on canopy trees in the actual 42-year-old stand.

Tree mortality was simulated stochastically (Botkin *et al.* 1972). An individual was given a low prob-

ability of dying each year such that 1–2% of the population reached maximum age. The maximum life span for *Liriodendron* was set at 300 years (Beck 1990). An additional mortality probability was imposed on individuals with a growth rate below 10% of the maximum potential rate. The additional mortality probability allowed only 1% survival over 10 years. Competitive effects of neighbours were largely responsible for suppression of individual tree growth.

SIMULATION PROCEDURES

The first set of simulations, characterizing succession, involved nine 800-year runs of forest dynamics on 0.4-ha simulation tracts. A second set of simulations followed this approach, but exogenous disturbances were incorporated at the old-growth stage (500 years). Disturbance regime components included patch size (*c.* 0.02–0.1 ha), return interval (50–> 300 years), severity and spatial dispersion. Severity of disturbance ranged from 10 to 25% mortality per 0.4-ha tract, and mortality was either dispersed over each tract without regard to tree locations or concentrated in certain areas. The latter mortality regime served to simulate multiple-tree disturbance patches.

Results

FOREST DEVELOPMENT AND *Liriodendron* POPULATION TRENDS

The 800-year simulations of forest development on bare tracts showed a sharp increase in stand basal area to high levels (> 55 m² ha⁻¹) by year 70 (Fig. 2). A gentle decline in stand basal area followed (100–250 years) and a steady state with basal area values predominantly in the 40–60 m² ha⁻¹ range was

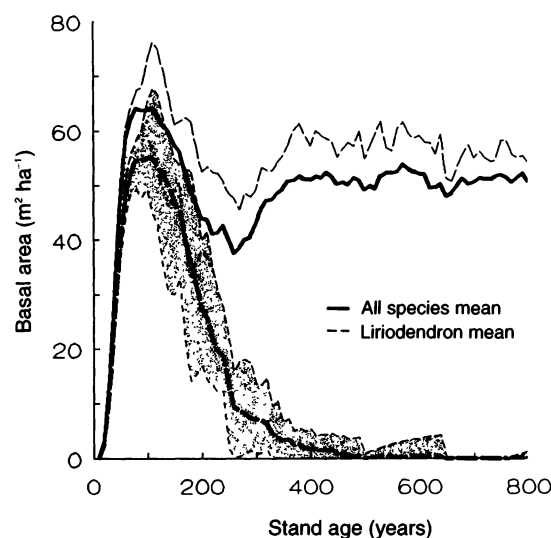


Fig. 2 Dynamics of total basal area and *Liriodendron* basal area during simulated forest development. Mean, minimum and maximum values for nine model runs are plotted; values for *Liriodendron* lie within the shaded envelope.

approached by year 400. *Liriodendron* basal area also increased sharply to maximal levels ($> 40 \text{ m}^2 \text{ ha}^{-1}$) by year 70 and *Liriodendron* clearly dominated the stand for at least a century (years 50–150; Fig. 2). Thereafter, it declined to less than $10 \text{ m}^2 \text{ ha}^{-1}$ on all tracts by year 400 and mean values were very low ($< 3 \text{ m}^2 \text{ ha}^{-1}$). *Liriodendron* was absent from some tracts as early as year 350.

The simulations captured the essential features of *Liriodendron* population dynamics in cove forests. As expected, it rapidly colonized bare sites and dominated the forest within 40 years (Fig. 2 and Table 1). Regeneration increased after a lull from year 50 to year 100 (Fig. 3a and Table 1), but it never occurred at the high levels of the stand initiation phase. The relationships between *Liriodendron* tree growth and mortality, and density appeared reasonable as thinning in simulated stands approximated that of actual stands (Fig. 4). Finally, *Liriodendron* was sometimes present in stands > 400 years old, but at low basal area levels ($< 10 \text{ m}^2 \text{ ha}^{-1}$ on any 0.4-ha tract; Fig. 2 and Table 1).

Disturbance patch size and frequency, changed

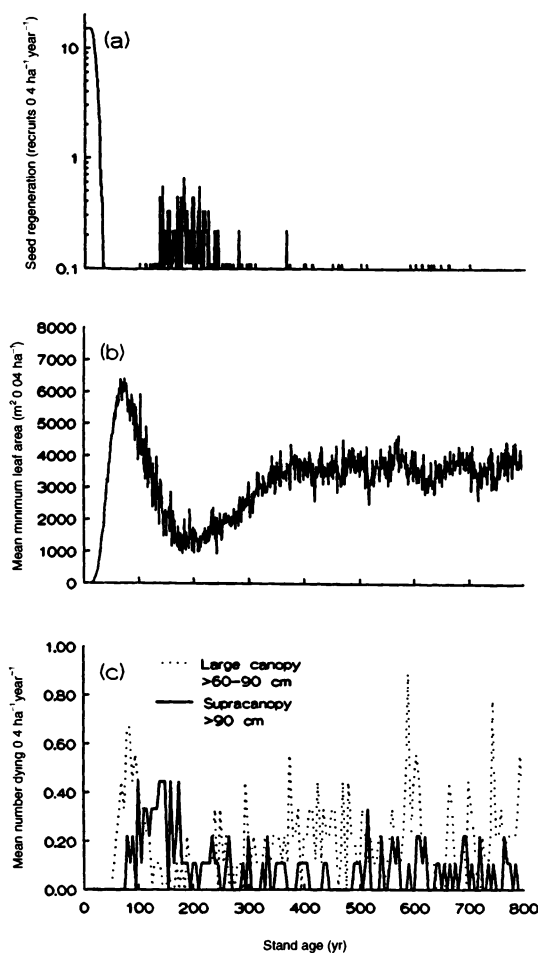


Fig. 3 Canopy dynamics and tree regeneration during simulated forest development: (a) dynamics of *Liriodendron* seed regeneration; (b) dynamics of mean minimum leaf area per 0.04 ha (high values indicate a lack of gaps > 0.04 ha); and (c) dynamics of large canopy tree mortality.

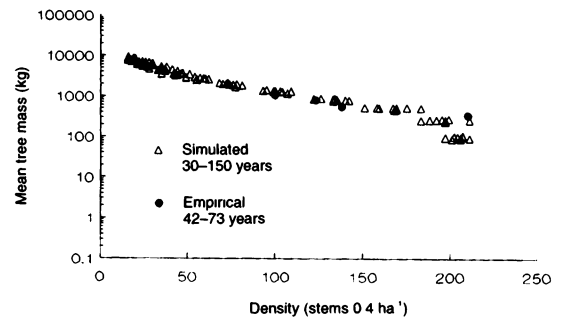


Fig. 4 Thinning relations for simulated and actual stands of *Liriodendron*. The empirical data are from the Long Branch plots (Table 1).

over the course of forest succession simulated as an autogenic process. How and when disturbance patches > 0.04 ha were created, and their effects on *Liriodendron* regeneration are considered here. Mean minimum leaf cover overlying 135 random, 0.04-ha samples showed that large gaps were absent from some stages of simulated forest development (Fig. 3b). For example, the interval from year 50 to year 100 had no large disturbance patches. The death of very large trees began at the end of this interval (Fig. 3c), and created gaps large enough to trigger *Liriodendron* regeneration (Fig. 3a). The frequency of large gap formation was high over the interval from year 150 to year 300 and moderate from year 300 to year 800. After 300 years, *Liriodendron* regeneration was infrequent.

EXOGENOUS DISTURBANCE AND *Liriodendron* POPULATION RESPONSES

Without exogenous disturbance, *Liriodendron* was often absent from 0.4-ha simulation tracts at the old-growth stage (> 500 years; Fig. 2). Mean basal area of *Liriodendron* was $< 2 \text{ m}^2 \text{ ha}^{-1}$. On any given tract, *Liriodendron* basal area did not exceed $5 \text{ m}^2 \text{ ha}^{-1}$.

The spatial pattern of disturbances did affect the response of *Liriodendron*. Imposing spatially diffuse disturbances of 10% and 25% mortality at year 500 did not produce a strong increase in *Liriodendron* basal area (Fig. 5a,b). By contrast, severe, single-patch disturbances at year 500 did produce a noticeable increase in *Liriodendron* basal area (Fig. 6a,b). The spatial pattern of disturbance was the primary reason for the difference in *Liriodendron* responses. For example, 10% of the trees were killed per tract in both the diffuse (Fig. 5a) and single-patch (Fig. 6a) disturbances, but only the single-patch disturbance produced a noticeable increase in *Liriodendron* basal area. The same argument held for the 25% mortality episodes (Figs 5b and 6b). Here, the response to single-patch disturbance was marked.

Effects of disturbance patch size on the success of *Liriodendron* were strong. Larger patch size (0.1 vs. 0.04 ha) clearly allowed higher *Liriodendron* regeneration and growth resulting in high basal area levels

for this species (Fig. 6). The 0.1-ha patch size was sufficient to elevate *Liriodendron* basal area on all simulation tracts, but the 0.04-ha patch size did not result in *Liriodendron* establishment on all simulation tracts. Apparently, it did not consistently colonize the smaller (0.04-ha) disturbance patches.

The effects of disturbance return interval were strong as well. A short return interval (50 years) elevated *Liriodendron* basal area (Fig. 6). In at least one case under this return interval, its basal area continued to rise at the end of the simulation period (Fig. 6f). A long return interval (> 300 years) produced population surges followed by declines. Duration of the decline depended on patch size, with larger patches generating larger *Liriodendron* populations that persisted for longer periods of time (Fig. 6a,b).

Discussion

Long-term population trends of *Liriodendron* can be explained by patch dynamics (Pickett & White 1985) and the role of regeneration in vegetation (Grubb 1977; Whitmore 1989; Veblen 1992). The effect of gap size on the regeneration and growth of different species is a key consideration. On the premise that large gaps are essential to regeneration and growth of *Liriodendron*, reasonable long-term trends in population dynamics of the species can be simulated.

The simulations of forest development free of exogenous disturbance demonstrate that endogenous processes alone affect gap size and frequency during succession. Various stages of forest development following major disturbances have different gap disturbance regimes. For example, the four stages recognized by Oliver (1981) are reasonably distinct in this respect. Based on the empirical data and simulation results, the stand initiation phase can be regarded as the colonization of one very large gap and *Liriodendron* regeneration is prolific. This phase lasts only a few decades in the simulations. It is followed by a stem exclusion phase where canopy trees are small, and consequently, the creation of large gaps is very

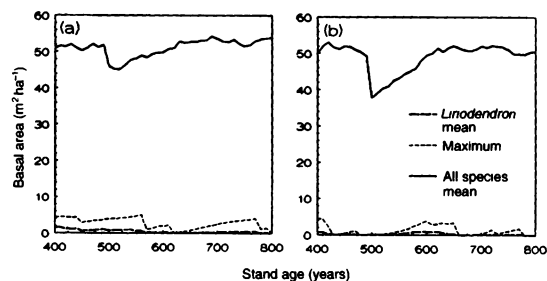


Fig. 5 Basal area levels of *Liriodendron*, and of all species combined, in old stands: (a) with 10% exogenous mortality at year 500; and (b) with 25% exogenous mortality at year 500. The exogenous disturbance episodes involve mortality that is random with respect to tree location. A diffuse pattern of mortality generally results. Mean and maximum values for nine model runs are provided.

infrequent. Intolerant species are unable to regenerate during this phase. By the end of the first century, this phase grades into the understorey reinitiation phase, characterized by an increase in large gap creation. Two means of large gap creation may be operating here. First, senescence of the colonizing cohort may lead to the contemporaneous mortality of adjacent canopy trees. Second, canopy trees may attain sizes large enough to create large gaps following the mortality of single trees. Although both means of large gap formation are likely to be operating, the simulations suggest that large gaps are strongly associated with large tree mortality (100–200 years, Fig. 3b,c). This supports the argument that changes in tree size during forest development affect the size of gaps. Without exogenous disturbance, the understorey reinitiation phase has the highest frequency of large gap creation of all the developmental stages. Although large gap creation is comparatively infrequent during the old-growth phase (> 400 years), it is sufficient to allow occasional regeneration of *Liriodendron*. However, the species is often absent from individual simulation tracts (and actual old stands) suggesting that lapses in establishment of this species in any given old-growth stand (*c.* 0.4 ha) may last for centuries.

Exogenous disturbances at the old-growth stage can trigger *Liriodendron* regeneration and increase its

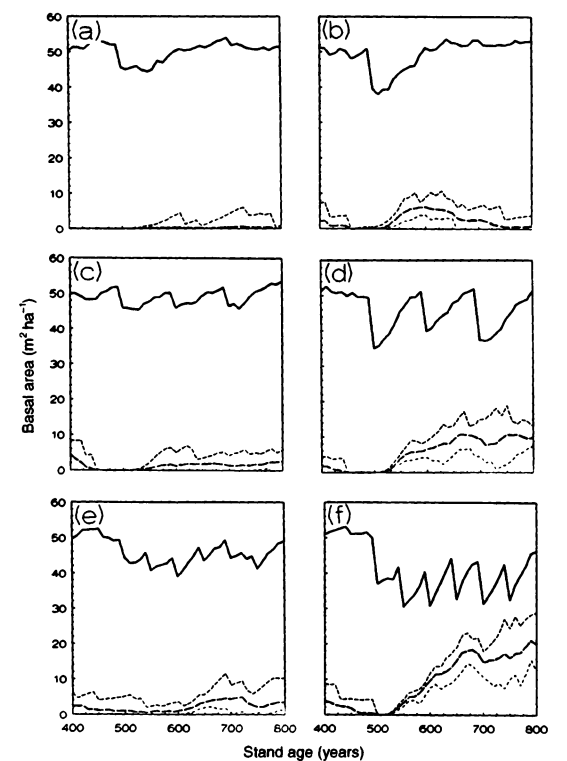


Fig. 6 Basal area levels of *Liriodendron*, and of all species combined, at disturbance patch sizes of 0.04 ha (a,c,e) to 0.1 ha (b,d,f) and return intervals of 300 years (a,b), 100 years (c,d) and 50 years (e,f). Exogenous disturbance begins at year 500. *Liriodendron* mean, minimum and maximum values for nine model runs are shown at the bottom of each panel; the upper line is the all-species mean.

relative dominance. Gap size greatly affects *Liriodendron* levels. A simulated stand with several small gaps < 0.04 ha in size has much lower *Liriodendron* regeneration than a stand with a single gap > 0.04 ha in size. Though more canopy trees may be killed in the former disturbance regime, the spatially diffuse pattern of small canopy openings is not conducive to successful regeneration of *Liriodendron*. So, the spatial pattern of canopy tree mortality can be an important aspect of the forest disturbance regime. Return interval of disturbances also affects *Liriodendron* dominance in old forests. Simulated return intervals less than its maximum life span (c. 300 years) tend to increase its mean basal area and its long-term persistence at the scale of 0.4 ha. Return intervals less than 50 years result in high *Liriodendron* relative dominance because of its ability to rapidly colonize large gaps.

How well do the simulated results for *Liriodendron* compare to actual levels of the species in eastern deciduous forests? As noted above, *Liriodendron* levels in southern Appalachian cove forests with a disturbance regime of small canopy gaps (predominantly < 0.04 ha) do correspond to the levels in old simulated stands without exogenous, large gap disturbances. *Liriodendron* is absent, or present at low basal areas, in both the actual and simulated stands. In an Appalachian forest with more frequent large-gap disturbance, *Liriodendron* basal area levels are considerably higher (mean = 14 m² ha⁻¹; Lorimer 1976). Exogenous disturbance regimes with 0.1-ha gaps at return intervals < 100 years imposed on old growth produce *Liriodendron* basal areas in this range (Fig. 6). Lorimer (1980) estimated that windfalls, each killing approximately 10% of the canopy trees, occurred at return intervals < 50 years. The simulated 0.1-ha disturbances presented above kill about 25% of the canopy trees and are therefore not fully compatible with Lorimer's regime. A more compatible simulation regime with gaps of this size killing 10% of the canopy at a 35-year return interval produces *Liriodendron* basal areas in the 5–20-m² range. On average, however, they are somewhat less than the actual values of Lorimer (1976).

Lorimer (1976, 1980) notes that many other primeval forests have even higher densities of *Liriodendron* than his Appalachian study stand. The species attains basal areas > 20 m² ha⁻¹ in at least some of these forests. Based on the simulations, repeated large gap disturbances > 0.04 ha are necessary to maintain such a high *Liriodendron* component (Fig. 6). One could argue that a single, very large gap could produce the same result (Johnson & West 1973), but in primeval forests *Liriodendron* canopy trees tend to occur as isolated individuals or in small clumps than in stands (McCarthy 1933; Buckner & McCracken 1978). So, very large disturbance patches are probably not responsible for the maintenance of *Liriodendron*. The simulations suggest that gaps, c.

0.1 ha in size, formed at intervals < 100 years by the mortality of c. 25% of the canopy trees stand wide, are sufficient to sustain such high levels of *Liriodendron*.

In conclusion, effects of disturbance regimes on forest population and community dynamics can be explained by patch dynamics theory. A continuum of forest responses to various canopy gap disturbances is demonstrated here. Given that intolerant species require large gaps for successful establishment, it is useful to know what kinds of forests (e.g. boreal vs. temperate deciduous), and what stages of forest development are prone to large gap disturbance. It is suggested that the size distribution of gaps changes over the course of succession, with young stands having a lower frequency of large gap creation. At later stages, intrinsic formation of large gaps is sufficient to maintain low levels of *Liriodendron* and other intolerants, but exogenous disturbances generating a higher frequency of large gaps can produce marked increases in the abundance of intolerant species.

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Appendix

The unique features and mathematical relationships of the SPACE model are described in Busing (1991). Further details of the model are available on request. Simulation of seed regeneration has been enhanced in the version employed here. Specific alterations are as follows. The KTIME parameter was deleted and three species-specific parameters (DISP, KRADIUS and LTIME) were added (Table 2). To simulate seed dispersal limitations, regeneration is not allowed on tracts lacking adult-sized trees of the species in question except when dispersal is likely. The value of DISP, a dispersal probability (ranging from 0 to 1, low to high), serves in the stochastic simulation of dispersal events at the population level. When adults of a species are present or when seed dispersal occurs NSEDL attempts at regeneration are made. KRADIUS defines the size of the circular neighbourhood over which leaf area is summed during each attempt at seed regeneration. It is related to the gap size requirement of a species. Input of each seedling is a probabilistic function of the total leaf area (SLA) within the neighbourhood of a randomly selected cell; input occurs when:

$$SLA < -CTOL \ln(u)$$

where u is a uniform random number ($> 0-1$). Finally, a time lag (LTIME) between seedling input and recruitment at sapling size is employed.

Table 2 Species parameters employed in the SPACE model. B3 and B2 are constants in the height to diameter relationship: $H = 137 + B2D - B3D^2$. ITOL is the shade tolerance class (1 = tolerant, 2 = intolerant). AGEMX is the maximum age (years). G is the growth scaling constant. SPRTND is the probability of a sprout replacing a tree following death; SPRTMN and SPRTMX are the lower and upper limits of sprouting tree diameter (cm). DISP is the probability of seed dispersal to tracts lacking reproductively mature individuals. CTOL is the canopy tolerance of potential recruits. LTIME is the time lag (years) between seedling establishment and recruitment. NSEDL is the maximum number of recruits per year. KRADIUS is the radius (0.5-m units) of the regeneration neighbourhood area

Species*	B3	B2	ITOL	AGEMX	G	SPRTND	SPRTMN	SPRTMX	DISP	CTOL	LTIME	NSEDL	KRADIUS
<i>Acer pensylvanicum</i>	0.7592	53.14	1	50	30.0	0.15	12.0	200.0	0.80	2.5	15	3	20
<i>Acer rubrum</i>	0.1439	48.06	1	150	20.0	0.05	12.0	200.0	0.80	2.5	15	4	20
<i>Acer saccharum</i>	0.1790	53.33	1	300	20.6	0.05	12.0	150.0	0.80	5.0	30	4	16
<i>Aesculus octandra</i>	0.1275	39.52	1	300	20.0	0.05	12.0	200.0	0.10	5.0	30	4	16
<i>Betula lenta</i>	0.1808	37.96	1	250	20.0	0.05	12.0	200.0	0.80	1.0	15	3	23
<i>Betula lutea</i>	0.1206	33.04	1	300	15.0	0.05	12.0	200.0	0.80	2.5	20	4	20
<i>Carya cordiformis</i>	0.3811	81.55	1	300	30.0	0.05	12.0	200.0	0.10	2.5	15	1	20
<i>Cornus florida</i>	0.5360	40.80	1	100	15.0	0.05	12.0	200.0	0.60	5.0	20	2	16
<i>Fagus grandifolia</i>	0.1566	46.97	1	350	15.0	0.20	6.0	200.0	0.10	8.0	40	1	11
<i>Fraxinus americana</i>	0.1632	48.97	1	300	20.0	0.05	6.0	200.0	0.80	1.0	15	3	23
<i>Halesia carolina</i>	0.1818	41.46	1	300	20.0	0.70	6.0	200.0	0.60	5.0	20	4	16
<i>Liriodendron tulipifera</i>	0.1115	51.29	2	300	40.0	0.05	12.0	200.0	1.00	0.5	10	15	23
<i>Magnolia acuminata</i>	0.1038	37.37	1	300	15.0	0.30	12.0	200.0	0.80	1.0	15	2	23
<i>Magnolia fraseri</i>	0.3950	58.46	1	300	35.0	0.50	12.0	200.0	0.80	1.0	15	2	23
<i>Prunus serotina</i>	0.1643	43.38	2	250	20.0	0.10	12.0	200.0	1.00	1.0	10	3	23
<i>Quercus rubra</i>	0.1401	51.55	1	400	20.0	0.05	12.0	150.0	0.10	1.0	30	1	16
<i>Robinia pseudoacacia</i>	0.1356	35.80	2	150	25.0	0.01	12.0	80.0	1.00	0.1	10	4	36
<i>Sassafras albidum</i>	0.6190	75.51	2	200	20.0	0.05	12.0	200.0	1.00	0.1	10	4	36
<i>Tilia heterophylla</i>	0.2841	65.91	1	150	25.0	0.50	12.0	100.0	0.40	5.0	30	1	16
<i>Tsuga canadensis</i>	0.1314	49.93	1	600	15.0	0.00	0.0	0.0	0.10	8.0	40	1	8

*Species nomenclature follows Radford, Ahles & Bell (1968).