

Competition and Tree Death

*Most trees die young in the struggle
for the forest's scarce resources*

Robert K. Peet and Norman L. Christensen

Tree deaths are often dramatic events. Fires can consume thousands of hectares of forest in a single conflagration. The powerful winds of hurricanes and tornados can flatten all the trees in their paths. More subtle events of synchronous tree mortality, such as those caused by defoliating insects or fungal diseases, may attract attention because of the ghostly skeletons that remain. But these dramatic forms of tree mortality are the exception; most tree deaths go unnoticed.

At best only a few of the many thousands of seedlings produced by a typical mature tree can survive and grow to achieve canopy position and reproductive status. Most die as a direct or indirect consequence of failure to compete successfully for light, water, or soil nutrients. This form of tree death has come to be called *natural thinning*, or *self-thinning* when applied to a relatively even-aged population of a single species. These terms contrast the process with *artificial thinning*, where less vigorous or unwanted trees are selectively removed by man. Although individually the deaths attributable to natural thinning are inconspicuous and unimportant, collectively they determine much about the structure, succession, and dynamics of forest ecosystems.

Robert K. Peet is an associate professor in the Department of Biology, University of North Carolina, Chapel Hill, NC 27514. Norman L. Christensen is a professor in the Department of Botany, Duke University, Durham, NC 27706. © 1987 American Institute of Biological Sciences.

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A general model of forest dynamics

Studies of forest succession in several divergent forest types have produced markedly similar conceptual models of postdisturbance forest development (Bloomberg 1950, Bormann and Likens 1979, Daubenmire and Daubenmire 1968, Day 1972, Horton 1956, Jones 1945, Oliver 1981, Peet 1981a, Raup 1946). In these models forest regrowth following disturbance is viewed as largely a population process wherein four relatively distinct phases can be recognized: the establishment phase, the thinning phase, the transition phase, and the steady-state phase. In this article, we present a generalized version of these models, which appears to apply broadly to forest regrowth following either natural catastrophe, such as wildfire, or human disturbance, such as agriculture and subsequent land abandonment.

Forests of the piedmont region of

North Carolina provide examples of many of the population processes important in forest development (see Christensen and Peet 1981, 1984, Peet and Christensen 1980a,b) and have a long history of ecological study. We use examples drawn from our work on these forests to explore the implications of our forest development model for tree mortality.

At the time of European settlement, piedmont forests were dominated by hardwood species, primarily oaks and hickories. Shade-intolerant species like shortleaf and loblolly pine were found occasionally, usually on sites with exceptionally poor soils or where competitive interactions with other trees had been temporarily reduced by some form of disturbance, such as windfall, fire, or aboriginal cultivation. Following settlement, much of the forest land was cleared for agriculture. Subsequently, less favorable economic conditions and decreased soil fertility resulted in widespread abandonment of land and its reversion to forest.

Establishment. Immediately following abandonment of agricultural land, few plants other than annual weeds are present. In this period of rapid, sometimes geometric, increase in vegetation, establishment of seedlings of numerous species is possible owing to the low level of competition. In piedmont old fields, pines are typically among the most numerous tree seedlings. These pine seedlings grow rapidly and after 5–15 years form a closed canopy above the other seedlings; only the occasional sweetgum

or yellow poplar manages to compete successfully and retain a position in the canopy. In most forest types, this establishment phase is characterized by extensive seedling establishment and rapid growth.

Thinning. Once a closed canopy has formed, competition becomes intense and most of the seedlings and saplings overtopped by the initial cohort of pines die, leaving the region near the ground relatively free of vegetation. Few if any pine seedlings can be found and only a few hardwood seedlings invade or persist from the initial establishment period.

As the pines get taller and their crowns larger, there is room for fewer of them in the canopy. The slower-growing, less vigorous individuals are not able to compete with the dominants in either height or root growth and eventually die. This period is the second or thinning phase of forest development. The number of trees in the stand steadily decreases and biomass steadily increases. In some forest types, though not typically in piedmont forests, more shade-tolerant tree species form a layer beneath the primary canopy.

Transition. The thinning phase continues until the canopy pines have reached full size and the overtopped individuals have mostly died, a process that in piedmont forests requires about 60 years after initial canopy closure. Subsequently, death of one of the pines results in the formation of a canopy gap that cannot be completely filled by lateral growth of adjacent trees. As a consequence, a patch of light and soil resources becomes available within the forest. In this patch, new seedlings can become established and previously established seedlings increase in size.

Seed availability and the size and other characteristics of a patch determine which species successfully exploit that particular patch. Tree death during this transition phase is often density independent (unrelated to competition) and a consequence of such factors as lightning, windthrow, and disease. This third phase, the transition phase, can be brief but dramatic if the canopy trees die synchronously, or it can last as long as 50–100 years.

Steady state. The fourth and final phase is the steady-state forest, which is dominated by hardwood species of varying age but often located in relatively even-aged patches coincident with previous canopy gaps. A forest in this phase can be viewed as a mosaic of patches of various sizes and ages, sometimes overlapping and sometimes distinct.

Within each patch the processes of establishment, thinning, and eventually gap formation are repeated. The only conspicuous deviation is that, because of their requirement of high light levels, pines and other early succession species regenerate only in the largest gaps of the steady-state forest. Thus, the final phase of forest development contains simultaneously all three of the preceding phases, only in miniature.

In his 1947 presidential address to the British Ecological Society, A. S. Watt described a general pattern of plant community dynamics wherein a community can be viewed as a dynamic mosaic with each of the tessera repeatedly cycling through phases of degeneration and recovery. This pattern has been observed in virtually all steady-state forests from the tropics to the boreal region. In this article we incorporate Watt's gap-phase regeneration as the final part of our four-phase model of forest development.

Applicability. The conceptual model described above for North Carolina piedmont forests should apply to essentially all forests where one or only a few tree species dominate the initial regrowth. Forests where similar developmental patterns have been reported include the conifer forests of the Rocky Mountain region (Daubenmire and Daubenmire 1968, Day 1972, Peet 1981a) and the Pacific Northwest (Oliver 1981), the boreal forests of Canada (Bloomberg 1950, Plochmann 1956, Raup 1946) and Scandinavia (Ilvessalo 1937, Siren 1955), and the mixed-hardwood forests of New England (Bormann and Likens 1979).

The applicability of the first three stages of the model to high diversity tropical systems is not yet clear, though the potential for such generalization is supported by Whitmore's (1984) description of forest development in the moist tropics of the Far

East. Extension to communities of lower stature or woodlandlike physiognomy is more problematic. Evidence from Rocky Mountain forests suggests that if tree establishment is sufficiently slow relative to the longevity of the trees, the thinning and transition stages can be almost completely passed over (Peet 1981a, 1987).

Patterns of tree mortality

Most postestablishment tree mortality takes place during the thinning phase. During this phase competition is most intense and tree density is highest.

For a given cohort of trees that becomes established during the initial stage of forest development, it is reasonable to predict a sigmoidal survivorship curve. That is, we expect an initial high level of survival during the establishment phase when competition is low, followed by much lower survival during the thinning phase, followed in turn by high survival after the trees have reached their maximum size and are no longer intensely competing for space. The increase in mortality during the thinning phase should be directly related to the initial density of stems entering into competition. Indeed, where the establishment rate for new trees is very low, the thinning phase might be bypassed altogether.

Unfortunately, because the longevity of trees generally exceeds that of most research projects, we have few data sets with which to verify the predicted changes in mortality. What few data we have are reasonably consistent with the predictions. For example, both Yarranton and Yarranton (1975), working with jack pine in Ontario, and Schlesinger and Gill (1978), working with the chaparral shrub *Ceanothus megacarpus* in California, have reconstructed stand histories from dead stems and have found sigmoidal survivorship curves of the sort we predict. Harcombe (1986) has provided evidence for a decline in mortality late in the thinning phase in a 130-year-old spruce-hemlock stand in Oregon. He used a combination of permanent plot data and extrapolation from forestry yield tables to suggest that mortality was much higher for the first 60 years of

stand growth than for the most recent 60 years.

Data from loblolly pine stands on the North Carolina piedmont are only partially consistent with our prediction of a sigmoidal survivorship pattern. As part of a study of tree mortality on the North Carolina piedmont, we examined 50-year records for seven loblolly pine stands of differing initial densities (Figure 1). The stands were eight years old when the observations were initiated by C. Korstian and other early members of the Duke University forestry faculty. The predicted initial period of low mortality was not observable at eight years in the densest stand, but lasted roughly 40 years in the least dense stand. The annual probability of death for a tree (the slope of a plot of log-density against time) varied di-

rectly with initial density and was generally constant within a stand for the duration of the thinning phase.

No support can be seen in these data for a final interval of high survival. It appears likely that by the time natural thinning reduced tree density to that typical of mature stands, the remaining trees were reaching senescence and were particularly susceptible to such dangers as bark beetles, fungal infection, and ice storms. Of course, it is possible that if observations were to continue for another 20 years the predicted plateau would be observed. Either way, the existence of a final period of constant mortality must be viewed as dependent on local site conditions and the biology of the colonizing species and not a necessary feature of our forest development model.

Although in the preceding studies we have assumed seedling establishment in a stand to be close to synchronous, variation in seed source proximity or climatic fluctuations can result in dramatic differences in the rate of stocking. Where establishment is slow, the onset of thinning can be significantly delayed. For example, lodgepole pine forests of the Rocky Mountains (Peet 1981a) and the Douglas-fir forests of the Pacific Northwest (Franklin and Hemstrom 1981) are typically described as strictly even-aged, postfire forests, yet the establishment period often extends over 50 years or longer.

In contrast to the thinning phase, mortality of canopy trees during the transition and steady-state phases is often a consequence of factors not directly related to resource availability, such as lightning, windthrow, ice damage, and disease. For example, Franklin¹ found at least 32% of tree deaths in old-growth coniferous stands in Washington and Oregon to result from wind (windthrow, windbreak, and crushing). In a relatively mature beech-magnolia forest in east Texas, Harcombe and Marks (1983) found 21% of tree mortality attributable to wind.

The duration and character of the transition phase is highly dependent on both the average survival following the cessation of thinning and the synchrony of mortality of the remaining members of the initial, postdisturbance cohort of trees. High postthinning longevity appears fairly common in conifer forests of western North America. Consequently, the transition phase is typically protracted in these forests. In contrast, loblolly pine forests in southeastern North America and aspen forests in northeastern North America generally have short to almost nonexistent transition phases, owing to the lesser longevity of their dominant trees.

Where the probability of mortality is constant for canopy trees, the transition phase will be one of relatively gradual change, whereas if cohorts show synchronous senescence, as Mueller-Dombois (p. 575, this issue) and Mueller-Dombois et al. (1983)

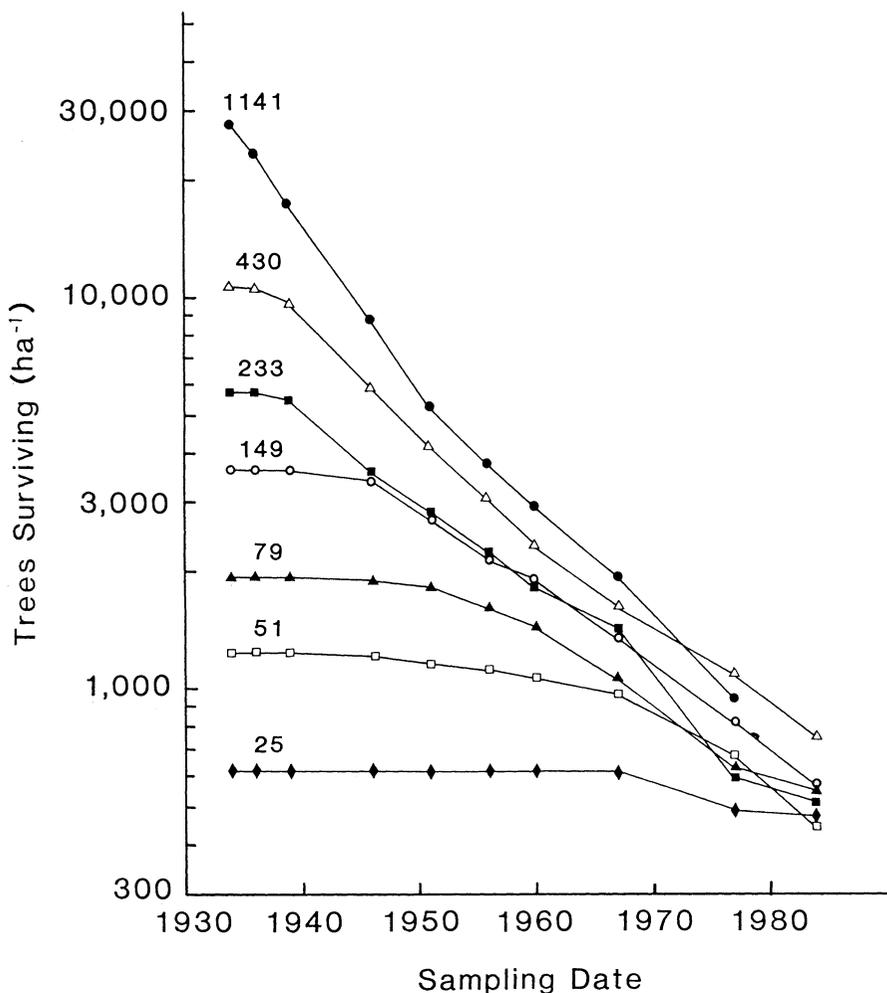


Figure 1. Survivorship in even-aged loblolly pine stands (stem diameters more than 1.25 cm) over a 50-year period. Despite extreme variation in initial density (25–1141 trees per 0.1-acre plot, indicated by figure labels), differential mortality resulted in convergence on a relatively narrow range of densities (18–31 trees per plot).

¹J. F. Franklin, M. Klopsch, K. J. Luchessa, and M. E. Harmon, 1986. Unpublished manuscript. Oregon State University, Corvallis.

have described for many forest types, the change will be abrupt. Indeed, if death of the canopy is nearly synchronous, a whole new cycle of stand establishment, thinning, and transition can be initiated (Peet 1981a, Plochmann 1956).

Tree mortality during the fourth or steady-state phase of forest development can be expected to be relatively constant from year to year. Given a large enough spatial scale, mortality is generally balanced by input of new stems. However, large-scale episodic factors such as windthrow and bark-beetle outbreaks prevent most stands from appearing stable.

For a group of trees observed over an extended period, we might expect mortality to decline slightly over a period of 200 or more years as the smaller trees die or grow to achieve canopy status. This proposal is difficult to test for piedmont forests, not only because of the shortage of long-term records, but also because few if any piedmont forests have been free of human disturbance long enough to be truly steady-state forests.

However, the 50-year record of tree death in a mixed-species hardwood stand (Figure 2) illustrates the expected patterns. This stand has never been clearcut, and it was undisturbed for at least ten years prior to the start of the observations. The depletion curve for all trees together is nearly straight, but that for the canopy-dominating oaks has a concavity consistent with the predicted decline in mortality with time and increasing average size.

The component species groups show various rates of loss consistent with their biology and canopy position. For example, flowering dogwood, an obligate understory tree, shows high mortality, probably because no stems ever escape the highly competitive understory environment. In contrast, oak (primarily white oak), a long-lived canopy tree with relatively few saplings, has the lowest mortality rate.

Seedling mortality

Our model of forest development also allows predictions about tree seedling mortality. During the establishment phase when competition is low, seedlings should have relatively low death

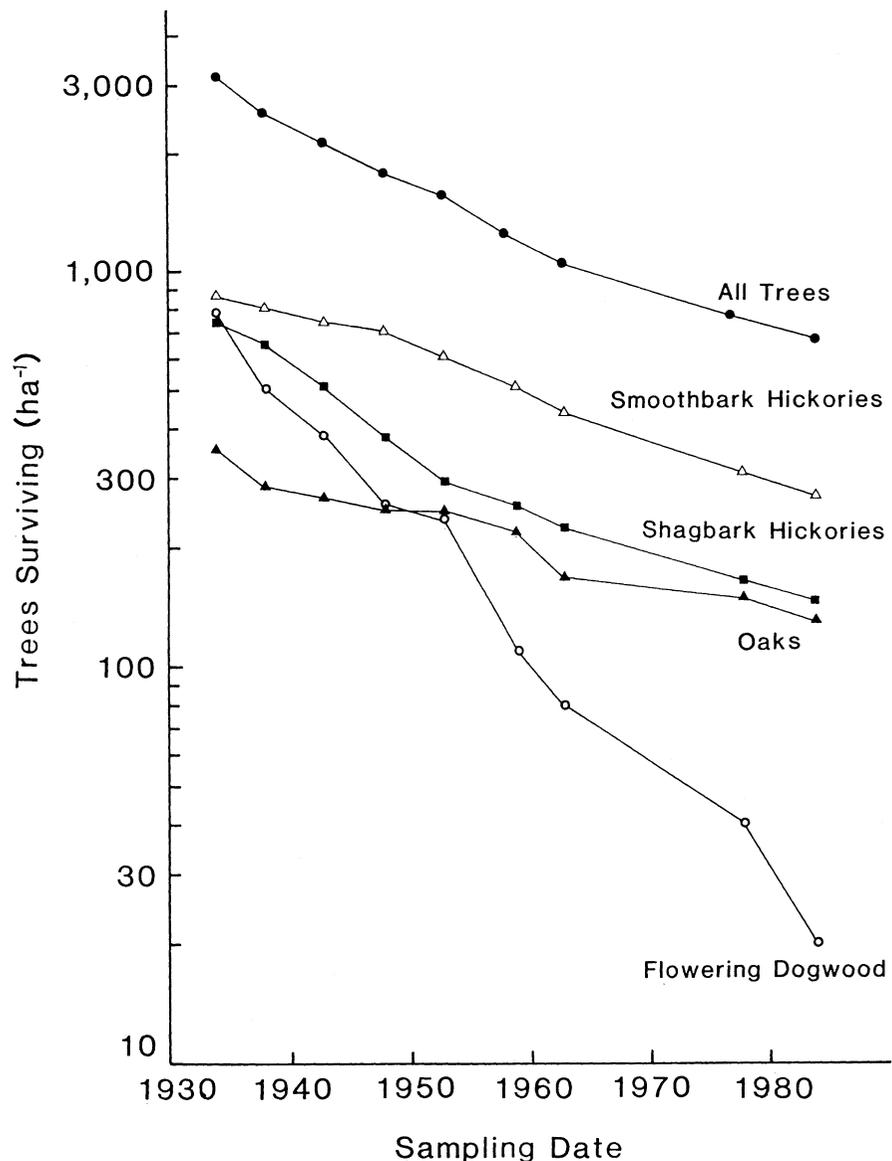


Figure 2. Depletion curves illustrating mortality rates of different tree species in an uneven-aged, mixed hardwood stand. Note that the overall depletion rate and the depletion rates within species remained relatively constant over 50 years.

rates. In contrast, the intense competition of the thinning phase (or "stem exclusion phase" as Oliver calls it) can be predicted to exclude virtually all seedling establishment. During the transition phase seedlings should again be able to become established by exploiting resources freed by deaths of canopy trees. Finally, an intermediate, but spatially highly variable, level of seedling mortality should be expected in steady-state forests.

It must be emphasized, however, that virtually all studies of seedling survival have shown high rates of

mortality, especially during the initial year following germination (e.g., Fowells and Stark 1965, Glitzenstein et al. 1986, Hett and Loucks 1971, Tappeiner and Helms 1971). Consequently, our predictions of differences in seedling mortality between the phases of forest development must be viewed as relative differences, set against a backdrop of consistently high absolute mortality.

Seedling establishment and survival probabilities of red maple and oak in piedmont forests illustrate typical changes during forest development (Table 1). Using size-based transition

probabilities for each stand obtained over a five-year period of annual observations, we calculated the probability that an individual new seedling would survive to a height of 50 cm.

These probabilities (PHT50s), although consistently low in an absolute sense, are relatively high in the youngest stands, which have just entered the thinning phase; relatively low during the middle of the thinning phase; and higher again during the transition phase. The survival probabilities are lower in the hardwood stands, though it is unclear whether these stands are in a moderate thinning phase resulting from selective cutting for railroad cross-ties and firewood early this century.

On severe sites, particularly in arid and boreal regions, seedling mortality can be exceptionally high—both in the absence of other competing plants and in the presence of a well-developed early successional herb community. On such sites the development of a few trees can serve to either ameliorate the physical environment or suppress the competing herb layer. Thus, the establishment of an initial cohort of a few trees can, in these circumstances, facilitate (Connell and Slatyer 1977) the survival of later seedlings. The result can be higher seedling survival in the thinning phase than in the establishment phase (see Pearson 1923, Peet 1981a, Shankman 1984, Stahelin 1943).

Constraints on size and numbers

During the thinning phase of forest development, total stand and average

tree biomass increase while tree density decreases. Therefore, surviving trees increase in size fast enough to more than compensate for biomass loss due to tree death. The quantitative relationship between average tree size and tree density has been the subject of considerable research (Hutchings and Budd 1981, Westoby 1984, White 1985).

In the seminal paper on the topic, Yoda et al. (1963) reported that the mean weight (or volume) of a plant in a thinning population is proportional to density taken to the $-3/2$ power. Subsequent studies, with plants ranging in stature from diminutive annual herbs to large trees, have shown this relationship to hold with almost law-like regularity (Westoby 1984, White 1985, but cf. Weller 1987). If applicable to trees, this relationship provides a convenient method for predicting the rate of mortality as a function of biomass increment, as well as a means of assessing plant competition in a stand.

The thinning rule leads us to predict an initial period of tree growth with little or no mortality. This is the establishment phase. Thereafter, during the thinning phase, a graph of changes in the logarithm of density and logarithm of mean weight should give a line whose slope is $-3/2$. White (1985) reports that for trees the intercept for this line generally falls between 3.5 and 4, assuming units of grams and stems/m².

As the thinning process proceeds and the transition phase is approached, the amount of biomass lost per tree death should increase. But fewer trees will survive to compensate

for the loss, so the rate of net stand biomass production will decrease. When the net biomass production matches loss to mortality, the slope of the thinning curve will be -1 , and if the rate of biomass loss is greater than the rate of net production, the slope will be greater (less negative) than -1 .

The thinning rule has repeatedly been shown to be consistent with forestry yield tables, but there have been few direct tests of the rule using long-term records of natural thinning in forest trees. Log-log plots of density versus mean tree volume (parabolic volume estimated from individual measurements of tree diameter and height) for permanent loblolly pine plots monitored for 50 years are shown in Figure 3. If the thinning process in a stand obeys the rule, then such a plot should yield a line of slope $-3/2$.

During the establishment phase of stand development, the slope is, as predicted, much less (more negative) than $-3/2$. However, as the canopy closes and resources become limiting, the plot converges on a $-3/2$ slope. The rate of convergence on a $-3/2$ slope is clearly dependent on initial density; at high stocking levels thinning begins very early, whereas at low stocking, convergence has not yet occurred after 50 years. As the stands age and approach maximum biomass, the thinning curves bend away from the theoretical upper limit set by the rule.

Thus, the mean weight-density relationship for each stand follows a curved trajectory, initially directed straight up, then bending to conform briefly to the $-3/2$ limit, then bending even farther away. While no one stand clearly defines the $-3/2$ thinning limit, all the stands together do define a line with a slope of nearly $-3/2$, which individual stand trajectories approach but never cross. How close any one stand is to this upper limit can be viewed as an index of the expected intensity of competition in the stand.

The thinning rule explicitly applies to even-aged populations of a single species. The extent to which the rule might be generalized to mixtures of species or uneven-aged assemblages of one or more species has not been fully explored. When we examined

Table 1. Seedling establishment rate (SER, in $n \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), and the probability of a seedling surviving to grow to a height of 50 cm (PHT50) for red maple and oak in an age-sequence of stands.

Stand age and type	Red maple		Oak	
	SER	PHT50	SER	PHT50
10–15 year pine	12,000	0.0573	7,500	0.235
20–25 year pine	14,000	0.0120	3,000	0.263
45–50 year pine	137,500	0.0037	2,300	0.055
55–60 year pine	329,000	0.0013	6,200	0.027
60–65 year pine	364,400	0.0032	3,000	0.033
75–80 year pine	393,600	0.0032	2,400	0.053
85–90 year pine	298,400	0.0056	3,600	0.094
Mixed pine-hardwoods	506,600	0.0064	22,300	0.047
Mature hardwoods	52,500	0.0038	10,675	0.013

tree growth and mortality records for a 50-year period for stems originally present in eight mixed-species, mixed-age hardwood stands, we found the thinning exponent to range between -1.40 and -1.72 .

When we looked at the thinning curves of the component species, however, there was much less conformity to the rule. Flowering dogwood and ironwood, both obligate understorey species, had slopes near -0.40 . In contrast, tulip poplar, an obligate successional overstorey species had a slope of -4.96 in one stand. Thus, the component species do not appear to conform to the thinning rule, whereas all the species in a stand together show at least moderate conformity. This result is consistent with those from a recent study by White (1985) of thinning in two mixed-species, mixed-age New England forests.

All these forests, both those studied by White and those we have studied, however, appear to be recovering from past disturbances and thus are undergoing a reduction in total number of trees. To what extent a true steady-state forest might conform to the thinning rule is unknown.

Who wins?

For predicting the likelihood of survival of an individual tree, the most useful information is different for each of the forest development phases. During the establishment phase, dispersal to safe sites is critical, and survivorship may depend both on small-scale spatial and temporal heterogeneity and on competition from shorter-lived pioneer species. These factors, plus genetic differences among individuals, result in considerable variation in size and vigor of individual trees as the population enters the thinning phase.

Because few trees survive the intense competition of the thinning phase, any tree that starts at a competitive disadvantage will almost certainly die. While not all forms of competitive disadvantage are readily measured, several, including size (diameter, height, and weight), vigor (diameter increment or weight increment), and proximity of competitors (calculated using distance to and size of neighboring trees), have been

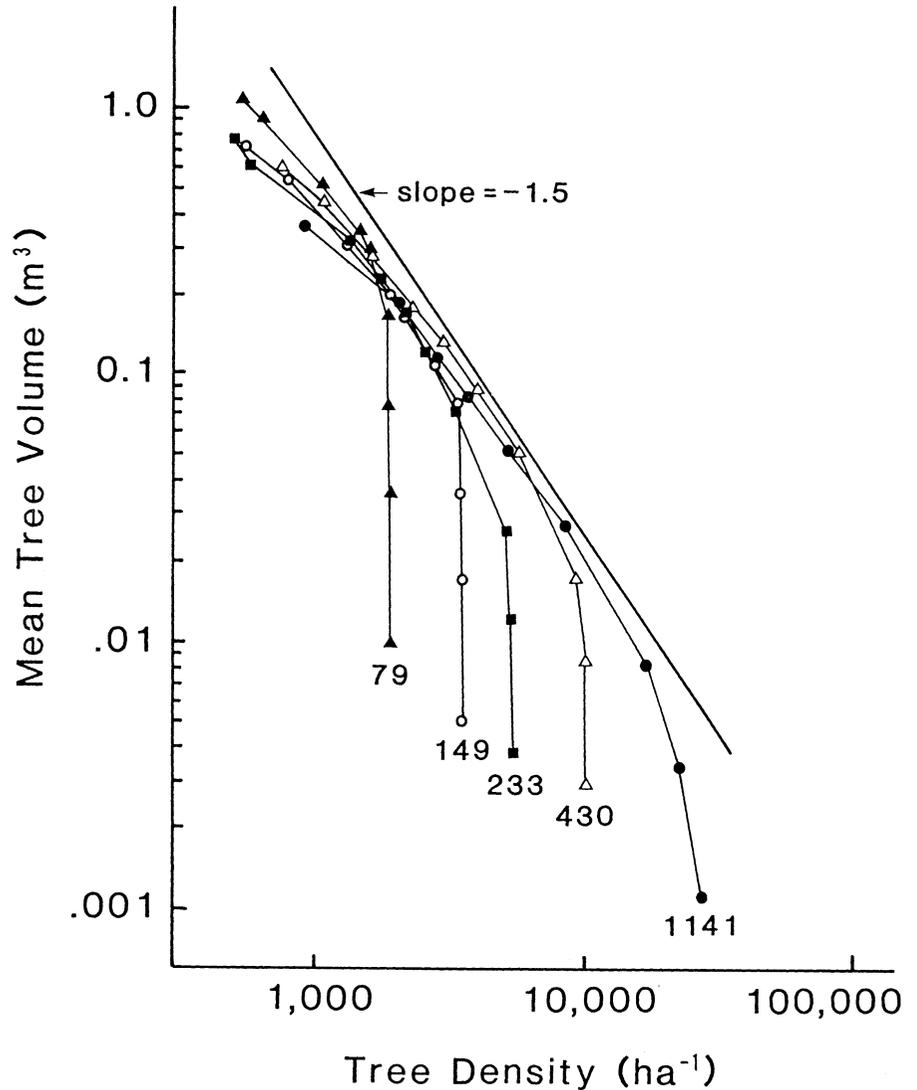


Figure 3. Relationship between mean tree volume and tree density for a series of loblolly pine stands over a 50-year period. The differing initial densities of the stands are indicated by the figure labels (79–1141 stems originally in the 0.1-acre plots). The straight line has a slope of -1.5 , as predicted by the law of thinning. The tree populations approach an upper limit defined by this $-3/2$ line, but no stand closely tracks that line.

shown to have high predictive value (Daniels 1976, Lorimer 1983, Monserud 1976, Weiner 1984).

If ability to extract critical resources from the environment is proportional to size, the larger plants should have the advantage. Recent studies on size inequality (Weiner and Thomas 1986) suggest that larger plants are at an advantage disproportionate to their size. As a consequence, mortality is concentrated in the smaller size-classes.

To illustrate the importance of size for survival, we summarize changes over a 50-year period in the distribu-

tion of sizes of trees in an even-aged loblolly pine stand (Table 2). For each sampling interval, mortality was concentrated in the smallest size-class, and most, if not all, trees in the largest size-class survived. During the observation period the surviving trees increased sufficiently in size that the 10–20-centimeter size-class (diameter at a height of 1.3 m) changed from being the largest size-class and having no mortality to being the smallest size-class and having high mortality. Thus, mortality appears closely linked, not to absolute size, but to relative size in the stand.

Table 2. Mortality of loblolly pine as related to tree diameter over a 50-year period of stand development. The number of trees in each size-class alive at the beginning of a sampling interval is shown together with the number of those trees that died during the interval.

Interval		Diameter-class in cm				Total
		1-5	5-10	10-20	20-40	
1935-1940	Original number	55	225	153	0	433
	Number of deaths	54	112	0	0	166
1940-1945	Original number	1	75	187	4	267
	Number of deaths	1	60	27	0	88
1945-1950	Original number	0	12	157	10	179
	Number of deaths	0	12	52	0	64
1950-1955	Original number	0	0	98	17	115
	Number of deaths	0	0	34	0	34
1955-1960	Original number	0	0	48	33	81
	Number of deaths	0	0	13	0	13
	Number cut	0	0	2	6	8
1960-1979	Original number	0	0	26	34	60
	Number of deaths	0	0	16	4	20
1979-1984	Original number	0	0	6	34	40
	Number of deaths	0	0	2	2	4

The most obvious explanation for why an individual tree might be larger than its neighbors is time of arrival. The first trees to arrive experience the least competition and have the greatest opportunity to preempt resources. Those plants that establish late generally find few resources readily available (Harper 1977).

In the loblolly pine stands of the Carolina piedmont, virtually all the dominant trees become established during a period of five years or less. Those trees that do become established later are usually among the first to die during self-thinning. In other regions where establishment is slower, such as the conifer forests of the Pacific Northwest or the Rocky Mountains, early arrival is still important but the windows for successful establishment can be much longer.

The location of an individual tree relative to other individuals in a population has been shown to affect its growth (Daniels 1976, Lorimer 1983, Weiner 1984) and must also affect its likelihood of survival. Because seed dispersal is not spatially homogeneous and the distribution of microsites favorable for establishment is often quite patchy, trees at the initiation of the thinning phase can be expected to have a clumped spatial distribution. To the extent that inter-tree distances influence competitive interactions and competition-related

mortality during the thinning phase, we should expect tree pattern to shift from clumped to random to regular. Such shifts have been documented in even-aged stands of sand pine (Laessle 1965) and to some extent in stands of ponderosa pine (Cooper 1961). With continued stand development seedlings and saplings again occur, typically in patches where canopy trees have died. As a consequence, spatial pattern shifts back toward greater clumping.

In steady-state forests, particular spatial patterns can be expected to be associated with particular size-classes of trees. As in the transition forests, regeneration is concentrated in gaps formed by canopy tree deaths. Thus, small trees can be expected to exhibit a clumped pattern. However, the individual risk of mortality increases with the proximity and size of neighboring trees. Thus, with increasing size-class we should expect progressively less clumping. For the extreme case of canopy trees, this process may reach the point where the spatial distribution is close to uniform.

Christensen (1977) has previously shown that small trees have greater clumping than large trees in the relatively mature, mixed-species hardwood forests of the Carolina piedmont. Elsewhere, others have found progressively less clumping with increasing tree size-class (Yeaton 1978)

and even some evidence for a regular distribution of the larger trees in a stand (Good and Whipple 1982, Whipple 1980).

A final variable important for determining whether a tree will win in competition is its species. Some species are simply more successful than others under competitive conditions. Under the high irradiance, water-limited conditions of the early establishment phase, hardwoods cannot compete with loblolly pine for a place in the canopy (Bormann 1953). In contrast, loblolly pine is not efficient enough at light capture to compete in a shady understory, whereas dogwood and red maple, and to a lesser extent oaks and hickories (Oosting and Kramer 1946), do well.

Implications of thinning

The consequences of the complementary processes of natural thinning and size-dependent mortality are most conspicuous in the changing distributions of tree sizes during forest development. Skewing appears to become progressively more positive as competition intensifies and a few plants assume dominance (Mohler et al. 1978). This trend continues until self-thinning starts, at which time the smaller individuals are selectively lost and the distribution can become more normal (Mohler et al. 1978, Weiner and Thomas 1986).²

By the end of the thinning phase, the typical even-aged stand has an approximately normal distribution of diameters with few, if any, small trees. During the transition phase, as establishment increases and the stand approaches a steady-state condition, the size distribution changes dramatically. The final, steady-state forest typically has a large number of small stems with progressively fewer stems in each subsequent size-class, the result being a reversed-J or negative exponential diameter distribution (Leak 1965, Meyer 1952). The size distributions in Table 2 illustrate the early portion of this process.

Knox has examined changes in the inequality of sizes of loblolly pines in the series of stands shown in Figures 1 and 3. Before the onset of self-thin-

²R. Knox, 1987. Unpublished manuscript. University of North Carolina, Chapel Hill.

ning, the inequality of sizes became progressively greater as a few individuals assumed dominance. This inequality was greatest in the most dense stands. During self-thinning, death of the smaller trees resulted in a significant decline in the size inequality.³

Change in community biomass also can be explained in terms of the processes that define the four stages of forest development (Bormann and Likens 1979, Peet 1981b, Sprugel 1985). Forest development starts with little biomass, but it increases steadily during the establishment and thinning phases. In forests where little regeneration takes place during the thinning phase, increased growth of previously suppressed trees cannot compensate for deaths of canopy trees in the late thinning and early transition phases. As a consequence, biomass declines. However, where there is a well-developed subcanopy of shade-tolerant trees, the decline is less conspicuous. In the steady-state phase at least a few patches in the mosaic are inevitably filled with small trees, so the average biomass never returns to the maximum achieved late in the thinning phase.

Changes in biomass over a 50-year period for a series of even-aged loblolly pine stands are shown in Figure 4. Biomass increased at a relatively constant rate for roughly 30 years, the stands with the largest numbers of trees initially having the highest biomass. However, as the end of the thinning phase was approached, the biomass values peaked and then dropped. After 50 years, stand biomass was more highly correlated with site quality as assessed from soil characteristics than with initial density.

Finally, many changes in species composition appear to result from differential death and establishment during the different stages of forest development. For example, differential growth and survival of the various species that invade together during the establishment phase have been reported to be responsible for many observed successional trends (Connell and Slatyer 1977, Egler 1954). Similarly, the differential inhibition of regeneration by the existing canopy species during the thinning phase can

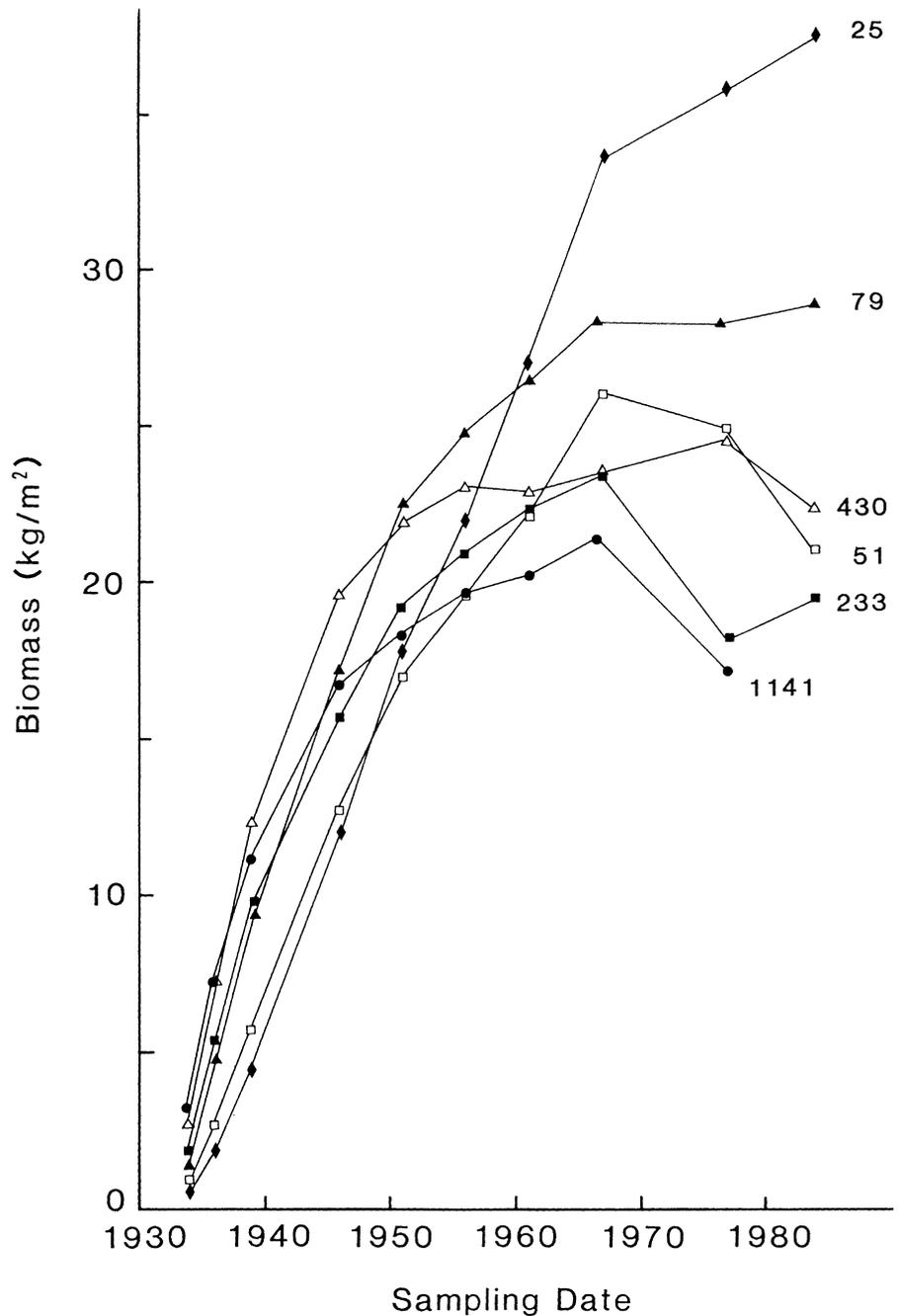


Figure 4. Changes in biomass over a 50-year period for a series of loblolly pine stands in which initial density ranged from approximately 600 to 28,900 stems per ha. The figure labels indicate original numbers of stems in the 0.1-acre plots.

be viewed as an important successional mechanism (Connell and Slatyer 1977, Peet and Christensen 1980a).

We have observed that relationships between herb- and tree-layer composition and site conditions in successional piedmont pine stands are most predictable, and most like those of mature hardwood stands, during the thinning phase, and less so during establishment and transition phases

(Christensen and Peet 1984). Thus, patterns of establishment and survival of hundreds of species in these forests are correlated with and probably determined by changes in resources associated with patterns of mortality in dominant tree populations.

Conclusions

We have described how a forest re-

³See footnote 2.

growing after a disturbance, such as wildfire or clearing, typically passes through four distinct phases that can be characterized by their dominant population processes. During the establishment phase, many new trees start growth and mortality is low. In the thinning phase, competition is extreme, few new trees enter, and many die as the survivors get larger. During the transition phase, competition is less important as a cause of tree death, and establishment of new trees resumes. Finally, in the steady-state or climax forest, large canopy trees are continually dying, thereby forming gaps in the forest wherein the establishment, thinning, and transition phases sequentially reoccur, though in miniature. This conceptual model appears to apply to the majority of the world's forests.

The changes in population processes during forest development represented in our four-phase model have implications for the structure and dynamics of forest ecosystems ranging beyond changes in tree density or average size. These population processes can be shown to determine changes in tree size-distributions, tree spatial-distributions, forest biomass, and even species composition. These results all suggest that the interdependent processes of tree death and tree establishment can provide the basis for understanding much of forest ecology.

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