

## SUCCESSION: A POPULATION PROCESS

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### Introduction

For over 80 years succession theory has played a central role in plant ecology, providing both a predictive tool and organizational scheme. Drawing on this long history of research and observation, Margalef (1968), Odum (1969), Whittaker (1975) and others have identified general trends in community development. Their synthetic treatments have helped focus the efforts of subsequent workers examining the empirical and experimental basis of succession theory (e.g. Connell & Slatyer 1977, Drury & Nisbet 1973, Egler 1975, Horn 1974, Pickett 1976, van Hulst 1978). This more recent work suggests that the classical succession paradigm is seriously flawed and that many long held concepts need to be reexamined.

The view of succession as a community or species replacement sequence driven by autogenic environmental modification has been rejected (Connell & Slatyer 1977, Drury & Nisbet 1973, Egler 1954, 1976, Niering & Egler 1955). In contrast to Odum's (1969) generalizations, successional changes in biomass and primary production can no longer be assumed to be consistently upward. Bormann & Likens (1979), Horn (1974), Loucks (1970), Major (1974) and Peet (1978, 1980a) all suggest that a more usual pattern is to find maximum productivity and biomass preceding the climax stage of forest development. Also in opposition to Odum's generalizations, Vitousek & Reiners (1975, Vitousek 1977) and Bormann & Likens (1979) suggest that the tightest nutrient cycles should be expected in the central portion of successional sequences. A similar reevaluation has proven necessary for patterns

in species diversity (Auclair & Goff 1971, Loucks 1970, Peet 1978, Whittaker 1972, 1977).

Simultaneous with the realization that succession is far more complex than classical theory suggests, there appeared in the literature a series of alternative approaches and formulations. These were not proposed as mutually exclusive, competing hypotheses, and should not be taken as such. Rather, they may all apply in varying degrees to any one successional sequence. What is of interest is the extent to which they are successful, either separately or in combination, in increasing our understanding of the succession process. The most important and frequently cited of these alternative approaches can be summarized in three groups.

1. *Succession as a gradient in time:* Drury & Nisbet (1971, 1973) argued that a successional sequence is simply a type of stress gradient to which plants are adapted. Their viewpoint was reductionistic, almost Gleasonian, and they suggested that '... a complete theory of vegetational succession should be sought at the organismic, physiological or cellular level and not in emergent properties of populations or communities.' Pickett (1976) also viewed the successional sequence as a form of gradient, along which species are competitively displaced. From this viewpoint the physiological and life-history characteristics of the component species are of central importance. 'Succession,' Pickett wrote, 'can be understood solely in terms of the interaction of evolutionary strategies without reference to a deterministic progress toward climax.' It is precisely this evolutionary strategy, life-history approach which Noble & Slatyer (1977, 1980) have been employing in their efforts to identify a minimal number of 'vital attributes' of plant species necessary to predict successional changes.

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2. *Differential longevity*: Egler & Niering (1955, Egler 1954, 1976) have argued that much of secondary succession is simply a consequence of differential longevity, that most of the eventual dominants enter a community in the earliest developmental stages when competitive pressures are low. Drury & Nisbet (1973) also considered initial conditions and species composition critical determinants of future community development. These arguments imply that failure of a species to become established early prevents, or at least greatly reduces its chances for subsequent dominance. Connell & Slatyer (1977) referred to this as the inhibition model in contrast to the classical facilitation model of Clements and others where in one species or set of species prepares the way for the next. If history is as important for vegetation development as Drury & Nisbet, Egler, and others suggest, convergence to climax may be too slow to be of practical significance, and perhaps does not occur at all.

3. *Succession as a stochastic process*: Horn (1975, 1976) has presented a model based on tree-by-tree replacement which has greatly popularized Markovian models. Central to every discrete Markov model is a matrix of transition probabilities. In Horn's model the matrix consists of the probabilities of a tree of any given species being replaced by a tree of the same species or any other species. Such a matrix can be used to calculate future forest composition and in this way provides a useful neutral model against which to compare reality. A necessary statistical consequence of this formulation is that convergence to a steady-state composition is inevitable, regardless of initial conditions. The interesting biology is, thus, not in the existence or even composition of the climax, but in the numbers comprising the transition matrix, especially their variation with site and stand development. Stochastic succession models need not be restricted to Markovian tree-by-tree replacement processes, but may be used at various hierarchical levels from trees of varying size-classes (e.g. Usher 1966, Moser 1972) to regional forest-types (e.g. Shugart et al. 1973), or may even be based on complex tree population simulations (e.g. Botkin et al. 1972).

Despite obvious differences, a common theme characterizes the preceding approaches; all are reductionist, emphasizing life-histories and competitive relations of component species rather than the emergent properties of communities. To date few data have been gathered appropriate for evaluating their relative utility or generality.

The intent of this contribution is not to further review previous studies, but to preview a research program we

have undertaken to evaluate in-depth, for one area, the utility of a reductionist, population-based approach to studying succession. Our approach is to view succession as a population process – a consequence of variation in rates of reproduction, establishment, growth and mortality. Species life-history and physiological characteristics determine, to a large extent, potential population responses to the changing competitive environment. Population processes in turn appear to strongly influence such community-level properties as species composition, rate of compositional change, diversity, productivity and biomass. Thus, we are taking a two-step or three-tier reductionist approach to the study of succession.

### The study area

Our study is being conducted primarily in the Duke Forest, an experimental forest owned by Duke University and located on the North Carolina piedmont. The legacy of prior research on the study area significantly influenced our study area selection. The papers of Billings (1938), Korstian & Coile (1938), Kozlowski (1949), Oosting (1942) and many others all have been based on studies conducted within the Duke Forest. Information on the physical environment of the area can be found in Billings (1938) and Oosting (1942).

Virtually all North Carolina piedmont vegetation is either the direct result of or has been greatly modified by human activities during the last 200 years. Most of the piedmont was at one time under cultivation, but changing economic conditions led to abandonment of much of this land and its reversion to forest. Typically, initial post-abandonment forest is dominated by pines; primarily *Pinus taeda* or *P. echinata*, or farther west, *P. virginiana*. All three species of *Pinus* occur within the study area and broadly overlap in their ecological requirements, but with *P. taeda* dominant on more mesic, nutrient rich sites and *P. virginiana* dominating a few of the edaphically least favorable sites. A number of light-demanding hardwood species often invade simultaneously with or slightly after the pines. The more rapidly growing of these species, especially *Liquidambar styraciflua* and *Liriodendron tulipifera*, occasionally codominate with pine, but are not commonly present in large numbers in the canopy.

The *Pinus* species in our region are light requiring and cannot regenerate successfully without large canopy gaps such as created by selective cutting or severe wind.

In contrast, a number of hardwood species are capable of invading beneath the pines. As a result, 80 to 100 years after land abandonment when the pine canopy is breaking up through natural mortality, numerous young hardwood saplings are available to fill the gaps. The composition of the new hardwood forest will probably change gradually for another 200 to 500 years as early invaders such as *Liriodendron*, *Liquidambar*, and *Acer rubrum* are replaced by more slowly invading species, especially species of *Quercus* and *Carya*. A more detailed description of the potential steady-state vegetation and its variation with site conditions can be found in Peet & Christensen (1979, Peet 1980b.)

## Methods

The study of plant population dynamics is best accomplished through long-term observations of marked individuals under carefully designed experimental conditions. As Harper (1977) has emphasized, the large size and great longevity of trees has largely precluded such critical demographic studies. Fortunately, we are heir to a set of per-

manent sample plots established within the Duke Forest during the early 1930's. In each plot the diameter and height of each tree was measured at roughly 5 year intervals until 1963, and then again 15 years later. Plots were typically established in sets with one or two designated as controls and the others subjected to various experimental regimes.

To illustrate the potential of a population-based approach for studying succession we have selected as examples three sets of permanent sample plots. The first set (12 - 23) started with twelve 8-year-old *Pinus taeda* plots of 0.1 acre (.04 ha) on a single hillside, but ranging in natural initial density from 25 to 1143. Seven of these were left as controls (Fig. 1). The second set (24-26) consists of three matched 19-year-old *Pinus taeda* plots which received different treatments. One plot (24) was 'thinned from above,' removing only the largest trees. The second plot (25) was 'thinned from below,' removing overtopped and intermediate trees. Both plots were thinned to a basal area of roughly 23 m<sup>2</sup>/ha (100 ft<sup>2</sup>/acre). The third plot (26) was retained as a control (initial basal area of .29.8 m<sup>2</sup>/ha). The third set (10,36,37) consists of three 0.25 acre (0.1 ha) plots dominated by mixed hardwoods, primarily species of *Quercus* and *Carya*. Plots 36 and 37 were similar except that 37 was significantly thinned by a hurricane in 1954 which reduced the basal area from 25 to 15 m<sup>2</sup>/ha, thus opening the canopy. Plot 10 differs from 36 in that it appears to represent an earlier successional stage, probably resulting from selective cutting in the late 19th century. Evidence for this is seen in several aspects of the 1934 data: basal area was lower (18.8 vs. 22.0 m<sup>2</sup>/ha), average diameter was lower (10.3 vs. 13.8 cm), average height was lower (9.8 vs. 11.5m) and density was higher (3152 vs. 1432 stems/ha).

Unfortunately the foresters who established these permanent plots were little interested in tree seedlings and initial tree establishment; only individuals over 1.25 cm dbh were measured. Therefore we have initiated a series of permanent plots for monitoring seedling establishment and survival. However, several more years of observation will be required before these can contribute substantially to our understanding of tree demography and successional processes.

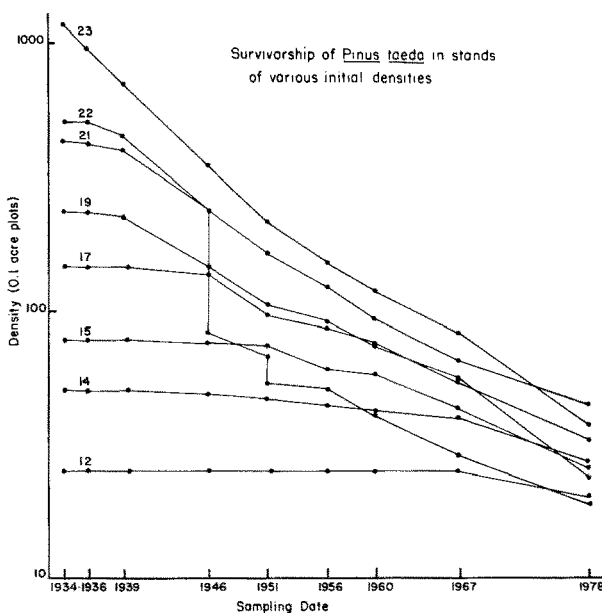


Fig. 1. Survivorship of marked *Pinus taeda* (> 1.25 cm dbh) in stands of differing initial densities over a 44 year period. Initial densities of trees in the 0.1 acre (.0405 ha) plots were 25 (plot 12), 51 (14), 79 (15), 149 (17), 234 (19), 431 (21), 511 (22), and 1172 (23). Sample plot 22 was twice thinned as represented by the vertical portions of its survivorship curve. Despite extreme variation in initial densities, differential mortality has led to convergence in density during the 44 year period.

## Results

### Mortality and thinning

Tree mortality is a process central to any consideration of

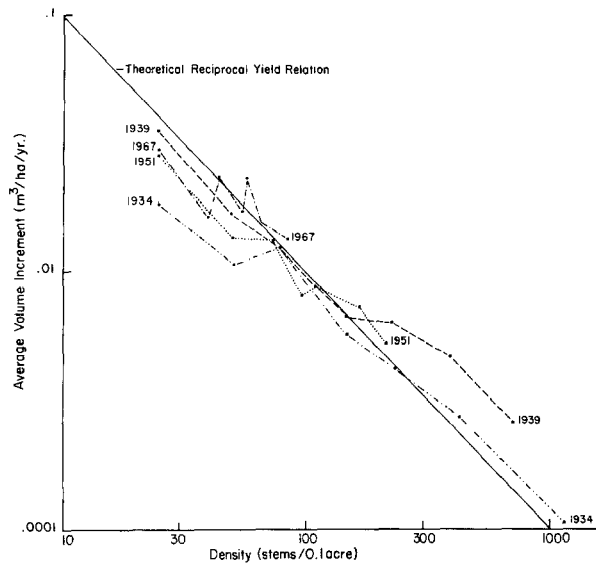


Fig. 2. Logarithmic graphs of average annual volume increment ( $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ ) versus stand density for the seven control stands illustrated in Figure 1. A reciprocal annual yield relationship would conform to a  $-1$  slope. Despite considerable variation in tree age, density and size among stands and among years, strong conformity to the reciprocal yield relation can be seen.

forest compositional change. Using the examples we have selected, aspects of mortality in both the *Pinus taeda* stage and the mixed hardwood stage can be illustrated.

Tree density strongly influences mortality as can be seen in Fig. 1. In each of the 7 matched stands, after a critical degree of crowding was reached, mortality showed a nearly perfect exponential decrease. (Lack of data for stands less than 8-year-old could partially explain failure of the data to fit either the power function suggested by Hett (1971) or the sigmoidal relation suggested by Goff & West (1975). Despite the broad dispersion of initial densities (25–1143/0.1 acre plot = 618–28244/ha) the plots converged within 45 years to a rather narrow range of densities (20–45/plot). In contrast, the experimentally thinned plot (22) never recovered from its initially high density; the initial high mortality rate continued after competitive release. Most likely some aspect of tree geometry was fixed by initial growing conditions. Our studies of the growth characteristics of *Pinus taeda* suggest that in dense populations a high ratio of height to diameter growth occurs with the resultant tall, thin trees being highly susceptible to wind and ice damage.

Given stands of markedly differing densities and developmental stages, such as in plots 12–23, it is interesting to consider the degree of their convergence in production.

As densities were sufficiently high to result in density dependent mortality, a reciprocal yield relationship (Harper 1977, Kira et al. 1953) was expected. Specifically, the reciprocal yield relation suggests that total productivity should be independent of density. Alternatively stated, a double logarithmic graph of average tree productivity versus density should yield a plot with a slope of  $-1$ . This relation has not to our knowledge been tested elsewhere for trees. Such a test must differ from work on herbaceous species; herbs can simply be harvested and weighed to provide a production estimate but this is not possible for trees. Instead, we have estimated net production using 'estimated volume increment' (Whittaker & Woodwell 1968, Whittaker & Marks 1975 – Assume a paraboloid of rotation based on tree height and diameter, and subtract a second such paraboloid calculated using height and diameter data from the previous year). The results, shown in Fig. 2, strongly support the applicability of the reciprocal yield relation to trees. Especially note-

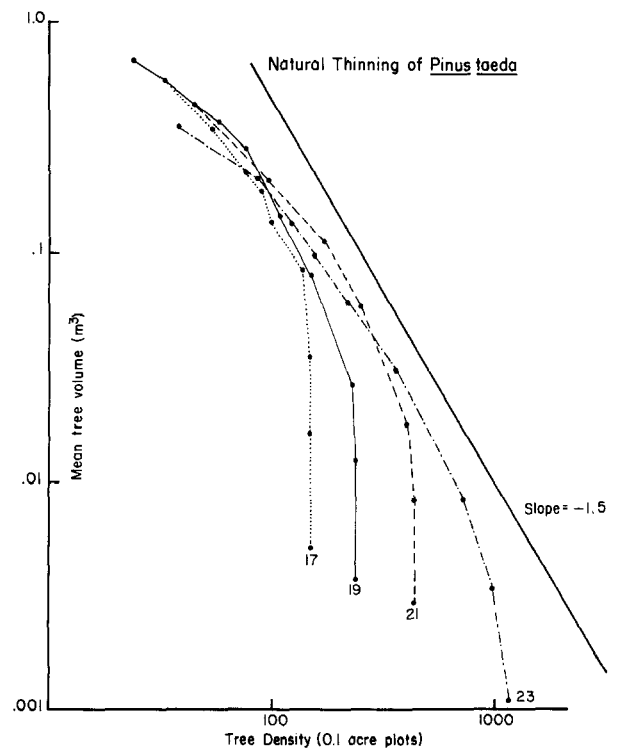


Fig. 3. Logarithmic plots of changing tree volume versus tree density for four sample plots of differing initial densities (149, 234, 431 and 1172 per 0.1 acre, .0405 ha) illustrate that Yoda's  $-3/2$  law of thinning does not strictly apply to even-aged *Pinus taeda* stands; the shift toward a  $-3/2$  relation is followed by a shift toward  $-1$  as trees mature and reach limiting dimensions.

worthy is the independence of production and age of the stand.

The link between site conditions, density, and mortality can be further examined by constructing double logarithmic graphs of single stands through time showing density versus average tree biomass (Fig. 3). Convergence toward a line with a slope of  $-3/2$  would imply agreement with Yoda et al.'s (1963) thinning law. This relation has only rarely been examined for time-series tree data (e.g. Drew & Flewelling 1977), and then with ambiguous results.

Our plots do not exhibit strong conformance with the Yoda relation. Rather, the plots at first shift toward slopes of  $-3/2$ , but continue past eventually approaching slopes of  $-1$ . This could be a result of trees reaching their

vertical growth potential well before diameter growth rates start to decrease.

Mortality data from uneven-aged, mixed hardwood stands are more ambiguous, primarily due to the unknown, ever-changing age structure of the populations, and the size dependence of mortality. Unless a stand can be shown to be at steady-state, which is rarely if ever the case, a depletion curve cannot strictly be interpreted as a survivorship curve. This limitation is important but does not prevent useful comparisons from being made.

Depletion curves for hardwoods alive in 1934 in plots 10 and 36 are shown in Fig. 4. As was the case for *Pinus taeda*, the curves conform well with a negative exponential model. Comparing the two stands, the difference in the overall or total depletion rate is conspicuous. A

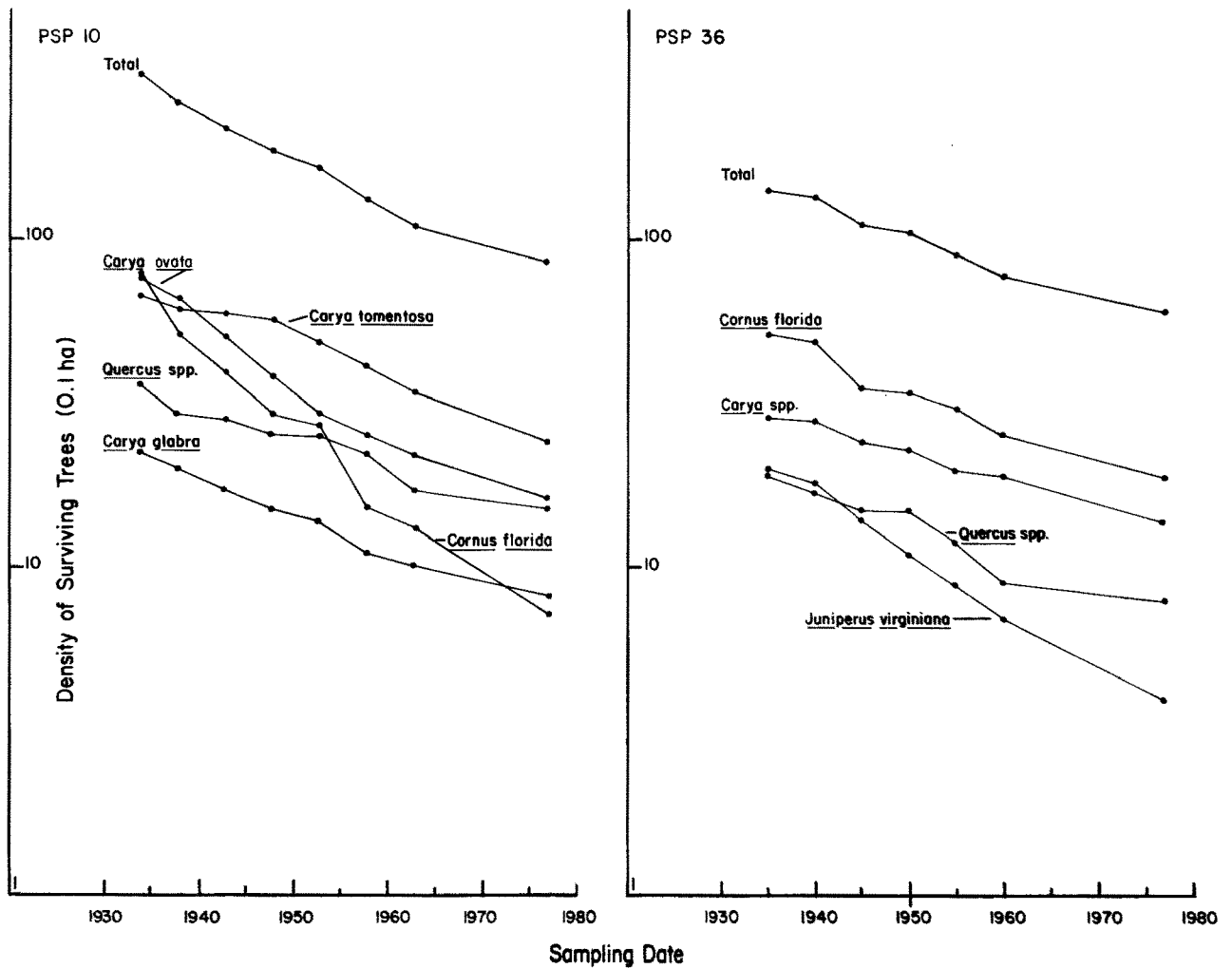


Fig. 4. Depletion curves illustrating differential mortality in trees from two upland, uneven-aged, mixed-species stands of differing successional status. The less mature plot 10 can be recognized by the greater rates of thinning and tree mortality (see text).

graph of the logarithm of stem density (stems  $\geq 1.25$  cm/ha) versus time (in centuries) yields a slope of  $-1.42$  for plot 10 compared to only  $-1.02$  for plot 36. The greater depletion rate in plot 10 may be symptomatic of its presumed earlier successional age where thinning processes dominate to a greater extent. In addition, species differences can be seen both within and between stands. Within plot 10 the three *Carya* species can be seen to be responding quite differently. *Cornus florida* appears as an average species in plot 36, but in plot 10 it has the highest depletion rate of any of the common species.

### Establishment

Complementary to tree mortality is establishment of new individuals. As future forest composition and structure are directly dependent on new tree establishment, an experimental examination of this process is critical for understanding succession.

A set of three permanent sample plots in what was initially a 19-year-old *Pinus taeda* forest provides an example of this experimental approach. In one plot the dominant trees were selectively cut (thinned from above),

in a second the suppressed understory trees were removed (thinned from below), and a third plot was left as a control. Table 1 shows stand composition after the initial treatment, and again 43 years later. The density of hardwoods ( $\geq 1.25$  cm dbh) in the control plot increased by a factor of 2.8 despite mortality of almost half of the stems alive at the start of the period. In the plot thinned from below most of the hardwoods were removed in the initial thinning producing an artificially low initial density. Nonetheless, hardwood density after 43 years was roughly equivalent to that on the control plot, an increase of 1440%. The greater age and size of the control hardwoods predictably led to higher basal area on that plot. In contrast to these two plots, the increase in hardwood density in the plot thinned from above was small, the final hardwood density being less than half that on either of the others. Greatest production, as indicated by basal area increment, occurred in the plot thinned from below, while the plot thinned from above had the lowest increment.

A major part of the increase in hardwood density in all the stands occurred in predominantly understory species such as *Cornus florida*, *Oxydendrum arboreum*, and *Acer rubrum*. *Nyssa sylvatica* and *Liquidambar* are less

Table 1. Effect of thinning on hardwood invasion of *Pinus taeda* forests.

Species	Year	Thinned from above			Thinned from below			Control		
		1934	1979 <sup>2</sup>	1979+ <sup>2</sup>	1934	1979	1979+	1934	1977	1977+
<i>Acer rubrum</i>		20 <sup>1</sup>	10	306	0	0	928	0	0	503
<i>Carya</i> spp.		267	100	100	20	10	50	60	30	30
<i>Cornus florida</i>		10	10	60	20	0	424	50	30	642
<i>Liquidambar</i>		168	90	405	60	30	494	415	227	721
<i>Nyssa sylvatica</i>		80	60	109	80	10	119	178	119	217
<i>Oxydendrum</i>		50	10	90	0	0	50	148	108	395
<i>Pinus</i> spp.		2510	435	464	1047	375	375	2311	355	355
<i>Quercus</i> spp.		0	0	30	0	0	100	0	0	40
Other		100	20	213	10	0	572	110	0	139
<b>Total Density</b>		<b>3205</b>	<b>735</b>	<b>1773</b>	<b>1237</b>	<b>425</b>	<b>3112</b>	<b>3272</b>	<b>869</b>	<b>3042</b>
<b>Hardwood Density</b>		<b>695</b>	<b>300</b>	<b>1309</b>	<b>190</b>	<b>50</b>	<b>2737</b>	<b>961</b>	<b>514</b>	<b>2687</b>
<b>Total Basal Area</b>		<b>23.4<sup>3</sup></b>	<b>29.5</b>	<b>32.0</b>	<b>22.8</b>	<b>39.2</b>	<b>44.5</b>	<b>30.8</b>	<b>35.8</b>	<b>40.9</b>
<b>Hardwood B.A.</b>		<b>0.9</b>	<b>1.9</b>	<b>4.3</b>	<b>0.2</b>	<b>0.7</b>	<b>5.9</b>	<b>1.2</b>	<b>4.4</b>	<b>9.6</b>

<sup>1</sup>Densities in stems  $\geq 1.25$  cm dbh per ha.

<sup>2</sup>1979 values contain only stems  $\geq 1.25$  cm dbh in 1934 surviving to 1979.

1979 + values include all stems  $\geq 1.25$  cm dbh in 1979.

<sup>3</sup>m<sup>2</sup>/ha.

Table 2. Effect of thinning on tree establishment in upland hardwood forests.

A. Control plot				B. Thinned plot (1954 hurricane)					
Diameter Class <sup>1</sup>	1934			1950			1977		
	1	2	3	1	2	3	1	2	3
<i>Oxydendrum a.</i>	1 <sup>2</sup>	11	5	3	10	6	5	10	8
<i>Quercus velutina</i>	0	1	2	0	0	3	0	0	2
<i>Carya spp.</i>	5	6	18	1	3	16	0	1	14
<i>Juniperus v.</i>	9	8	0	2	9	1	1	1	3
<i>Cornus florida</i>	7	43	2	12	27	6	46	22	3
<i>Quercus coccinea</i>	0	2	6	0	0	6	1	0	1
<i>Quercus alba</i>	1	1	5	0	1	5	0	2	4
<i>Acer rubrum</i>	0	1	1	1	1	1	4	0	2
<i>Liriodendron t.</i>	0	0	2	0	0	2	0	0	2
<i>Nyssa sylvatica</i>	0	3	0	0	0	2	0	0	2
<i>Quercus stellata</i>							1	0	0
<i>Quercus rubra</i>							1	0	0
<i>Carpinus</i>							3	0	0
TOTAL	23	76	41	21	54	46	65	36	40

Diameter Class <sup>1</sup>	1934			1950			1977		
	1	2	3	1	2	3	1	2	3
<i>Carya spp.</i>	2 <sup>2</sup>	13	2	0	7	3	75	2	0
<i>Cornus florida</i>	3	25	1	0	26	2	29	24	1
<i>Quercus alba</i>	0	5	23	0	2	23	11	1	0
<i>Juniperus v.</i>	3	2	1	2	2	1	13	13	0
<i>Oxydendrum a.</i>	0	6	2	2	2	3	31	10	1
<i>Quercus rubra</i>	0	2	0	0	1	1	1	0	1
<i>Acer rubrum</i>	0	1	0	6	1	0	92	16	11
<i>Nyssa sylvatica</i>	0	1	0	0	1	0	4	1	0
<i>Ulmus alata</i>							1	0	0
<i>Pinus virginiana</i>							1	12	2
<i>Pinus taeda</i>							5	27	1
<i>Sassafras a.</i>							16	6	0
<i>Prunus serotina</i>							9	2	0
<i>Diospyros v.</i>							4	1	0
<i>Quercus velutina</i>							21	4	0
<i>Ostrya v.</i>							1	2	0
<i>Liriodendron t.</i>							20	12	0
<i>Chionanthus v.</i>							1	0	0
TOTAL	8	55	30	10	42	33	335	133	17

<sup>1</sup>Diameter classes of trees are (1) 2.5–5 cm, (2) 5–10 cm, and (3) > 10 cm.

<sup>2</sup>Densities are in stems per 0.1 ha.

shade tolerant species which usually become established early in succession, a fact which could account for their greater abundance in the control plot. Species of genera normally associated with the climax forests of the region, *Quercus* and *Carya* (see Oosting 1942), show very small levels of increase. A combination of the lack of nearby mature individuals and large seed size (i.e. poor dispersal) could largely explain their failure to reinvade.

The influence of thinning on mature hardwood forests (Table 2) is illustrated in a second example. A hurricane severely damaged one plot in 1954 decreasing its basal area from 25 m<sup>2</sup>/ha in 1950 to 15 m<sup>2</sup>, whereas the control plot received only minor damage. Low levels of regeneration of all tree species except *Cornus florida* have been the norm for the control since 1934 whereas the experimental plot showed a dramatic increase in regeneration of most species following the hurricane. Of particular

interest is the negligible level of *Carya*, *Quercus*, *Pinus* and *Liriodendron* regeneration in the control plot, and in the experimental plot prior to perturbation, an observation consistent with most reported studies of *Quercus-Carya* forests in eastern North America (e.g. Buell et al. 1966, Christensen 1977, Good 1965, Keever 1973, Peet & Loucks 1977). The obvious post-disturbance increase in regeneration of these species in the experimental plot suggests that a dynamic, temporally patchy type of forest regeneration characterizes these species in climax forests.

#### Discussion and conclusions

Establishment and mortality are complementary population processes which together directly determine changes in

community composition and structure. Unfortunately, the difficulty of studying tree populations (see Harper 1977) has precluded all but a very few applications of population based approaches to forest succession research (e.g. Hartshorn 1975, Sarukhan 1978). Shortcuts such as inference from size structure have more often been employed (e.g. Peet & Loucks 1977). For example, pine replacement by hardwoods is anticipated from comparisons of saplings with mature trees in Table 1. Similarly, compositional differences between saplings and mature trees in the mixed *Quercus*, *Carya* stands of Table 2 are suggestive of successional trends (see Christensen 1977). However, only through direct observation of permanent plots can structural properties, such as size distributions, be firmly linked with successional processes, and only through experimental manipulation of such plots can causal mechanisms be identified.

In some stages of forest development mortality processes dominate. Changes in the *Pinus taeda* plots shown in Fig. 1 have been solely due to mortality. Similarly, mortality has been the dominant factor for over 45 years in the hardwood stands shown in Fig. 4. The reverse situation of the establishment process dominating forest change is represented by the hurricane damaged plot shown in Table 2b.

The experimental thinning treatments shown in Table 1 illustrate the shifting importance of mortality and establishment. While all three plots had marked *Pinus* mortality, the plot which was thinned from above was distinctive in its low rate of hardwood establishment. The experiment suggests that if a mature canopy is greatly disturbed, the understory saplings will be released to compete for canopy dominance. Intense competition should follow with little regeneration possible under the resulting dense, even-aged stand. This contrasts with the case of limited canopy damage represented by the plot thinned from below (or the hardwood plot thinned by the 1954 hurricane) which allowed increased regeneration, but not sufficient understory growth to quickly eliminate further establishment.

The preceding observations suggest a general pattern. Initially after severe disturbance the establishment process dominates. However, after a relatively short period, a dense stand of trees develops, precluding further establishment. From this point forest succession becomes a thinning process which lasts either until a subsequent disturbance, or until natural thinning opens the canopy and a balance is achieved between patches which are thinning and patches dominated by establishment. Parallel to the

compositional changes will be changes in such 'community properties' as biomass and diversity. Diversity should be minimal during the thinning stage when herbs, like small trees, are less common on the forest floor. Biomass will initially increase but restricted establishment will eventually cause it to plateau and then drop somewhat, allowing establishment to resume. Similar results have been suggested by Bormann & Likens (1979) and Peet (1978).

The alternative formulations of succession theory outlined in the introduction all fall into an establishment-mortality model. Connell & Slatyer's (1977) proposed facilitation and inhibition mechanisms apply strictly to the influence of canopy individuals on establishment. The differential longevity approach applies to the growth phase when mortality dominates. The idea of time as a gradient is easily applied with different species populations simply responding through variation in their mortality and establishment rates. Stochastic models can be based on mortality and establishment rates (see Botkin et al. 1972), though some of the simpler Markovian models proposed do not allow changes in rates over time, thus precluding their meaningful application to short-term successional situations.

## Summary

Recent critical reviews suggest the need for a reductionistic approach to the study of secondary plant succession. We propose viewing succession as the result of the underlying plant population dynamics. This approach is being developed using nearly 50 years of permanent sample plot records.

After initial establishment *Pinus taeda* shows an exponential depletion with stands of various densities conforming to the reciprocal yield relationship. Uneven-aged hardwoods also show exponential depletion. Canopy disturbance can enhance the establishment process, though severe disturbance and the consequent abundant regeneration can lead again to dense, even-aged stands with low levels of establishment. These results suggest a general pattern of forest development wherein establishment is initially important, but is quickly replaced by mortality as the dominant process when the dense, even-sized stand starts to thin. Eventually, failing additional disturbance, natural mortality will again open the canopy allowing development of a balance between establishment and mortality.



## References

- Auclair, A.N. & F.G. Goff. 1971. Diversity relations of upland forests in the Western Great Lakes area. *Amer. Nat.* 105: 499–528.
- Billings, W.D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.* 8: 437–499.
- Bormann, F.H. & G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, N.Y., 253 pp.
- Botkin, D.B., J.F. Janak & J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60: 849–872.
- Buell, M.F., A.W. Langford, D.W. Davidson & L.F. Ohmann. 1966. The upland forest continuum in northern New Jersey. *Ecology* 47: 416–432.
- Christensen, N.L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. *Amer. Midl. Nat.* 97: 176–188.
- Connell, J.H. & R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.* 111: 1119–1144.
- Drew, T.J. & J.W. Frewelling. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey Pine plantations. *For. Sci.* 23: 517–534.
- Drury, W.H. & I.C.T. Nisbet. 1971. Inter-relations between developmental models in geomorphology, plant ecology and animal ecology. *Gen. Sys.* 16: 57–68.
- Drury, W.H. & I.C.T. Nisbet. 1973. Succession. *J. Arnold Arb.* 54: 331–368.
- Egler, F.E. 1954. Vegetation science concepts. 1. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412–417.
- Egler, F.E. 1976. Nature of vegetation. Its management and mismanagement. Conn. Cons. Assoc., Bridgewater, Conn., 527 pp.
- Goff, F.G. & D. West. 1975. Canopy-understory interaction effects on forest population structure. *For. Sci.* 21: 98–108.
- Good, N.F. 1968. A study of natural replacement in six stands in the highlands of New Jersey. *Bull. Torrey Bot. Club* 95: 240–253.
- Harper, J.L. 1977. Population biology of plants. Academic Press, N.Y., 892 pp.
- Hartshorn, G.S. 1975. A matrix model of tree population dynamics. In: F.B. Golley & E. Medina (eds.), *Tropical ecological systems*. p. 41–52, Springer-Verlag, N.Y.
- Hett, J.M. 1971. A dynamic analysis of age in sugar maple seedlings. *Ecology* 52: 1071–1074.
- Horn, H.S. 1974. The ecology of secondary succession. *Ann. Rev. Ecol. Syst.* 5: 25–37.
- Horn, H.S. 1975. Markovian properties of forest succession. In: M.L. Cody & J.M. Diamond (eds.), *Ecology and evolution of communities*. p. 196–211, Belknap Press, Cambridge, Mass.
- Horn, H.S. 1976. Succession. In: R.M. May (ed.), *Theoretical ecology: principles and applications*. p. 187–204. Blackwell, London.
- Hulst, R. van. 1978. On the dynamics of vegetation: patterns of environmental and vegetational change. *Vegetatio* 38: 65–75.
- Keever, C. 1973. Distribution of major forest species in southeastern Pennsylvania. *Ecol. Monogr.* 43: 303–327.
- Kira, T., H. Ogawa & K. Shinozaki. 1953. Intraspecific competition among higher plants. 1. Competition-diversity-yield interrelationships in regularly dispersed populations. *J. Inst. Polytech. Osaka City Univ. D* 4: 1–16.
- Korstian, C.F. & T.S. Coile. 1938. Plant competition in forest stands. *Duke Univ. For. Bull.* 3: 125 pp.
- Kozłowski, T.T. 1949. Light and water in relation to growth and competition of piedmont forest tree species. *Ecol. Monogr.* 19: 207–231.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *Amer. Zool.* 10: 17–25.
- Major, J. 1974. Biomass accumulation in successions. In: R. Knapp (ed.), *Vegetation dynamics, Handbk. Veg. Sci.* 8: 195–203. Junk, The Hague.
- Margalef, R. 1968. Perspectives in ecological theory. Univ. Chicago Press. 111 pp.
- Moser, J.W. 1972. Dynamics of an uneven-aged forest stand. *For. Sci.* 18: 184–191.
- Niering, W.A. & F.E. Egler. 1955. A shrub community of *Viburnum lentago*. stable for twenty-five years. *Ecology* 36: 356–360.
- Noble, I.R. & R.O. Slatyer. 1977. Post-fire succession of plants in Mediterranean ecosystems. In: H.A. Mooney & C.E. Conrad (eds.), *Symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems*. p. 27–36. U.S.D.A. For. Serv. Gen. Tech. Rpt. WO-3.
- Noble, I.R. & R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: ...–....
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262–270.
- Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Amer. Midl. Nat.* 28: 1–126.
- Peet, R.K. 1978. Forest vegetation of the Colorado Front Range: Patterns of species diversity. *Vegetatio* 37: 65–78.
- Peet, R.K. 1980a. Forest vegetation of the Northern Colorado Front Range, U.S.A.: II. Forest structure. *Vegetatio* (in press).
- Peet, R.K. 1980b. Ordination as a tool for analyzing complex data sets. In: E. van der Maarel (ed.), *Advances in vegetation science: Classification and Ordination. Vegetatio* 42: ...–....
- Peet, R.K. & N.L. Christensen. 1979. Hardwood forest vegetation of the North Carolina piedmont. *Veröff. Geobot. Inst. ETH, Stiftung Rübel*, 1979 (in press).
- Peet, R.K. & O.L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. *Ecology* 58: 485–499.
- Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. *Amer. Natur.* 110: 107–119.
- Sarukhan, J. 1978. Studies on the demography of tropical trees. In: P.B. Tomlinson & M.H. Zimmermann (eds.), *Tropical trees' as living systems*, p. 163–184. Cambridge Univ. Press, Cambridge.
- Shugart, H.H., T.R. Crow & J.M. Hett. 1973. Forest succession models: a rationale and methodology for modeling forest succession over large regions. *For. Sci.* 19: 202–212.
- Usher, M.B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *J. Appl. Ecol.* 3: 355–367.

- Vitousek, P.M. 1977. The regulation of element concentrations in mountain streams in the northeastern United States. *Ecol. Monogr.* 47: 65-87.
- Vitousek, P.M. & W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25: 376-381.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Whittaker, R.H. 1975. *Communities and ecosystems*. MacMilland, N.Y. 385 pp.
- Whittaker, R.H. 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10: 1-67.
- Whittaker, R.H. & P.L. Marks. 1975. Methods of assessing terrestrial productivity. In: H. Lieth & R.H. Whittaker (eds.), *Primary productivity of the biosphere*. *Ecol. Stud.* 4: 55-118. Springer-Verlag, N.Y.
- Whittaker, R.H. & G.M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven forest, New York. *J. Ecol.* 56: 1-25.
- Yoda, K., T. Kira, H. Ogawa & H. Hozumo. 1963. Self-thinning in overcrowded pure stands under cultivation and natural conditions. *J. Biol. Osaka City Univ.* 14: 107-129.

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