Reproductive Strategies and the Co-occurrence of Climax Tree Species

Abstract. *In a central New Hampshire forest, three co-occurring tree species were found to occupy different positions on a reproductive strategy gradient. These reproductive strategy differences, in part, described separate niches for the species. The three-species complex is hypothesized to form a dynamic climax overstory characterized by cyclical replacement of one dominant species by another.*

The simultaneous occurrence of species with similar ecological roles and with the same apparent habitat requirements in a climax ecosystem seems to refute the competitive exclusion principle (*1*). Although many mature plant communities contain several species that appear to have similar ecological roles, there have been few attempts to examine the comparative behaviors or niches of co-occurring plant species. Ecologists, however, have increasingly recognized the importance of evolved behavioral differences among plant species, particularly at early developmental stages, and research on this subject has recently intensified (*2*).

To describe the reproductive strategies of three forest dominants and to address the question of how different species contribute to the ecosystem's stability, a study of trees < 2.0 cm in diameter at breast height (dbh) (*3*) was conducted on the Hubbard Brook Experimental Forest in central New Hampshire. One forested watershed was stratified and 400 permanent plots were randomly chosen within it; each plot was observed six different times to determine the pattern, structure, and population dynamics of the seedling layer (*4*). Nearly 90 percent of the trees in the canopy of the stand, whose composition appears representative of the climax (*5*), are sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Brit.) (*6*). The three species comprise approximately equal portions (*7*) of the dominant trees at Hubbard Brook and occur synectically—that is, intimately co-occur—as dominants in many northern hardwood forests (*8*). Additionally, although changing in relative importance with elevation, all three species occur abundantly throughout the elevational range in the study stand (*6*).

Density, frequency, and biomass indicate that the beech seedling population exhibits the most stable behavior and that yellow birch is the most opportunistic of the three species (Table 1). The average density of the latter species exceeds that of both sugar maple and beech, but a comparison of maximum and minimum density values recorded during the study shows that the beech seedling population had the greatest numerical stability and the yellow birch population, the least. Over the 3-year period, yellow birch seedlings were observed on 92 percent of the permanent study plots. Although yellow birch was more widespread than the other species, particularly beech, its relative frequency in any one year was sometimes very low (*9*). Also, yellow birch seedlings were significantly more clumped than those of the other species.

Life tables show that the comparative stability of the beech population resulted in part from the generally higher survival rates of its seedlings (Table 2). Under the closed canopy that exists over most of the forest, beech seedlings experienced high mortality during the first year of life, but mortality rates became progressively less as the cohort's age increased. Once beech seedlings survived several years, their life expectancy was considerably higher than that of sugar maple. Sugar maple's survivorship curve can be described as intermediate between classical type II and type III survivorship (*10*), type II describing a population with a constant mortality rate regardless of age and type III a population with a decreasing mortality rate, as exemplified by the beech data. The survivorship of yellow birch is best fit by an extreme type III curve. Its tiny seedlings (Table 1) become established on very specialized, disturbed microsites in the forest (*11*). The necessary conditions for establishment do not occur simultaneously in many areas of a climax stand. At Hubbard Brook at the present time, most adequate sites for the establishment of yellow birch are created by the falling of isolated large trees. Yellow birch trees produce frequent large crops of very small seeds, which flood the forest and germinate throughout the summer months. However, new germinants usually do not survive for long, as indicated by a minimal mortality estimate of 97 percent 14 months after germination. Sugar maple was intermediate in its seedling population density, frequency, stability, and average individual size.

Association analyses of the occurrence of seedlings, saplings, and overstory trees (*12*) were made employing correlation analysis, chi square, and Cole's index of association (*13*). Seedlings and saplings of sugar maple were positively associated with a yellow birch overstory, and sugar maple's occurrence in the canopy tended to be associated with beech seedlings and was highly associated with beech saplings. In contrast, beech overstory and yellow birch seedlings and saplings were not strongly associated with the seedlings, saplings, or trees of the other two species. A striking result of the association analyses was that in this stand, even though the seedlings of a species were associated with its occupancy of the canopy, in no case did this association extend to include the sapling size-class. Yellow birch and beech canopies were negatively associated with their respective saplings, while the overstory and saplings of sugar maple showed no association. However, as might be expected, beech saplings of sprout origin were strongly associated with a beech overstory.

The association analyses indicate that the dynamic nature of this climax forest extends to its overstory (*14*). The apparent reproductive strategies of the three climax species can be integrated in the following microsuccessional scheme (Fig. 1).

Yellow birch is usually the first of the three species to reach areas where disturbance has been sufficient to create openings with exposed soil. The species grows relatively rapidly following its establishment, stabilizes the area in the process, and initiates a pocket of tree succession within the generally stable matrix of the forest. Next, a sugar maple understory becomes established in preference to beech, either because of its greater mobility or be-

Table 1. Comparative species data for seedlings (*12*). The first four parameters were calculated from measurements made in six individual surveys of permanent plots during 1967 to 1970; index of clumping is David and Moore's *I*, where larger values indicate greater contagion (*17*). Mean weight is for oven-dry seedlings and is based on a minimum sample of 496 seedlings of a species. Abbreviations: *d*, average density; $d_{\min}$, minimum density; $d_{\max}$, maximum density; and *N*, number of seedlings.

Species	d (N/m^2)	$(d_{\min}/d_{\max}) \times 100$ (%)	Plots containing seedlings at least once (%)	I	Mean weight (mg)
Yellow birch	21.3	2	92	24.5	8
Sugar maple	10.0	57	73	5.4	268
Beech	3.9	66	55	2.1	569

cause of subtle interspecies relationships that favor sugar maple compared to beech under a yellow birch canopy.

Assuming that sugar maple eventually replaces yellow birch in the canopy of many sites, its dominance in the overstory appears to be accompanied by the establishment of beech seedlings and saplings. Based on the association indices of progressively larger or older classes, sugar maple seedlings appear to develop poorly compared to beech seedlings under a sugar maple canopy.

The occurrence of beech in the canopy is negatively associated with the occurrence of the other two species, and the most strongly associated seedling-sapling component beneath the beech canopy is comprised of beech sprouts. If beech sprouts can mature to replace overstory casualties, the beech overstory–beech sprout sapling microcommunity could represent the end point of the proposed succession. However, the successful differentiation of beech forests from sprouts in this region is questionable. The appearance of many beech tree–beech sprout microcommunities suggests that dominance of an area by beech may be temporary, at least partially due to biotic factors such as aging processes, insects, and disease. Wind may curtail the dominance of a weakened beech microcommunity, only to restart a pocket of microsuccession with the influx of yellow birch. This hypothesized cyclic succession (*15*) would assure the co-occurrence of the three species in the community through times of infrequently occurring exogenous disturbance.

The interrelationship of space and the rates of various reproductive processes is important to forest composition as well as to a species' survival. For example, the reproductive strategy of beech is not only one of stability, it can also be characterized as slow. Yellow birch, on the other hand, although capable of long durability once it achieves the canopy, has an opportunistic reproductive strategy. If many sites were suitable for yellow birch occupancy, its behavior would enable it to become rapidly established on those areas. In contrast, there may be many areas of the forest now suitable for beech seedlings and saplings, but the poor mobility of that species delays its occupancy of these areas. The likelihood of continued survival and the importance of a very tolerant, but poorly mobile, climax species would be enhanced if it evolved a mechanism of decreasing the population size of more mobile species, even if the mechanism did not directly augment the species' own tree population. For example, even if beech sprouts do not become overstory trees, their role in delaying the occupation of previously beech-dominated sites by yellow birch, and also sugar maple, would lead to increased importance of beech in the forest through time.

Table 2. Synopsis of life table information on Hubbard Brook seedlings. The yellow birch table was truncated at 14 months because of the small size of its older seedling population.

Age interval (years)	Number of cohort alive at beginning of interval		
	Beech	Sugar maple	Yellow birch
0–1	1000	1000	1000
1–2	410	583	70
2–3	262	317	<30
3–4	188	225	
4–5	138	166	
5–6	121	118	
6–7	110	84	
7–8	92	54	
8–9	87	48	
9–10	83	42	

Sugar maple's prominence in the forest would probably decrease if the importance of beech increased, but sugar maple will also continue to be an important member of the overstory. Although the niche of sugar maple, like those of the other species, is defined by numerous dimensions (*16*), it is probable that the reproductive strategies of beech and yellow birch have contributed to the evolution of its niche. Yellow birch is too intolerant to establish advanced reproduction in its own shade, and poor mobility slows the advance of beech into undisturbed areas. Even without postulating additional interference mechanisms, and assuming the competitive superiority of beech over sugar maple to be absolute throughout the forest, the intermediate reproductive strategy of sugar maple would seem to insure its continued, although spatially shifting, occurrence in the ecosystem.

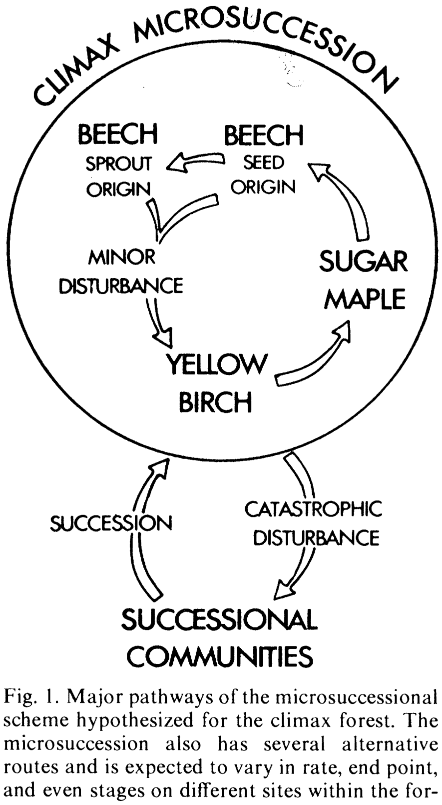

Fig. 1. Major pathways of the microsuccessional scheme hypothesized for the climax forest. The microsuccession also has several alternative routes and is expected to vary in rate, end point, and even stages on different sites within the forest, with the interaction of disturbance and with stochastic aspects of any species' regeneration.

The seedling research was not designed to examine whether the niches of three synectic forest dominants are distinct, but it does indicate that their niches do not entirely overlap. The broad range of behaviors displayed by the three-species complex on a reproductive strategy gradient, one extreme of which is approached by mobile yellow birch and the other by very tolerant beech, also confers on the forest an efficient mechanism for recovering from various degrees of disturbance. Thus, the evolved reproductive strategies of sugar maple, beech, and yellow birch, which are probably essential for their coexistence, also appear to be partially responsible for the stability of the near-climax ecosystem.

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References and Notes

1. The competitive exclusion principle states that two species competing for the same limited resource cannot coexist indefinitely. For further description of the principle and summaries of studies of competitive exclusions in animals. see F. J. Ayala, *Nature (Lond.)* **224**, 1076 (19 *Science* **171**, 820 (1971); *Am. Sci.* **60**, 348 (1972). Ayala's laboratory studies with *Drosophila* have shown that the competitive exclusion principle may not hold if the competitive relationships of two species vary with their ontogenetic stage and population densities. However, W. B. Leak [*Nature (Lond.)* **236**, 462 (1972)] presented evidence that the density-dependent competitive ability of two northern hardwood tree species appears to hasten the exclusion of one species.
2. M. F. Willson, *Biologist* **55**, 74 (1973).
3. Diameter at breast height is the diameter of a stem measured 1.37 m (4.5 feet) above the ground surface.
4. A description of the methods, statistical procedures, and study area is given in L. K. Forcier, thesis, Yale University (1973).

R. H. Whittaker, F. H. Bormann, G. E. Likens, T. G. Siccama, *Ecol. Monogr.* **44**, 233 (1974).

F. H. Bormann, T. G. Siccama, G. E. Likens, R. H. Whittaker, *ibid.* **40**, 373 (1970).

7. Importance values for trees ≥ 10 cm in dbh at Hubbard Brook are 33 for sugar maple, 28 for beech, and 25 for yellow birch. The maximum importance value is 100; importance is based on a species' relative density, frequency, and basal area (*6*).
8. For example, see E. L. Braun, *Deciduous Forests of Eastern North America* (Blakiston, Philadelphia, 1950); R. O. Curtis and F. M. Rushmore, *J. For.* **56**. 116 (19 T. G. Siccama, *Ecol. Monogr.* **44**, 325 (1974).
9. During one survey, yellow birch seedlings were recorded on only 15.7 percent of the permanent seedling plots.
10. E. S. Deevey, *Q. Rev. Biol.* **22**, 283 (1947).
11. To become established, yellow birch usually requires a disturbed seedbed such as scarified soil or decaying wood; higher light intensity than that under a full canopy, but not so much light as to cause overheating of the soil; and a substantial moisture supply (*4*).
12. In the description of the spatial association, seedlings are individuals of seed origin < 0.5 m in height; saplings are ≥ 0.5 m in height and < 2.0 cm in dbh; and trees are ≥ 2.0 cm in dbh. Beech sprouts are root sprouts in the sapling size class.
13. L. C. Cole, *Ecology* **30**, 411 (1949).
14. The possible variation of canopy composition in time has been postulated by Bormann *et al.* (*6*). These authors offered two alternatives to explain

the lack of correspondence of the patterns of the overstory and smaller size-classes of a species on a two-dimensional environmental gradient. One alternative is that overstory composition would change in time. This change could be directional with one species gaining prominence at the expense of another, or the overstory composition in any portion of the forest could fluctuate through time. The other alternative is that there might be differential mortality in the understory layer that would cause the canopy pattern to remain relatively unchanged.

15. A. S. Watt, *J. Ecol.* **35**, 1 (1947).
16. G. E. Hutchinson, *Cold Spring Harbor Symp. Quant. Biol.* **22**, 415 (1957).
17. E. C. Pielou, *An Introduction to Mathematical Ecology* (Wiley-Interscience, New York, 1969).
18. This is a contribution of the Hubbard Brook Ecosystem Study, funded by the National Science Foundation. Support during manuscript preparation was from the Montana Forest and Conservation Experiment Station.

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Occurrence of *S*-Methyl Thioesters in Urines of Humans After They Have Eaten Asparagus

Abstract. *Gas chromatography-mass spectrometry was used to determine the odor-causing agent (or agents) present in the urines of humans after they have eaten asparagus.* S-*Methyl thioacrylate and* S-*methyl 3-(methylthio)thiopropionate were identified from methylene chloride extracts of such urines and appear to be the odor-causing compounds. Methanethiol, the previously reported odor-causing agent, was not detected in these methylene chloride extracts.*

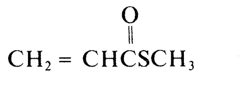
It has been recognized for many years that, after eating asparagus, some humans excrete a substance or substances which produce a characteristic odor in the urine (*1*). This strong odor appears within an hour after only a few spears of asparagus have been consumed (*2*). Allison and McWhirter found evidence that the ability to produce the odor is controlled by a single autosomal dominate gene (*3*). In a random sample of 115 individuals, 46 were found to produce the odor after eating asparagus and 63 did not. The odor-bearing compound was tentatively identified as methanethiol in 1891 by Nencki who distilled the urines of four individuals who had eaten a total of 7 kg of asparagus (*1*). Identification was based on the odor of the distillate and precipitation of mercury and lead mercaptides. Allison and McWhirter also reported the compound as methanethiol on the basis of the isolation of the silver methyl mercaptide (*3*).

Recently, dimethyl disulfide was identified as a normal trace volatile of human urine (*4*). The presence of the free mercaptan methanethiol would not be expected, however, because the compound is rapidly oxidized to the disulfide by oxygen. In addition, small doses of methanethiol injected into rats are reported to be metabolized rapidly to inorganic sulfate and carbon dioxide (*5*).

Efforts to identify methanethiol in odorous urine (kept at 80°C) by passing its vapors through a mercuric chloride solution in an attempt to isolate the mercaptide were unsuccessful. An attempt to trap the CH_3SH by reaction of the urine or its methylene chloride extract with 1-fluoro-2,4-dinitrobenzene (DNFB) was also unsuccessful. A water sample containing ~ 1.0 μmole of CH_3SH gave the DNFB derivative that was easily assayed by gas chromatography-mass spectrometry (GC-MS). Attempts to find by the use of GC-MS abnormal amounts of dimethyl disulfide in ethyl ether and methylene chloride extracts of the urines of humans who had eaten asparagus were also unsuccessful.

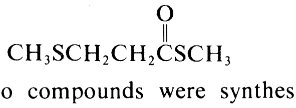
Analyses were carried out on urine samples of approximately 500 ml, which were collected over a period of 12 hours on several occasions after the subject had eaten a standard diet. When included in the diet, ~ 100 g of asparagus was prepared by cooking for 10 minutes in boiling water. The urine samples were collected in a flask containing 50 ml of methylene chloride (distilled in glass) and cooled to 3°C. The flask and contents were shaken for 1 hour and the resulting emulsion was separated by centrifugation; the organic layer was evaporated at 40°C to a small volume in a stream of nitrogen. The resulting concentrated methylene chloride solution was examined with an LKB 9000 GC-MS (*6*).

Closer examination of the GC-MS data of these extracts, however, revealed the presence of compounds with molecular ions and fragmentation patterns corresponding to *S*-methyl thioacrylate (M^+, m/e = 102)



$$CH_2=CH\overset{\overset{\displaystyle O}{\|}}{C}SCH_3$$

and its methanethiol addition product *S*-methyl 3-(methylthio)thiopropionate (M^+, m/e = 150)



$$CH_3SCH_2CH_2\overset{\overset{\displaystyle O}{\|}}{C}SCH_3$$

These two compounds were synthesized (*7*), and were found to have the same gas chromatographic retention times and mass spectra as the two compounds found in the urine (*8*). The addition of these synthesized compounds to nonodorous urine produced the characteristic odor found in the urine after the subjects had eaten asparagus. In addition to these compounds smaller amounts of other sulfur compounds were also detected on occasion. These included dimethyl trisulfide CH_3SSSCH_3, tetrahydrothiophene $\overline{CH_2CH_2CH_2CH_2S}$, and an unidentified compound (M^+, m/e = 126) containing two sulfurs (*9*). None of these compounds could be detected in the urine unless asparagus had been consumed. The expected ease of hydrolysis of these compounds to produce methanethiol under the distillation or reaction conditions (or both) used by previous investigators would account for their identifications of methanethiol as the odoriferous compound.

Since the amount of dimethyl sulfone excreted in a 24-hour period is known to be relatively constant (between 4 to 11 mg) (*10*), dimethyl sulfone was used as an internal standard for quantifying *S*-methyl thioacrylate and *S*-methyl 3-(methylthio)thiopropionate in urine. The two thioesters are present in approximately equal amounts after ingestion of asparagus. Furthermore, they occur at levels comparable to that of dimethyl sulfone. Therefore from 2 to 5 mg of each of the thioesters appears to be excreted in the urines of humans within 12 hours of having consumed ~ 100 g of asparagus.

Previous work has demonstrated the presence of two unusual sulfur-containing compounds in asparagus; these include 2,2′-dithiolisobutyric acid (*11*) and a methylsulphonium salt of methionine (α-aminodimethyl-γ-butyrothetin) (*12*). Ingestion of 10 mg of 2,2′-dithiolisobutyric acid by two individuals produced no odor in the urine (*13*). The methionine analog has also been found in cabbage and parsley, neither of which produce the urine odor observed after the eating of asparagus, which would indicate that this compound is not responsible for the production of the odor (*13*). Although *S*-methyl thioacrylate and *S*-methyl 3-(methylthio)thiopropionate have been identified as the odor-causing compounds, their metabolic origin remains an open question.

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6. Separations were effected with a glass column (1.8