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Seedling Tolerance as a Factor In Bottomland Timber Succession

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The problem of perpetuating valuable subclimax species in bottomland areas is one of the greatest difficulties in bottomland timber management. After cutting, areas that had supported good stands of cottonwood and sycamore commonly revert to or become semi-stabilized in inferior species such as the elms.

Numerous investigators have reported the successional sequence of bottomland timber species and, in general, the picture is one of valuable species being replaced by less valuable species and these, in turn, being slowly replaced by more valuable species. Steyermark (1940) found that along the smaller streams of the southeastern Missouri Ozarks, the first stage of woody succession on sand and gravel near a stream was commonly characterized by a temporary community or associes of willow-witch hazel. Sycamore may occur as a single dominant on gravelly, sandy deposits, or it may occur in associations with Ward's willow and witch hazel. Another variation in close proximity to water may be an alder-witch hazel-sycamore associes.

Farther away from the margins of the streams, Steyermark reports a different associes of silver maple-eastern cottonwood. River birch, black willow, green ash, and red gum also may make an appearance in this stage. Steyermark notes that river birch may come in before black willow, cottonwood, and silver maple. The next forest community development away from a stream, according to Steyermark, is an American elm-green ash associes with a persistence of large sycamore, cottonwood, and black willow from the previous or streamward successional stage. Steyermark states that this elm-ash associes may last almost indefinitely, depending upon pH of the soil and flooding activities of the stream. Shumard oak and bur oak may be present in this elm-ash stage. Steyermark found that the final or climax stage of floodplain succession is characterized by the development of a sugar maple-bitternut hickory association. Winged elm is a common component of climax forest as well as the gums, hackberries, oaks, and many other species.

Steyermark describes the development of a white oak-red maple association in acid soil areas such as slight draws in ravines, heads of stream tributaries, and the upper slopes of hills and ravines. The first stage of this white oak-red maple association is described as a dogwood-blackgum associes that may have, in combination or as alternates, witch hazel or Ward's willow. As drainage areas become more deeply dissected, red maple, mockernut hickory, and winged elm are dominants; and the final development is white oak-red maple.

In his phytosociological studies of the plant communities of the North Carolina Piedmont area, Oosting (1942) includes an analysis of the bottomlands. Although somewhat oversimplified, the general successional trends are: (1) alder-willow, (2) to river birch, or sycamore, or boxelder, or mixed or predominantly red gum and yellow-poplar, and (3) to red maple-elm-ash.

Oosting studied intensively three stands of birch and three of sycamore. He found that in a six-year-old stand of river birch, birch reproduction was predominant, with sycamore, winged elm, and red maple making up the bulk of the remainder in the order named. In a 14-year-old birch stand, reproduction tallies indicated an almost complete absence of birch, while red maple, red gum, and winged elm were most abundant. In a 36-year-old birch stand, no birch reproduction was in evidence and red maple-elm-ash made up 50 percent of the total. In 22-year-old, 30-year-old and 35-year-old sycamore stands, there was no sycamore reproduction; and in all three stands, red maple, elm, and ash, in varying proportions, were the major constituents.

Field data collected by the author in bottomlands of the southeastern Missouri Ozarks indicate that in stands of sycamore, river birch, and cottonwood, reproduction of these species is almost completely curtailed with the development of canopy strata. As a canopy develops, various kinds of reproduction are found including red gum, sugar maple, oaks, mulberry, etc., but with a strong tendency toward elms.

It is evident then, that if a merchantable stand of sycamore or cottonwood is cut, the next cut may be limited to species that are characteristic of the next stage of succession. In the southeastern Ozarks of Missouri and the North Carolina Piedmont, this next unfavorable successional development is often toward some combination of elm, ash, and/or maple.

The objective of this investigation was to determine why reproduction of the trees typical of the early stages of primary and secondary succession in bottomland areas fails to continue coming in under canopies, consisting in part of these same species. In general, it can be stated that the successional trend is toward more shade-tolerant species. However, the tolerance of sycamore is a matter of debate as Baker (1949) points out. Thus, as a preliminary investigation, it seemed advantageous to ascertain the relative light tolerances of young seedlings of tree species representing the several stages of bottomland succession. Sycamore (*Plantanus occidentalis* L.), river birch (*Betula nigra* L.), red maple (*Acer rubrum* L.), American elm (*Ulmus americana* L.), winged elm (*Ulmus alata* Michx.), and hazel alder (*Alnus rugosa* [Du Roi] Spreng.), were selected as representing early, middle, and late stages of small stream, bottomland succession.

PROCEDURE

Four light intensities were used: full, one-half, one-third, and one-fifth sunlight. One-fifth full sunlight was used as a minimum because such an intensity, according to Shirley (1943), is common under canopies and it is in this light range that seedling establishment is greatest. The one-half intensity resulted from the filtering effect of an unwashed greenhouse roof, and the two lower intensities were obtained by screens of cheesecloth. Full sunlight was obtained in an open area immediately adjacent to the greenhouse.

Each treatment was applied to 50 seedlings in units of five per six-inch pot. The seedlings had been transplanted into the pots after the appearance of the first true leaves and were then allowed to stabilize for three days before being subjected to the light treatments. As soon as seedling size permitted, the surfaces of the pots were covered with a one-half-inch layer of granulated vermiculite. The indoor pots were set on cinder beds, and the outdoor pots were partially buried in sand. The soil used was a light potting soil with a wilting percentage of 9.93% and a field capacity of 19.73%.

The one-third and one-fifth screens were so constructed that two sides were suspended three inches above the cinders to allow air circulation.

The pots were arranged in the same order by species in each treatment so that any shading effect of the pots upon each other would be of the same magnitude. This within-treatment shading effect was judged to be at a minimum because of ample spacing.

By frequent watering and the use of the vermiculite mulch, an attempt was made to keep the moisture content of the soil at field capacity or slightly above it. This was possible for the treatments within the greenhouse, but not in the outdoor or full sunlight treatment. The light soil and underlying cinder and sand beds provided rapid drainage.

Survival, height growth, weight of the tops, and the weight of roots per pot were recorded at the end of 15 weeks for sycamore, 14 weeks for alder, 13 weeks for red maple and the elms, and 10 weeks for river birch.

Relative humidity, air temperature, and sunlight intensities were recorded for 10 days during the experiment. Temperatures under all treatments in the greenhouse were never more than 4°F apart, but the outdoor temperatures were at different times 13°F higher and 6°F lower than the indoor readings. Outdoor relative humidities proved to be consistently lower than the indoor humidities. The higher outdoor temperatures, steeper atmospheric moisture gradients, and lower soil moistures produced a consistently drier environment in the full sunlight treatment.

In analyzing the growth data, it was felt that due to the pronounced environmental differences of the outdoor treatment, the growth results for full sunlight would have to be evaluated separately instead of pooling all residuals. The analysis of indoor data could have been made on a pooled 27 degrees of freedom, but the precision on 9 degrees of freedom was so close to that gained on 27 that pooling seemed unwarranted. Hence, all treatments were analyzed separately by species. Standard errors of individual treatments were used in calculating significance of mean differences.

RESULTS

The percentages of survival by species in each treatment are presented in Table 1.

Height growth of the seedlings and the ratios of top weight to root weight per pot were analyzed statistically (Tables 2 and 3).

Height growth of red maple did not differ significantly in any of the light intensities, and the top-root ratio differences are significant for full sunlight only. Height growth and top-root ratio of sycamore are significantly less for full sunlight than for lower light intensities, and the difference is significant for the ratios developed under one-fifth and one-third light.

The elms differ from each other in that one-third light resulted in the significantly greatest height growth of American elm, while one-half light resulted in the greatest height growth of winged elm. Interestingly, the difference between the top-root ratios of one-fifth and one-third light is significant for winged elm and not American elm, as are all the responses of both under full light in comparison with those of reduced intensity.

Sycamore, American elm, and alder had their highest top-root ratios under the light intensities which produced their greatest height growth, indicating perhaps, that best height growth resulted in the relatively poorest root growth. However, actual root development, as measured by weight, was greatest at this intensity for American elm, but not for sycamore and alder.

Like winged elm, the alder and river birch have their best growth at one-half sunlight, but unlike elm, their height growth in full sunlight is significantly better than at one-fifth and one-third sunlight intensity.

Representative pots of the species that displayed significant height growth responses are presented in Figs. 1 and 2.

TABLE 1 -- PERCENTAGE SURVIVAL OF SEEDLINGS GROWN UNDER FOUR SUNLIGHT INTENSITIES (△)

Species	Treatment			
	1/5 △	1/3 △	1/2 △	Full △
Red Maple	95.0	95.0	100.0	62.5
Sycamore	92.5	97.5	100.0	100.0
American Elm	100.0	100.0	100.0	90.0
Winged Elm	100.0	97.5	100.0	62.5
Alder	100.0	97.5	90.0	45.0
River Birch	87.5	100.0	100.0	77.5

TABLE 2 -- MEAN HEIGHTS OF SEEDLINGS AND THEIR DIFFERENCES AS INFLUENCED BY FOUR SUNLIGHT INTENSITIES (△)

Species	Mean Ht. Per △				Differences Between Means					
	1/5 △	1/3 △	1/2 △	Full △	1/3 △- 1/5 △	1/2 △- 1/3 △	Full △- 1/5 △	1/2 △- 1/3 △	Full △- 1/3 △	Full △- 1/2 △
	Cm.	Cm.	Cm.	Cm.	Cm.	Cm.	Cm.	Cm.	Cm.	Cm.
Red maple	25.53	27.13	29.40	26.16	1.60	3.87	0.63	2.27	- 0.97	- 3.24
Sycamore	42.56	41.10	40.13	32.73	- 1.46	- 2.43	- 9.83*	- 0.97	- 8.37*	- 7.40*
Am. Elm	72.71	81.26	68.56	36.84	8.55	- 4.15	-35.87*	-12.70*	-44.42*	-31.72*
Wing. Elm	58.86	71.26	76.41	28.17	12.40*	17.55*	-30.69*	5.15	-43.09*	-48.24*
Alder	21.34	19.78	37.67	29.81	- 1.56	16.33**	8.47*	17.89*	10.03*	- 7.86*
Riv. Birch	26.01	33.26	51.58	41.22	7.25*	25.57*	15.21*	18.32*	7.96*	-10.36*

*Significant at the 5% level

TABLE 3 -- MEAN TOP/ROOT WEIGHT RATIOS OF SEEDLINGS AND THEIR DIFFERENCES AS INFLUENCED BY FOUR SUNLIGHT INTENSITIES (△)

Species	Mean Ratio Per △				Differences between Means					
	1/5 △	1/3 △	1/2 △	Full △	1/3 △- 1/5 △	1/2 △- 1/5 △	Full △- 1/5 △	1/2 △- 1/3 △	Full △- 1/3 △	Full △- 1/2 △
	Gm.	Gm.	Gm.	Gm.	Gm.	Gm.	Gm.	Gm.	Gm.	Gm.
Red Maple	4.095	3.666	3.463	1.995	-0.429	-0.632	-2.100*	-0.203	-1.671*	-1.468*
Sycamore	4.594	3.451	4.078	2.039	-1.143*	-0.516	-2.555*	-0.627	-1.412*	-2.093*
Am. Elm	3.063	3.248	3.022	1.673	0.185	-0.041	-1.390*	-0.226	-1.575*	-1.349*
Wing. Elm	5.213	3.933	4.433	1.914	-1.280*	-0.780	-3.299*	0.500	-2.019*	-2.519*
Alder	3.434	3.513	4.743	2.821	0.079	1.309*	-0.613	1.230*	-0.692*	-1.922*
Riv. Birch	13.393	9.292	8.265	3.617	-4.101*	-5.128*	-9.776*	-1.027	-5.675*	-4.648*

*Significant at the 5% level

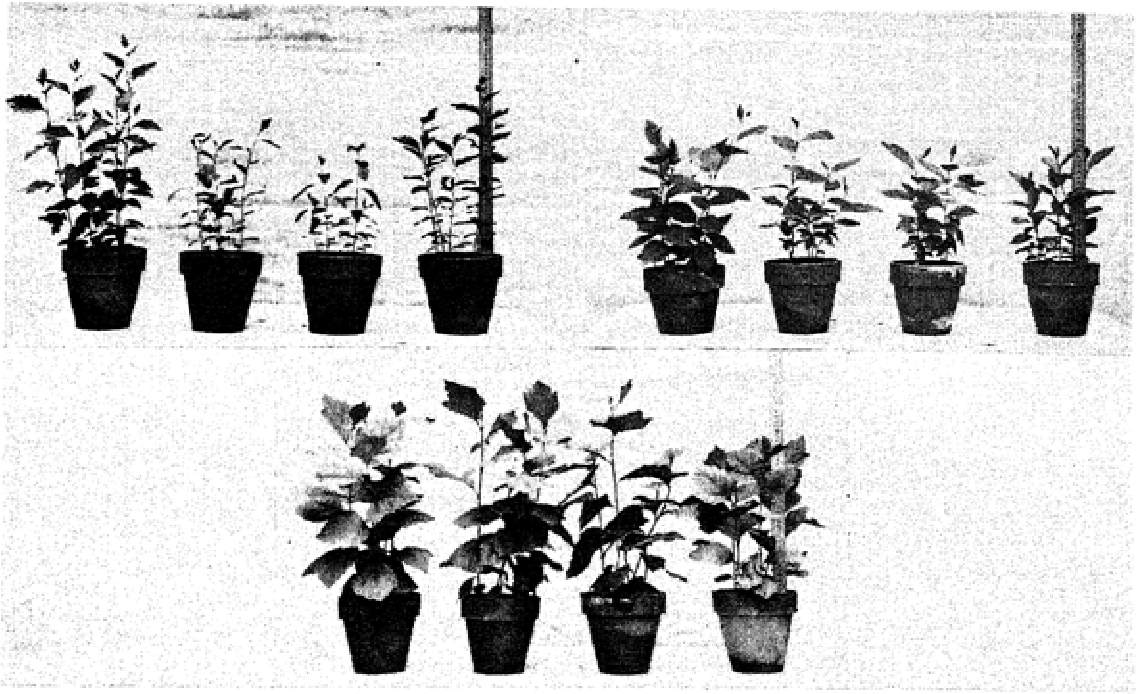

Fig. 1—Representative pots of river birch 10 weeks old, alder 14 weeks, and sycamore 15 weeks old grown, from left to right, in one-half, one-third, one-fifth and full sunlight.

Fig. 2—Representative pots of winged elm and American elm 13 weeks old grown, from left to right, in one-half, one-third, one-fifth, and full sunlight.

DISCUSSION AND CONCLUSIONS

The growth of the seedlings under different light intensities has application as an indirect means of evaluating the relatively successful establishment of a germinated seed. Furthermore, it may provide a general scale of species tolerance. Such a scale may be an indicator of competitive ability of the seedlings with established trees, and perhaps of equal importance, of competitive ability of tree seedlings with herbaceous plants.

In addition to height growth, an indicative and important growth response is the weight of the roots, or the ratio of top weight to root weight. This importance lies in the fact that if, as Kramer and Coile (1940) suggest, root extension into the soil supplies a large part of the water used by a plant, then a poorly developed seedling root system might result in a localized depletion of soil moisture, brought about by a slow extension of the root system. If the same species develops a larger root system in higher light intensities, seemingly the increased water availability resulting from root extension on into new soil areas is proportionately greater than the amount consumed in and by the additional top increment.

An interpretation of both height growth and top-root ratios of young seedlings of the six species used in this experiment indicates that the light tolerance of alder, river birch, American elm, winged elm, and red maple correspond in general to their successional relationships in bottomland forest communities. Sycamore seedlings appear to be at least as shade tolerant as the elms, despite the more advanced successional relationship of the elms. Thus, it is apparent that a successional shift to elm-ash (and red maple in the Piedmont of North Carolina) from a river birch-sycamore level can be accounted for by the low shade tolerance of river birch, but not sycamore. Putnam (1951) cites river birch and sycamore as intolerant, and American elm, winged elm, and red maple as tolerant. Baker (1949) in his poll of American foresters found that they regard sycamore as tolerant, intermediate, and intolerant with emphasis on the latter. To be sure, tolerance tables such as Putnam's and Baker's are based upon all phases of species growth. And, under mature stands of many allegedly tolerant species (particularly western conifers), reproduction of any kind is conspicuously scarce. But, in early stages of primary and secondary succession in bottomlands, there is reproduction but often of a more advanced successional stage. This suggests that the absence of very young sycamore seedlings in stands of sycamore successional status, where a canopy is developing, may be due to the development of seedbed conditions that are prohibitive to sycamore germination and immediate establishment of the germinated seed. By the same token, the development of such conditions would be advantageous to the germination of seed and immediate establishment of germinated seed of the maple-elm-ash stage.

SUMMARY

In the successional sequence of bottomland timber species, an early shrub stage often characterized by alder is replaced by a stage in which sycamore and river birch may be prominent. This stage in turn, is commonly replaced by a maple-elm-ash community. In general, it can be assumed that there is a shift from intolerant to tolerant species as this alder to sycamore-birch, to maple-elm transition takes place. To test this assumption, very young seedlings of alder, sycamore, river birch, American elm, winged elm, and red maple were grown in four sunlight intensities: full, one-half, one-third, and one-fifth.

On the basis of height growth and top-root ratios, it was found that alder and river birch are quite intolerant, American elm and winged elm, moderately tolerant, and red maple, tolerant. Contrary to expectations, sycamore seedlings are at least as tolerant as the elms. Thus, the fact that sycamore reproduction is lacking in sycamore stands, and that the tendency is commonly toward elm reproduction, is not primarily due to differences in light tolerance. The suggestion is made that as succession proceeds in bottomland timber areas, it appears that seedbed conditions become prohibitive for the sycamore stage and are improving for the elm stage.

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