REGENERATION OF SOUTHERN HARDWOODS:

SOME ECOLOGICAL CONCEPTS

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ABSTRACT

Classical concepts of post-disturbance succession through well-defined seral stages to a well-defined climax stage(s) are not a useful conceptual framework for predicting species composition of regeneration resulting from the application of regeneration treatments in complex southern hardwood forests. Hardwood regeneration can be better understood, and more useful prediction models can be developed, using the concepts of initial floristic composition and vital ecological attributes.

INTRODUCTION

In the ecology, silvics, or silviculture courses that most if not all of us attended, we studied concepts associated with forest succession, which has been a major area of study in ecology for more than 70 years. Attempts to explain successional phenomena have created a rich body of literature that I will not attempt to review here. It is sufficient to say that there are several schools of thought on what succession is and how it should be studied. The classical concept of succession includes seral stages leading to a climax(s). My own conclusion, based on the literature from ecology and forestry, is that this concept creates more confusion than understanding when it is applied to silvicultural systems and regeneration methods in southern hardwood forests. For example, it is unlikely that any consensus could be reached on a classification of 'climax' vegetation in the Southern Appalachians. Further, identical treatments in stands with very similar species composition growing on very similar sites can produce widely differing species composition of regeneration (Loftis 1989). And among stands with very similar species composition growing on very similar sites, different treatments have resulted in very similar species composition of regeneration (Loftis 1983a). So, classifying seral stages and linking them with particular kinds and levels of disturbance also present difficulties.

Rather than force observed responses into a conceptual framework in which they apparently do not fit, more effort must be directed at understanding the process of regeneration. I therefore will discuss two concepts–initial floristic composition and vital attributes–that may form the basis for understanding regeneration in managed hardwood forests. My focus will be on species composition of regeneration, where regeneration is the result of planned, recurrent disturbance designed to create a new age class of trees. Therefore, the spatial scale to which I apply these concepts is the stand, and the temporal scale is the rotation length.

INITIAL FLORISTIC COMPOSITION

The first of these concepts was proposed by Egler (1954). He presented two contrasting patterns of vegetation development following abandonment of agricultural land. The first pattern he called 'relay floristics,' in which groups of species appear and are replaced by other groups of species until some relatively stable community is attained. As an alternative, he proposed another pattern he called 'initial floristic composition,' in which the site receives an initial load of propagules and a plant community develops without additional input of new individuals. The apparent dominance of different groups of species is the result of differential development or growth of different species or groups of species. Regardless of its applicability to old-field succession, many investigators have recognized, either explicitly or implicitly, the broad applicability of the initial floristic composition pattern to hardwood stand development following disturbance (e.g., Oliver 1981, Leopold et.al. 1985, Shugart 1984, Drury and Nisbet 1973). The essential feature of the initial floristic composition concept that makes it useful for modeling is that the individuals of species that form the dominant canopy 50 to 100 years

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after disturbance come from the initial load of propagules. A corollary to this concept is that variations in species composition 50 to 100 years after disturbance may result from variations in this initial load of propagules. We know that for hardwood stands the initial load of propagules after harvest cutting will be comprised of:

1. New seedlings
2. Advance reproduction
3. Stump or root sprouts.

VITAL ATTRIBUTES

It is important, then, to understand more about this initial load of propagules. Noble and Slatyer (1980) suggested that species composition of stands that develop after disturbance could be predicted from 3 vital attributes of species:

1. The method of arrival or persistence of a species at a site during and after a disturbance.

2. The ability to establish and grow to maturity in the developing community.

3. The time needed for an individual of a species to reach critical life stages.

Because of time constraints, I will discuss only the first two of these vital attributes. The first can be illustrated by grouping species by their primary mode of arrival or persistence during and after disturbance. On mesic sites in the Southern Appalachians, for example, new seedlings established during or soon after disturbance are an important source of regeneration for only a few species (Table 1).[2] Most species are advance-growth dependent, i.e., they *must* persist as advance reproduction or develop from stump or root sprouts. A species' shade tolerance generally indicates the likelihood that its advance reproduction will be present on the site as we approach a regeneration cut. Shade-intolerant species are unlikely to be present as large advance reproduction. To the extent that shade-intolerant species can germinate under closed stands, the establishment-mortality cycle tends to be fairly rapid. Shade-tolerant species are more likely to be well represented as large advance reproduction or larger advance growth. Species listed as intermediate in shade tolerance can usually germinate and survive for a few years under closed stands, but typically show little development. For example, northern red oak (*Quercus rubra* L.) seedlings become established after good seed crops, but survival of a cohort is likely to be less than 10% after 10 years, and those that do survive will have grown very little (Loftis 1983b).

Generalizations about seedling population dynamics based on species' shade tolerance should be viewed cautiously. We need to know much more about the dynamics of seedling populations of individual species under mature stands and the factors that influence these dynamics.

Given some initial load of propagules, how do we approach the second vital attribute, the ability to grow to maturity in the developing community? Again, let me use northern red oak to illustrate one approach. Recall that red oak is an advance growth dependent species. It is well established that growth of red oak stems after harvest is related to the size of the advance reproduction (Sander 1971, 1972). Based on this information, we have developed from experimental data a model that relates the probability of a stem becoming dominant or codominant (dominance probability) in the next stand to its preharvest basal diameter and the quality of the site on which it grows (Loftis 1988a). The dominance probability increases with increasing preharvest basal diameter and decreases with increasing site quality. We attribute the inverse relationship with site quality to the increasing level of competition with increasing site quality. If we have knowledge about the numbers in each size class of red oak that are present in the stand at the time of harvest, we can roughly predict the number of dominant and codominant red oaks that will be present in the next stand. Similar models have been developed for oaks on more xeric sites (Sander et.al. 1984)

As I have suggested in an earlier paper (Loftis 1989), this probabilistic, population-based approach is quite attractive for predicting the amount of a single species to be expected in the stand that develops after harvest. However, for predicting species composition in multispecies stands, there are several drawbacks to this approach. The most serious, in my view, is that competition is considered implicitly in the model as a function of site quality. One simple approach to modeling species composition in multispecies stands, which explicitly considers competition, is to rank relative post-harvest performance by species and regeneration source. Applying such a ranking to information collected from stands prior to harvest, say using 0.01 acre plots, would provide a basis for predicting species composition. The expected species composition on each plot, based on the ranking, could be combined to provide a picture of stand-level species composition.

[2] See also Beck (1988), Kelty (1988), and Johnson (1989).

TABLE 1. Reproduction sources and shade tolerance of some Appalachian species.

Regeneration from new seedlings established after cutting

Species	Shade tolerance
Yellow-poplar	intolerant
Sweet birch	intermediate
*Black cherry	intolerant
Yellow pines	intolerant

Advance-growth-dependent species (from advance reproduction and stump sprouts)

Red oak	intermediate
White oak	intermediate
Chestnut oak	intermediate
Black oak	intermediate
Scarlet oak	intermediate
White ash	intermediate
*Black cherry	intolerant
Cucumbertree	intermediate
White pine	intermediate to tolerant
Hickories	intermediate to tolerant
Basswood	intermediate to tolerant
Red maple	intermediate to tolerant
Sugar maple	tolerant
Beech	tolerant
Buckeye	tolerant
Hemlock	tolerant

* Based on detailed preharvest inventories and stem analysis data, black cherry sometimes regenerates successfully from new seedlings, while in other cases, it appears to require advance growth to compete successfully (Loftis, unpublished data). The conditions under which these 2 regeneration strategies operate have yet to be determined.

SOME IMPLICATIONS FOR REGENERATION METHODS

If one accepts these concepts as a rational basis for understanding hardwood regeneration, then devising regeneration methods to influence species composition requires treatments that will effect changes in the initial load of propagules. These changes may involve discriminating against some regeneration sources, changing the size-class structure of regeneration sources, or some combination of the two. Again, consider red oak in the Southern Appalachians. As you might expect from the information I have already presented, red oak is difficult to regenerate. Successful regeneration depends on the presence of large advance reproduction in the initial load of propagules, but large advance reproduction will not develop in the absence of disturbance . We have devised a method to regenerate red oak that involves treating midcanopy and lower canopy trees with herbicides about 10 years prior to overstory removal. This level and kind of disturbance simultaneously enhances the growth of advance red oak reproduction prior to overstory removal and eliminates sprouts from midcanopy and lower canopy trees from the initial load of propagules after overstory removal (Loftis 1988b).

FINAL THOUGHTS

I have drawn heavily on some of our work in the Southern Appalachians, but I believe these concepts apply generally to managed hardwood forests. I am optimistic that we will be able to develop, for managed forests, predictive models of species composition. In his excellent review paper, White (1979) emphasized the importance of understanding disturbance regime in studies of succession. He dealt with natural (non-anthropogenic) disturbance and its implications for species compositional dynamics on an indeterminate temporal scale. White suggested that disturbances can be described by such parameters as frequency, predictability, and magnitude. In "naturally" disturbed communities, a great deal of uncertainty can be associated with disturbance regime. In silviculture, however, we exert considerable control over the parameters of disturbance. If we can understand the effects of timing and type of disturbance, we will be able not only to predict predict species composition, but also to control it.

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