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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 **an** other 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 **in-**

volves 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 **mid-canopy** 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 **suc-**

cession. 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 species **composition**, but **also** to control it.

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