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Defining species guilds in the Central Hardwood Forest, USA

Elaine Kennedy Sutherland[1,2], Betsy J. Hale[1] & David M. Hix[3]
[1]*Northeastern Research Station, Delaware, Ohio 43015-8640, USA;* [2]*present address: Rocky Mountain Research Station, P.O. Box 8089, Missoula, Montana 59807-8089, USA;* [3]*School of Natural Resources, The Ohio State University, Columbus, Ohio 43210-1085, USA*

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Abstract

Tree regeneration outcomes are challenging to generalize and difficult to predict. Many tree species can establish new propagules in a variety of post-disturbance environments and many different reproductive mechanisms may be used. In order to develop conceptual models that accurately reflect reproductive potential, we need a better understanding of the similarities in regeneration ecology among species. We used information from the forest ecology literature to evaluate the reproductive attributes of sixty-two tree species in the central hardwood region of the eastern United States. Each species was classified categorically for features such as flowering, seed production and dispersal, seed dormancy, germination requirements, seedling characteristics, and vegetative reproduction. Cluster analysis (Jaccard's similarity coefficient, complete linkage method) and ordination (homogeneity analysis) were used to separate nine groups (guilds) of species that had similar reproductive attributes. Individual attributes that had high variance in the first and second dimensions included: seed banking, seed dispersal, seedling shade tolerance, and seedbed requirements. Members of each guild had similar levels of reproductive specialization and guilds were either pioneer-like, opportunistic, or persistent. Pioneer guilds included: short-lived or fugitive species that colonize sites rapidly and are too shade intolerant to replace themselves; shade-tolerant species that colonize frequently disturbed sites; and stress-tolerant pioneers that survive on dry or nutrient-poor sites. Opportunistic guilds contained species that are remarkably versatile in their reproductive effort. The most flexible opportunists can colonize new sites, maintain seed in a seed bank, sprout from existing stems and persist as a seedling or sapling bank. Persistent guilds contain species that develop and maintain advance regeneration. These include: species with moderate understory tolerance that regenerate via cycles of dieback and resprouting; and more tolerant species that maintain seedling or sapling banks. Our regeneration guilds may provide a useful approach for more realistically representing large and diverse sets of tree species in forest ecosystem models.

Introduction

The regeneration of trees is complex, difficult to generalize and consequently challenging to predict. Yet, the need exists to better understand forest dynamics and to predict forest composition. In the face of environmental change, the composition of existing communities is a poor predictor of future composition. Communities disassemble and reassemble in new configurations (Delcourt & Delcourt 1991). Species move individually and not in concert with other members of a given assemblage. How do we predict the migration and extirpation of individual species, and the consequent composition of new communities?

Predicting tree regeneration outcomes is particularly challenging in the hardwood forests of the eastern United States, with variability in both the characteristics of releasing disturbances and the regeneration potential of a diverse tree flora (Runkle 1985; Peterson & Carson 1996). There are many types of disturbance in eastern forests, and they vary in intensity, frequency, and spatial extent. Windstorms, fire,

floods, and drought are common. The impact of these disturbances on future forest composition depends on existing site conditions, species composition, and stage of stand development (Watt 1947; White 1979; Oliver & Larson 1996). The life history attributes of the surviving species determine which species are available to establish new cohorts (Sousa 1984; Peterson & Pickett 1995; Smith et al. 1997). Many tree species can establish new propagules in a variety of post-disturbance environments, and several reproductive mechanisms can be used to establish new cohorts (Canham & Marks 1985; Oliver & Larson 1996).

Generalization is a necessary prerequisite to prediction. Several approaches have been used to generalize patterns of tree regeneration. In categorizing species according to reproductive potential, researchers have used predominant mechanisms (e.g., windblown seed, stump sprouts, advance growth) or only a few attributes (e.g., seed size, dispersal mode, seedling shade tolerance) to sort species into ecological groups or guilds (Bormann & Likens 1979; Kelty 1988; Brzeziecki & Kienast 1994; Smith et al. 1997; Barnes et al. 1998). For example, Smith et al. (1997) described propagule guilds that represent various sources of tree reproduction that may arise after severe or releasing disturbances. Seed inputs (i.e., newly-dispersed seed, stored or buried seed) and forms of on-site reproduction (i.e., vegetative sprouts, advance-growth seedlings or saplings) were used to define these guilds.

Barnes et al. (1998) ranked tree species according to a single attribute, seedling shade tolerance, and then divided the continuum into three disturbance-driven establishment types. Pioneers follow major disturbances (e.g., fire or flooding); gap-phase species establish in the understory but then must be released by gap-forming events (e.g., windstorms); extremely shade-tolerant species establish in the understory and can remain suppressed for many years before small canopy openings allow them to grow into the overstory. Bormann & Likens (1979) used several reproductive attributes (fruiting, seed size, dispersal, seed banking, seedling shade tolerance) and other life history features (longevity, height growth rate, crown and leaf characteristics) to distinguish two groups of species (exploitative and conservative) that reclaim severely disturbed sites in the northern hardwood forest. Exploitative species are those likely to appear immediately after disturbance while conservative species are suited to conditions occurring at a later stage of stand development.

Reproductive attributes also have been used to group species that are adapted to a particular type of disturbance. For example, many fire-adapted trees are differentiated by the nature of their seed banking (serotinous cones, soil seed banks), resistance to fire (sprouting ability), and seeding characteristics that allow them to colonize and establish in various post-fire seedbeds (Whelan 1995; Smith et al.1997).

Reproductive behavior has been at the core of more general grouping schemes such as those based on gap-size preferences (Whitmore 1975; Denslow 1980; Swaine & Whitmore 1988). With these, tree species fall into two categories: those that establish and grow in large gaps (intolerant, or light-demanding 'pioneers') and those that are more shade adapted and can regenerate in small canopy openings or in the shade of canopy trees ('non-pioneers'). Features used to separate pioneers from non-pioneers include seed size, dispersal mechanisms, and growth rates (Whitmore 1989).

Although each of these grouping schemes can help predict basic regeneration outcomes, they do not fully account for the complexity of the reproductive process. Often, group characteristics are defined by the attributes of only one or several typical species, so it can be difficult to assign other species to their most representative group. Also, it has been commonly assumed that each species has a preferred or adaptive mode of reproduction, but many species have a suite of contrasting regenerative traits (Houle 1991).

To predict forest compositional change at the landscape level, we need to characterize and generalize regeneration processes for large and diverse groups of tree species. Moreover, many elements of the 'regeneration niche' (sensu Grubb 1977) such as seed availability (seed rain or seed bank), seedling ecology (timing of germination, microsite preferences), and seedling longevity (potential to survive until the next disturbance) should be considered because the importance of any one reproductive feature may change under different disturbance scenarios (Whitmore 1988). There have been few attempts to categorize a diverse set of species based on a broad array of features (e.g., Loehle 1988; Brzeziecki & Kienast 1994). Our objectives were to use a comprehensive set of reproductive attributes to define groups of similar species and identify which traits differ among these groups. We examined species common throughout the central hardwood region of the eastern United States (representing 32 genera), and used multivariate classification techniques to provide an objective and broadly based

view of reproductive similarities. From these patterns of similarities and the traits that define them, we could then integrate the mechanistic processes of regeneration with the observed pattern in the central hardwood forest.

Methods

Regeneration attributes

To compare reproductive traits, we defined a set of attributes that reflects the main components of regeneration: seed production, seed dispersal, germination, and establishment. Our attribute set was derived from the silvical characteristics of tree species in the eastern United States, but it could be easily adapted to use in other forest types.

Using information from the forest biology and ecological literature, we evaluated each attribute for 62 common tree species in the central hardwood region of the eastern deciduous forest (Clark & Hutchinson 1989). Major sources included Lamb (1915), van Dersal (1938), USDA Forest Service (1948), Fowells (1965), Schopmeyer (1974), and Burns & Honkala (1990 a, b). Nomenclature follows Burns & Honkala (1990a, b).

Evaluating reproductive attributes for a diverse set of tree species presented several problems; many attributes are qualitative (e.g., seedbed requirements, seedling shade tolerance, or seedling root form) while others represent quantitative variables for a wide geographic range (e.g., dates of flowering and seed dispersal). Given the diversity in the species evaluated, and because we gathered information from a variety of published sources, we developed a categorical assessment scheme (Table 1). When possible, we compared information from several sources and each species was represented by its central tendencies. Attribute values that might occur only at the extremes of a species' range or in atypical habitats were not used. Seed type, dispersal mechanism and average dispersal distance were combined to reflect dispersal potential. Dispersal distances associated with rare or occasional events were not included. Some species considered shade intolerant or intermediate at later stages of development are more shade tolerant as seedlings. If this disparity occurred, we used seedling shade tolerance values. Basal sprouting and root suckering were poorly documented for some species, so we only separated species by whether these forms of reproduction were common or uncommon. If a species rarely sprouts or suckers, or does so only under unusual circumstances, or not at all, vegetative reproduction was considered 'uncommon'. The categorical data are shown in Appendix 1.

Data analysis

Because we assigned categorical values to the attributes of each species, the data were nominal, not ordinal, and did not conform to the normal distribution. Consequently, our data analysis was constrained to statistical methodologies appropriate for nominal data. We used a data reduction approach, applying cluster analysis to classify natural groupings and correspondence analysis to to identify key attributes that drove the groupings (Jobson 1992). (The multiple correspondence analysis also provided useful information in determining groups.) Similar approaches, applying cluster analysis in conjunction with principal components or correspondence analysis, have been used to analyze species traits in studies of North American pines (McCune 1988), Mediterranean shrubs (Aronne & Wilcock 1994), prairie vegetation (Kindscher & Wells 1995), and riverine macrophytes (Henry et al. 1996).

Cluster analysis is a common multivariate approach used to detect grouping patterns among objects (Sneath & Sokal 1973; Romesburg 1984). In our case, the objects are tree species and the variables are the regeneration attributes; our objective was to determine similarities among the species. Jaccard's similarity coefficient is the appropriate measure to calculate the distance matrix for species from nominal data (Sneath & Sokal 1973). We developed a procedure in the S language using SPLUS (Statistical Sciences 1993) to calculate Jaccard's coefficient. We then performed hierarchical clustering using complete linkage with the HCLUST procedure in SPLUS (Statistical Sciences 1993).

We used homogeneity analysis (or HOMALS, for Homogeneity Analysis by Means of Alternating Least Squares, sometimes called multiple correspondence analysis) to analyze our nominal data. Homogeneity analysis is useful for interpreting the underlying structure of nominal data, and has been used to analyze species traits (Van der Burg 1985). It is a weighted principal components analysis of a contingency table, decomposing the table into row and column coordinates that can be displayed graphically (SAS Institute, Inc. 1989). Homogeneity analysis optimizes the separation of objects as far as possible from each

Table 1. Categorical scheme used for regeneration attributes.

Code	Attribute	Category		
FLWR	Flowering date:	(1) early spring (March 1–April 15)	(2) late spring (April 15–May 31)	(3) summer (June–August)
FRST	Flowers susceptible to frost	(1) yes	(2) no	
POLL	Pollination agent(s):	(1) wind only	(2) insects, some wind possible	(3) insects only
SAGE	Age when first seed is produced:	(1) < 15 years	(2) 15–30 years	(3) 30–50+ years
SPRO	Optimum seed production begins:	(1) before age 50	(2) 50–75 years	(3) after age 75
SFREQ	Frequency of good seed crops:	(1) annually	(2) every 2 years	(3) 3–4 years
SFALL	Seedfall begins:	(1) spring-summer	(2) early fall (Sept.–Oct.)	(3) late fall-winter (Nov.–Feb.)
SBANK	Seed banking:	(1) transient, < 1 month	(2) transient, up to 1 year	(3) short-term persistent, 2–10 years
		(4) serotinous/semi serotinous cones	(5) long-term persistent, 10+ years	
SDISP	Seed type/dispersal mechanism:	(1) nuts & pods/gravity & animals to 50 m	(2) small nonwinged/wind & gravity to 50 m	(3) berries & drupes/birds & gravity to 100 m
		(4) winged seeds I/wind to 100 m max.	(5) winged seeds II/wind, 100 to 200 m	(6) plumed seeds/wind, >200 m
STRAT	Stratification required:	(1) yes	(2) no	
GTIME	Season of germination:	(1) early spring – late summer	(2) summer – fall	
GLITE	Light:	(1) open conditions required (high light levels)	(2) can germinate under canopy (shaded)	
GBED	Seedbed requirements:	(1) bare mineral soil	(2) litter/humus	(3) variable
GMOIS	Seedbed moisture:	(1) wet required	(2) moist required	(3) moisture neutral
GTEMP	Seedbed temperature:	(1) cool/cold seedbed required	(2) temperature neutral	(3) warm seedbed required
TOL	Shade tolerance at seedling stage:	(1) very intolerant	(2) intolerant	(3) intermediate (mid-tolerant)
		(4) tolerant	(5) very tolerant	
ROOT	Form of seedling root system:	(1) taproot	(2) variable	(3) shallow-spreading
VSPR	Seedling sprouts[a] or stump sprouts:	(1) common	(2) uncommon	
RSCKR	Root suckers:	(1) common	(2) uncommon	
CORIG	New cohort is:	(1) from seed origin	(2) mixed origin (seeds and sprouts)	(3) sprout dependent

[a]Dieback and resprouting at seedling root collar.

other using the same optimization technique used for nonlinear principal components analysis and nonlinear canonical correlation (Gifi 1991). The resulting Euclidian distances approximate chi-square distances (Van der Burg 1985). We performed the homogeneity analysis using PROC CORRESP in SAS (SAS Institute, Inc. 1989).

The eigenvalues resulting from homogeneity analysis measure how much of the categorical information is accounted for by each dimension. (There are potentially as many dimensions as there are variables, but most variation is represented in low-dimensional space.) The proportion of variance accorded to each attribute in each dimension is evaluated as the discrimination measure. These measures are useful in interpreting the contribution of each attribute to the distance between species in each dimension. This information indicates which attributes are shared by many objects and which ones are not (Van der Burg 1985). Then, the classification of groups of objects (in our case, species) follows from interpreting the configuration of the objects in space. The distances between

species in multivariate space are represented by object scores. By viewing plots of these scores we interpreted species relationships. In general, in any dimension, objects (species) that are close to each other are similar, while distant objects are dissimilar. Further, attributes with high discrimination measures contribute most to the distances between objects in that dimension. Where many objects were clumped together and groups were difficult to discern, we examined object scores in the third and fourth dimensions, where distances between species were driven by attributes different from those in the first two dimensions.

Of the 20 variables in the initial data set, susceptibility to frost damage, seedbed moisture, seedbed temperature, and root suckering had low discrimination measures in all four dimensions. Since these variables did not contribute to the objective of determining groups with related regeneration attributes, they were removed from the data set and the cluster and homogeneity analyses were repeated.

Results

The central hardwood region includes a wide diversity of environments ranging from wet to dry and nutrient poor to nutrient rich. Most tree species are angiosperms; there are only six common conifer species. The species we evaluated occur in several forest types (Eyre 1980) and they represent a variety of life-history strategies.

Regeneration attributes of central hardwood species

Flowering and seed production. Most trees in the central hardwood region flower from mid-April to late May. Nine species flower in early spring (March and into the first week of April) and eight species flower during the summer. Most species (75%) are exclusively wind pollinated and seed production is well established by age 30 (84%). Early seedbearing also is common; 21 species can produce seed before age 15. However, such early maturity usually occurs on vigorous sprouts or open-grown trees. Frequency of good or bumper seed crops is a more variable attribute, but most mature trees produce at least some seed every year. Eighteen species have intervals of 5 or more years between good seed crops, but six of these species have prolonged seed viability. Seeds of many species (35%) remain viable for more than 1 year, however the length and type of dormancy varies. Some exhibit physical dormancy because of impermeable seed coats (e.g., *Gleditsia* and *Robinia*). Others have various degrees of physiological or morphological dormancy that must be broken by fluctuations in light, moisture or temperature, or additional embryo growth (Hills & Morris 1992; Baskin & Baskin 1998). We did not distinguish between these various types and levels of dormancy because dormancy characteristics may vary within the species' geographic range (Krugman et al. 1974; Peroni 1995) and among seedbed environments (e.g., in clearcuts vs. under partial canopies) (Marquis 1975).

Dispersal and germination. Some species disperse seeds in May or June, but for most (77%) dissemination occurs in late summer or fall. Spring-dispersed seeds typically germinate shortly after dispersal in the moist conditions of late spring and early summer. Most seed dispersed at the end of the growing season requires some period of cold stratification before germination can occur. Acorns of white oaks (subgenus *Lepidobalanus*) are an exception; they germinate in the fall soon after dispersal. Their epicotyls remain dormant (Farmer 1977), but a vigorous root system develops before winter (Rogers 1990).

Dispersal distance is inversely related to seed size, though some small non-winged seeds (*Oxydendrum arboreum* and *Tilia* spp.) travel only short distances. Most large seeds are dispersed by gravity but some may be transported by secondary dispersal agents (birds and rodents), which can significantly increase dispersal distances (Darley-Hill & Johnson 1981, Tamura & Shibasaki 1996).

Nearly every species requires a moist seedbed and moderate temperatures (20–30 °C) for germination (Krugman et al. 1974). Some exceptions include chestnut oak (*Quercus prinus*), which can germinate on droughty soils, and sugar maple (*Acer saccharum*), which germinates in cold seedbeds (< 10 °C) during early spring.

Establishment. Many species in the central hardwood forest are more tolerant of shaded conditions as seedlings than at later stages of development (Cope 1948; Trimble 1975; Dean et al. 1982). In our set, 17 species need full sun or open conditions to germinate. The others can germinate under canopy cover and persist for at least several years.

Root systems of most species accommodate a variety of litter and soil conditions. Only nine species are limited by shallow roots. One-third of the species have distinct seedling taproots that may enable ger-

minants to penetrate a thick humus layer. Seedlings of some oaks (*Quercus* spp.) quickly develop deep taproots allowing them to withstand seasonal moisture deficits and survive on dry or exposed sites (Pallardy & Rhoads 1993).

Vegetative reproduction. For nearly all hardwoods and several conifer species, basal sprouting is a common mode of reproduction. Several species sprout so prolifically that root or basal sprouts are the primary means of regeneration. The shallow root systems of *Liquidambar styraciflua*, *Sassafras albidum*, *Salix nigra*, *Robinia pseudoacacia*, *Populus grandidentata*, and *Populus tremuloides* develop dense thickets of new sprouts when parent stems are damaged (Burns & Honkala 1990b). *Tilia* spp. also sprout prolifically from cut stems and numerous sprouts may develop over a wide range of diameters (Perala 1974). For most species, however, small stems (usually those less than 30 cm dbh) have the best sprouting potential (Lamson 1988).

Clustering and homogeneity analysis

The cluster analysis dendrogram shows 10 distinct groups at the 0.25 similarity measure (Figure 1). High similarity occurred among red oaks and hickories, and among white oaks (Cluster 8). The largest group (Cluster 5), contained mainly tolerant and very tolerant mesophytic species. Common pioneers were grouped in Clusters 9 and 10, and Cluster 1 contained species that typically regenerate in large canopy gaps. In general, species in the smaller clusters shared traits that were less common among the central hardwoods. For example, Cluster 2 species have fleshy seeds that are dispersed in spring or summer. Cluster 3 species rely on insects for pollination and have large, gravity-dispersed seed. Cluster 4 species are shade-intolerant conifers that regenerate primarily from seed. Species in Cluster 6 have small, gravity-dispersed seed.

Homogeneity analysis object scores (first and second dimensions) (Figure 2) showed associations similar to those produced by the cluster analysis. Oaks and hickories formed two distinct groups in object space, occupying the upper left quadrant. Species that formed Cluster 9 in the dendrogram also were discrete in object space, plotting in the upper right. Most shade-tolerant species plotted below the origin and shade-intolerant species plotted to the right of the origin. Still, many species object scores discriminated poorly in the first and second dimension, so we also examined object scores in the third and fourth dimension. In these dimensions, insect-pollinated species (*Robinia pseudoacacia*, *Cercis canadensis*, and *Gleditsia triacanthos*) and the buckeyes (*Aesculus* spp.) were easy to discern along with the summer flowering species (*Tilia* spp., *Oxydendrum arboreum*, *Nyssa sylvatica*, *Magnolia acuminata*, and *Liriodendron tulipifera*).

Attributes that defined the groupings

The first two dimensions of the homogeneity analysis together account for 25.8% of the variation in regeneration attributes. Discrimination measures, or weightings, for the individual variables are plotted in Figure 3. Seedling shade tolerance (TOL), mode of seed dispersal (SDISP), length of seed viability (SBANK), seedbed (GBED), and season of seed dispersal (SFALL) discriminate in both the first and second dimensions. Variables that separated species in the second dimension included stratification (STRAT), season of germination (GTIME), and age of optimum seeding (SPRO).

Shade tolerance. Differences in shade tolerance define several species groups. In Figure 1, Clusters 9 and 10 contained spring-dispersed species that share many attributes, e.g., short-lived seed, excellent dispersal potential, and a preference for mineral seedbeds, but Cluster 10 species have much greater understory tolerance than those in Cluster 9. Conspicuous groups of mid-tolerant species were identified with both analyses as well. These include the oaks and hickories, which plotted together in the upper-left quadrant (Figure 2) and also formed a separate branch in the dendrogram (Figure 1). Most other intermediates were found in Cluster 1, but their object scores show no clear association.

Dispersal. This attribute reflected both seed type and dispersal distance. Traditional pioneers (e.g., *Salix nigra* and *Populus* spp. with small, widely-dispersed seeds) and the oaks and hickories (large seeds, limited primary dispersal) were separated in object space (Figure 2). Other large-seeded, gravity-dispersed species (*Aesculus* spp., *Cercis canadensis*, *Gleditsia triacanthos*, and *Juglans* spp.) were not as well segregated. Species whose seeds (fleshy fruits) are dispersed by birds occurred in three branches of the dendrogram; their object scores discriminated best in the second dimension, plotting below the origin.

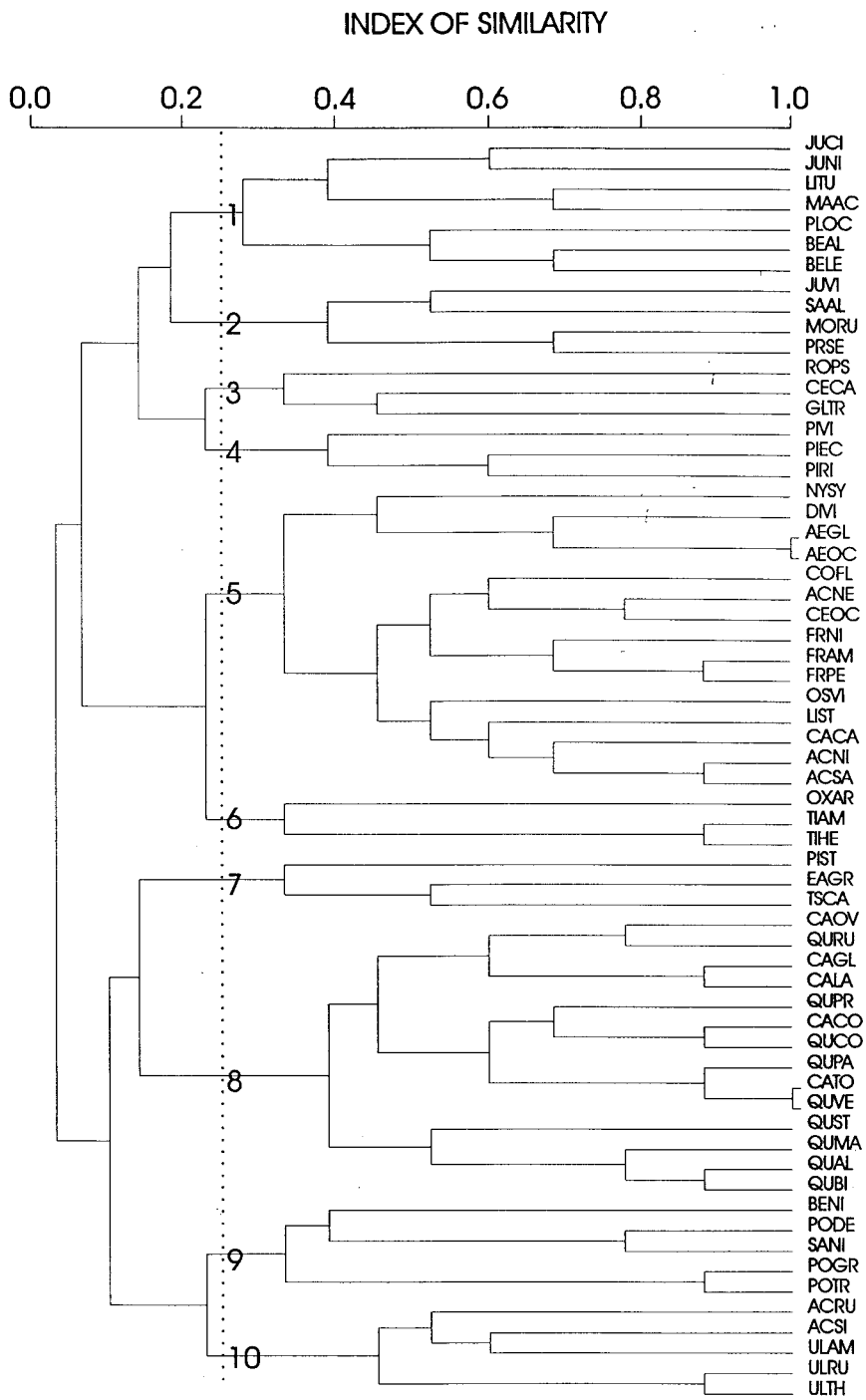

Figure 1. Dendrogram of 62 central hardwood species as a function of regeneration attributes. See Appendix 2 for species abbreviations.

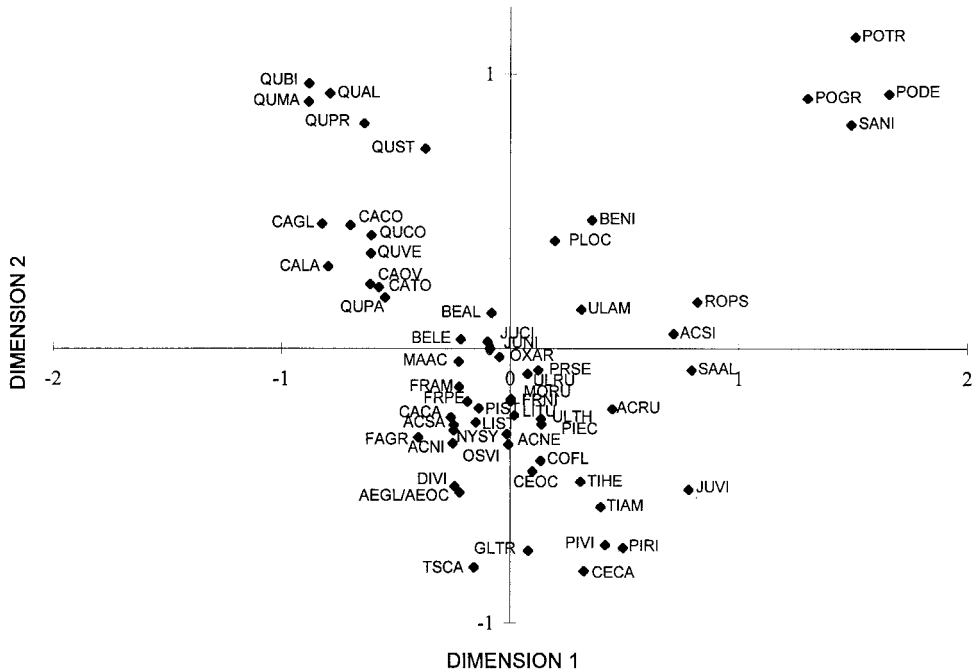

Figure 2. Homogeneity analysis object scores (first and second dimensions) of 62 central hardwood species. See Appendix 2 for species abbreviations.

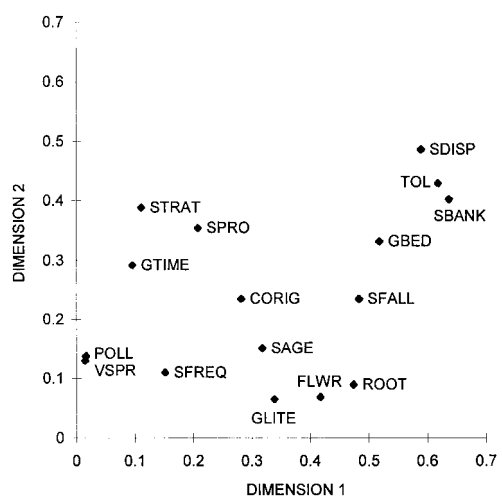

Figure 3. Homogeneity analysis discrimination measures (first and second dimensions) of individual regeneration attributes. Attribute codes are given in Table 1.

Seed banking. Seed banking was an attribute of species in Clusters 1, 2, and 3, and several seed banking species formed a branch of Cluster 5. In the object score plots, this variable was perhaps the most important in distinguishing groups of species that lack seed banking as a reproductive mode. Species whose seeds remain viable only for several weeks (e.g., *Populus* spp. and *Salix nigra*), formed a discrete group in object space (Figure 2, upper right). Others with limited seed viability (generally a year or less) plotted to the left of the origin. Object scores of most seed banking species occurred throughout the lower right quadrant.

Seedbed. In the dendrogram, species that require mineral-soil seedbeds occurred in two groups (Clusters 4 and 9); the litter-dependent oaks and hickories formed Cluster 8. These groups also were well separated in the first dimension of object space (Figure 2). For the most part, central hardwood species can germinate in a variety of seedbeds so long as soil moisture is sufficient; therefore, this variable was not as important in distinguishing groups in this data set as it might be in other forest types.

Season of dispersal. Dispersal season was another important attribute separating species in the first dimension of object space. Most central hardwood species disperse seeds toward the end of the growing season or in the autumn and winter months. All spring-dispersed species plotted to the right of the origin; most were included in Cluster 9 or 10.

Stratification. A period of cold stratification is required before the majority of central hardwood species

can germinate. Among the fall-dispersed species, only the white oaks germinate before overwintering; they plot as a distinct group above the red oaks and hickories in the second dimension (Figure 2). Spring-dispersed species also germinate without stratification. Only those included in Cluster 9 of the dendrogram are clearly separated in the second dimension of object space. The more shade-tolerant, spring-dispersed species from Cluster 10 plot nearer the origin.

Season of germination. This variable also contributed to the separation of the white oaks from the red oaks and hickories. The white oaks are the only fall-germinating species among the central hardwoods.

Age of optimum seeding. Species that reach their optimum seed-producing years later in their life include the oaks and hickories as well as the aspens (*Populus* spp.), *Betula alleghaniensis*, *Magnolia acuminata*, *Oxydendrum arboreum*, *Platanus occidentalis*, and *Pinus strobus*. Nearly all of these species plot above the origin in the second dimension (Figure 2).

Seeding frequency. One might have expected seed frequency (SFREQ) to be more important in grouping species as this reproductive feature is commonly used as a defining attribute of pioneer and non-pioneer species. Fast-growing, shade-intolerant species are more likely to be regular and abundant seeders, whereas species that are slow-growing and shade-tolerant are more likely to produce seed infrequently (Barnes et al. 1998). These tendencies were not apparent among the central hardwoods. Frequency of good seed crops varied greatly within species groups. Several oaks and hickories have regular seed crops and some birches and aspens seed at infrequent intervals. Other factors not addressed in our attribute set may control this aspect of reproduction (see Farmer 1997).

Although a small set of variables was important in determining species groups, other attributes we examined may be critical factors in successful germination and establishment. For example, sprouting potential (VSPR) and age at which a species begins to produce seed (SAGE) may determine which species are available to reclaim a site following a given disturbance. Further, many variables in the data set may be useful as filters to determine regeneration potential for specific site conditions or climate scenarios. Juvenile root form, seedbed moisture, or temperature requirements may preclude successful establishment of certain species on moisture- or nutrient-limited sites. Flowering dates, susceptibility to frost, or cold-stratification requirements could limit or direct patterns of species migration if the climate became warmer and rainfall distribution changed.

Species groups and reproductive similarities From the relationships shown in the cluster analysis we could distinguish nine species groups that had definite similarities. Several clusters of the dendrogram (Figure 1) were subdivided, and species were regrouped based on the object score plots and a review of their individual attributes. Although strictly speaking, this reduced the objectivity of the results, clusters are generally viewed as heuristic, not rigid classifications (McCune 1988).

The cluster analysis placed *Pinus strobus*, a mid-tolerant conifer, with extremely shade-tolerant *Fagus grandifolia* and *Tsuga canadensis* in Cluster 7. *Liquidambar styraciflua*, a fast-growing, shade intolerant, was clustered with very tolerant species in Cluster 5. We added both species to the group of shade intolerants and intermediates found in Cluster 1. Cluster 2 contained species that have fleshy fruits which are dispersed during the spring or summer. This cluster was split, and *Morus rubra* and *Prunus serotina*, whose seeds remain viable for several years, were placed with other seed-banking species from Cluster 5 (*Cornus florida*, *Acer negundo*, *Celtis occidentalis*, and the ashes (*Fraxinus* spp.). The shade intolerants, *Juniperus virginiana* and *Sassafras albidum*, were placed in two different groups. *Juniperus virginiana* was grouped with the pines (Cluster 4) because it has similar pioneer characteristics (e.g., it readily colonizes open sites and seedlings are well-adapted to dry or nutrient-poor sites). Furthermore, even though most dispersal occurs when the berrylike cones open in early spring (February and March) the seeds mature in late summer or fall and can be dispersed by birds and animals throughout the autumn and winter. Thus, like the pines, *Juniperus virginiana* has a prolonged period of dissemination. *Sassafras albidum*, an old-field pioneer and prolific sprouter, was regrouped with other pioneers that readily sprout under a variety of conditions (Cluster 3). *Nyssa sylvatica*, *Diospyros virginiana* and *Aesculus* spp. formed a separate branch in Cluster 5; they were combined with other insect-pollinated species (Cluster 3). The remaining shade-tolerant species from Clusters 5, 6 and 7 were combined to form a group of understory tolerants

having a wide range of dispersal modes and seedbed preferences.

Group 1 (Betula alleghaniensis, Betula lenta, Juglans cinerea, Juglans nigra, Liquidambar styraciflua, Liriodendron tulipifera, Pinus strobus, Magnolia acuminata, Platanus occidentalis)
Species in this group are relatively shade intolerant and long-lived. Most new cohorts originate from both seeds and seedling or stump sprouts. Seed production begins before age 30 and good seed crops are infrequent (every 3–5 years). Seed is widely dispersed, except for the large seeds of *Juglans* spp. All but *Liquidambar styraciflua*, *Pinus strobus*, and *Platanus occidentalis* have seeds that remain viable in the seed bank. Each species can germinate on a variety of seedbeds although mineral soil favors germination of *Betula alleghaniensis*, *Liriodendron tulipifera*, and *Platanus occidentalis*. *Juglans* spp. and *Liquidambar styraciflua* seedlings are intolerant of shade, so they need large openings for successful establishment. Most others require canopy openings for germination and establishment as well, though they are somewhat tolerant of shading.

The object score for sycamore (*Platanus occidentalis*) is an outlier (Figure 2), reflecting shade intolerance and long seed-dispersal potential. Sycamore shares many traits with spring-dispersed pioneers (see Group 9), however its seeds mature in the autumn, overwinter in persistent fruiting-heads, and then are dispersed in the spring. As a result, sycamore was clustered with *Betula* spp., which have similar 'pioneer' attributes but whose seeds require stratification.

Group 2 (Juniperus virginiana, Pinus echinata, Pinus rigida, Pinus virginiana) These species, all conifers, grow on dry sites and are shade intolerant. New cohorts arise almost entirely from seed. They mature much earlier than those in Group 1 but have good seed years only every 3–5 years. Although pines have wind-dispersed seed, dispersal is comparatively local. Birds disperse *J. virginiana* seeds so dissemination may occur over a wide area. For all species in this group, germination is best in disturbed seedbeds with exposed mineral soil. Some seed remains dormant and may germinate the second or third year after dispersal. Vegetative reproduction is common only in a few eastern conifer species; small stems of *P. rigida* and *P. echinata* can produce vigorous sprouts when damaged by fire (Little & Somes 1956) and *P. virginiana* may resprout when young stems are cut (Stone & Stone 1954). Seedlings of *J. virginiana*, *P. echinata*, and *P. virginiana* may survive for several years under a sparse overstory even though these species are viewed as shade intolerant. *P. virginiana* lacks such understory tolerance, and establishes only in open, highly disturbed conditions that follow fire or logging (Carter & Snow 1990).

Group 3 (Acer negundo, Celtis occidentalis, Cornus florida, Fraxinus americana, Fraxinus nigra, Fraxinus pennsylvanica, Morus rubra, Prunus serotina)
Most species in this group are fast-growing, small to medium-sized trees with enough shade tolerance to persist in lower canopy positions. Only *Fraxinus americana* and *Prunus serotina* are common in the upper canopy. New cohorts originate from both seeds and seedling or stump sprouts. All species in this group mature early and produce abundant seed crops; many maintain seed banks. The ashes (*Fraxinus* spp.) have the longest interval between good seed years (5 or more years), but their seeds remain viable for as many as 8 years. Seeds of the other species remain viable for 3–4 years, however, little is known about the longevity of *Acer negundo* and *Morus rubra* seed. Wide dispersal usually is assured. Birds disperse seeds of *Prunus serotina*, *Celtis occidentalis*, *Cornus florida*, and *Morus rubra*; the small samaras of *Fraxinus* spp. and *Acer negundo* can be blown 100 m or more from parent trees. Seedlings establish in the understory on a variety of seedbeds.

Group 4 (Acer nigrum, Acer saccharum, Carpinus caroliniana, Fagus grandifolia, Ostrya virginiana, Oxydendrum arboreum, Tilia americana, Tilia heterophylla, Tsuga canadensis)
Species in this group are extremely shade tolerant, slow-growing and long-lived. New cohorts originate from both seeds and seedling or stump sprouts. Exceptions include *Tsuga canadensis* which originates only from seed, and *Tilia*, which usually originates from sprouts. Seed production becomes well established at 15–30 years of age, though optimum seeding occurs later in *Fagus grandifolia* and *Tsuga canadensis* (usually after age 75). *Acer nigrum*, *Acer saccharum*, *Carpinus caroliniana*, *Fagus grandifolia*, and *Tsuga canadensis* have good seed years every 3–5 years; *Ostrya virginiana*, *Oxydendrum arboreum* and *Tilia* spp. are regular and prolific seeders. *Tilia* spp. also maintain a large seed bank (Houle 1991) and *Ostrya virginiana* seed may remain viable for several years. Most of the other shade-tolerant, seed-banking species

are in Group 3. Maple and hemlock seeds are disseminated by wind and have the greatest dispersal potential in this group. *Carpinus* seed is attractive to birds and thus may be broadly dispersed as well. The other species have small non-winged seeds and more limited dispersal. Seedlings establish on a variety of seedbeds and because of their extreme shade tolerance form a persistent seedling or sapling bank.

Group 5 (Aesculus glabra, Aesculus octandra, Cercis canadensis, Diospyros virginiana, Gleditsia triacanthos, Nyssa sylvatica var. sylvatica, Robinia pseudoacacia, Sassafras albidum)

Both shade tolerant and intolerant species occur in this group. It is a mixture of late-spring and summer flowering species that are insect-pollinated (an attribute that defined this group in the third dimension of object space). Most species are fast-growing, short-lived, small to medium-sized trees, but *Aesculus* spp. and *Gleditsia triacanthos* are moderately long-lived. All species can sprout from seedlings or from stumps. *Aesculus* spp. and *Cercis canadensis* produce new cohorts mostly from seed, whereas *Robinia pseudoacacia* and *Sassafras albidum* usually originate from sprouts. All species mature at an early age (before age 15) and produce good seed crops nearly every year. *Nyssa sylvatica* matures somewhat later but is an abundant seeder. Seed pods of *Cercis canadensis* and *Robinia pseudoacacia* and the large capsules of *Aesculus* spp. open when ripe so that seeds fall near the parent tree. The indehiscent seed pods of *Gleditsia triacanthos* also have limited dispersal. *Diospyros virginiana*, *Nyssa sylvatica*, and *Sassafras albidum* have fleshy fruits that are dispersed by birds. For most species, germination can occur in the understory and on a variety of seedbeds. Only *Cercis canadensis* and *Robinia pseudoacacia* need mineral soil to germinate; both *Sassafras albidum* and *Robinia pseudoacacia* require open conditions for establishment.

Group 6 (Carya cordiformis, Carya glabra, Carya laciniosa, Carya ovata, Carya tomentosa, Quercus coccinea, Quercus palustris, Quercus rubra, Quercus velutina)

The oaks and hickories were distinct in both the cluster analysis (Figure 1) and the plot of species object scores (Figure 2). These species share many regeneration attributes and differ primarily in age of optimum seed production and frequency of good seed crops. Because the white oaks (subgenus *Lepidobalanus*) germinate in the fall without stratification, we considered them as a separate group (see Group 7). For the red oaks (subgenus *Erythrobalanus*) and hickories, seed production is well established by age 50; *Carya glabra*, *Carya laciniosa*, and *Quercus palustris* produce good seed crops nearly every year. Good seed years are somewhat less frequent for the other species; only *Q. coccinea* has sporadic and unpredictable seeding (Burns et al. 1954). Mature seeds drop in the autumn and require cold stratification before germination the following spring. Seed predation is high and nuts and acorns rarely survive in the seed bank for more than 1 year (Nixon et al. 1980; Beck 1993; McCarthy 1994). If their seed is sound, both oaks and hickories germinate readily in the understory. Litter cover favors oak establishment because it helps preserve acorn viability and provides protection and mechanical support (Korstian 1927). Litter and duff seedbeds also are beneficial for hickory seed germination (Minckler & Jensen 1959). New seedlings have only intermediate shade tolerance so that their shoots cannot survive in the understory for more than several years. Subsequent sprouting from well-developed root systems allows oaks and hickories to persist in the understory (Liming & Johnson 1944; Sander & Clark 1971).

Group 7 (Quercus alba, Quercus bicolor, Quercus macrocarpa, Quercus prinus, Quercus stellata)

This groups differs from Group 6 in that acorns of white oaks do not require stratification, and germination occurs shortly after dispersal (Schopmeyer 1974). Although species in this group can produce seeds at an early age (20–25 years), optimum seedbearing does not begin until trees are 50–75 years old. Annual seed crops are almost entirely consumed by animals and insects so that regeneration depends on bumper seed crops every 4–5 years (Beck 1993). Like the red oaks, seedlings develop a large root system that helps them survive in the understory. These oaks also have intermediate shade tolerance, so long-term survival in the understory depends upon their ability to resprout.

Group 8 (Acer rubrum, Acer saccharinum, Ulmus americana, Ulmus rubra, Ulmus thomasii)

New cohorts of all but one species (*Ulmus thomasii*) in this group originate from both seeds and seedling and stump sprouts. The group contains shade-tolerant species that disperse their seeds in spring and early summer. Each species starts producing seed early (age 15–30) but the elms do not seed abundantly until after age 40. Good seed crops are produced nearly every year; wind is the primary dispersal agent. Seeds gen-

erally fall within 100 m of a parent tree though water also may be an important dispersal agent. Seeds can be carried several kilometers during spring floods. Although germination is favored on moist mineral soil, other seedbeds (e.g., moist hardwood litter or moss) are suitable. Canopy cover does not hinder germination, but seedling survival ultimately depends on the species composition of the overstory.

Group 9 (Betula nigra, Populus deltoides var. deltoides, Populus grandidentata, Populus tremuloides, Salix nigra)

Root suckers are the primary regeneration mechanism used to replace *Populus tremuloides* and *P. grandidentata*, and new cohorts of the other species originate from both seeds and seedling or stump sprouts. Like Group 8, these species also disperse seed during spring, but they are shade intolerant and seeds are more widely dispersed. Like Group 8, these trees mature before age 30 and seed crops are both frequent and abundant. Seeds do not require cold stratification and germination occurs soon after dispersal. *Populus* spp. and *Salix nigra* have plumed seeds that can travel long distances by wind or water. Moist/wet seedbeds are essential to maintain seed viability and support the rapid growth of new germinants. Seed viability is short, about 2–4 weeks. Disturbed, mesic uplands or scoured stream banks provide the open conditions and mineral-soil seedbeds that are essential for successful establishment

Discussion

We developed a set of 20 regeneration attributes that reflected seed production, seed dispersal, germination, and establishment. By surveying available literature we determined a categorical value for each attribute, for each of 62 tree species in the Central Hardwoods forest type. Because we parameterized the regeneration attributes for each species using a review of the literature, of necessity we had to choose the central tendencies of each species for each regeneration attribute. Readers with some familiarity with these species may have experience of behaviors of particular species in specific instances that are different from those given in Appendix 1. From this data set, we applied multivariate statistical approaches to classify groups of species with similar sets of regeneration attributes and determined which were the most important variables in driving the grouping, and finally, described the species groups.

Species groups as regeneration guilds

Our species groups are the result of a detailed assessment of reproductive attributes and demonstrate associations among central hardwood species. These groups can be positioned along the continuum set out in previous classification schemes (Bormann & Likens 1979; Swaine & Whitmore 1988; Barnes et al. 1998), but they clearly show that many tree species possess attributes associated with both exploitative (or pioneer) and conservative (or non-pioneer) strategies. Further, many central hardwood species can use a variety of regeneration modes to establish new cohorts. The most flexible species can colonize new sites, maintain seed in a seed bank, sprout from existing stems, stumps, or surface roots, and persist under a canopy as a seedling bank or sapling bank.

We view these groups as regeneration 'guilds' because species within a group share principal reproductive features and have similar levels of specialization that influence regeneration potential. The nine groups we identified can be arranged into three broad guild types: pioneer, opportunistic, and persistent. Each species and its regeneration guild is listed in Appendix 2.

Pioneer guilds

Pioneer guilds contain species that regenerate where disturbances are frequent or severe enough to create large openings and kill existing vegetation. Seasonally flooded areas, abandoned fields, or areas subjected to high-intensity fires are the most likely to be colonized by pioneer guilds. Seeds come from outside the disturbed site or are stored on site as buried seed or in an aboveground seed bank (serotinous cones). We identified three pioneer regeneration guilds: short-lived or fugitive pioneers that colonize sites rapidly and are too shade intolerant to replace themselves; persistent pioneers that colonize frequently disturbed sites more slowly and are shade tolerant; and stress-tolerant pioneers that survive on dry sites.

Spring-dispersed, moist-site intolerants (Group 9). This guild includes short-lived, shade-intolerant species that require moist or wet seedbeds to maintain seed viability and support germination. Species in this guild most closely fit the traditional definition of pioneers (Swaine & Whitmore 1988, Barnes et al. 1998). They grow rapidly, mature early, and seed crops are copious and widely dispersed. Since full sunlight and mineral-soil seedbeds are essential for successful

germination and establishment, they rarely regenerate under existing stands.

Spring-dispersed, moist-site tolerants (Group 8). This guild contains species that are more shade tolerant than those in the other two pioneer guilds. These species are most common on moist or wet sites, but they also occupy mesic uplands. Although they have many pioneer characteristics such as fast growth and wide seed dispersal, they are neither as short-lived nor as intolerant as those in Group 9. Abundant seed crops, longer seed viability, and less restrictive germination requirements allow them to establish in a variety of situations so long as there is sufficient light to maintain growth. Often these more shade-tolerant pioneers persist for many years beneath the light overstories of less tolerant species (e.g., spring-dispersed, moist site intolerants) and eventually replace them.

Dry-site intolerants (Group 2). This guild includes highly competitive, shade-intolerant conifers that colonize dry uplands and abandoned fields. Species begin seeding early, but unlike trees in the other pioneer guilds, seed crops are infrequent and dispersal is limited to nearby areas. Although these species may establish and survive under pine or hardwood canopies on dry or nutrient-poor sites, regeneration is most favored where disturbances create large openings.

Opportunistic guilds

Opportunistic guilds contain species that use several reproductive mechanisms and thus can regenerate following a range of disturbance types. Frequent seeding or extended seed viability ensure that seeds are continually available; sprouts from damaged individuals also may provide an additional source of propagules. Shade-tolerant opportunists maintain seedling or sprout banks that readily respond to canopy openings. Three of our species groups are opportunistic:

Long-lived intolerants and intermediates (Group 1). This guild includes some of the fastest growing species in the central hardwood forest. These species are common on mesic sites and are long-lived, highly competitive overstory dominants. Large canopy openings and disturbed seedbeds favor germination; all but *Pinus strobus* are vigorous sprouters. Reproduction of *Platanus occidentalis*, *Juglans* spp., and *Betula* spp. depends on continued high light levels for successful recruitment into the canopy. Seedlings and sprouts of the other species are more tolerant of overhead shade, and new cohorts may survive for several years in the understory.

Fast-growing understory tolerant (Group 3). This guild contains shade-tolerant opportunistic species that are relatively fast-growing and long-lived. Most species are small to medium-sized trees. Abundant seed is available for germination because they produce good seed crops frequently and seeds remain viable for several years. Understory light levels are sufficient for germination and reproduction quickly reaches sapling size. Some species may form a subcanopy layer that persists or gradually dies out depending on overstory composition. Others become less shade tolerant with age; their saplings may persist for several years in the shaded understory, but eventually they must be released by canopy openings to survive.

Dispersal-limited (large-seeded or sprout dependent) (Group 5). These species are considered opportunistic because they mature early, produce seeds frequently and germinate on a wide range of seedbeds. We note however that some species fit the profiles of other guild types, and this guild does contain species with contrasting successional roles. For example, *Sassafras albidum* and *Robinia pseudoacacia* are old-field pioneers, whereas *Aesculus octandra* and *Diospyros virginiana* are understory tolerants

Most species in this guild have large seeds with a limited dispersal range; colonization of new areas is possible, however, because birds, small rodents, or livestock often act as dispersal agents. Large seeds also provide food reserves that allow new seedlings to establish on a broad range of sites. Survival rates usually are high because taproots or wide-spreading root systems support vigorous growth.

Root suckering also is common in this guild, and many new cohorts of *Sassafras albidum*, *Robinia pseudoacacia*, and *Gleditsia triacanthos* arise on or adjacent to previously occupied sites. Dense thickets of root sprouts also are found around the more shade-tolerant *Diospyros virginiana* and *Nyssa sylvatica*. The ability to form dense clones from root sprouts provides these species with an additional source of reproduction. The buckeyes (*Aesculus* spp.) have the most limited regeneration potential in this guild. Their large seeds quickly lose viability if they are not kept moist, so germination is restricted to mesic, litter-covered sites.

Persistent guilds

Persistent guilds contain species that develop and maintain advance regeneration. Many persistent species have large seeds with energy reserves sufficient for germinants to establish in shade or on dry sites. Large cohorts often develop as a result of mast seeding or other occasional events (e.g., wet years). Species with moderate understory tolerance may survive with a cycle of dieback and resprouting, whereas more tolerant species maintain seedling or sapling banks. Small canopy gaps maintain the regeneration pool for these species, but individuals do not enter the overstory until more significant canopy disturbances occur. Two persistent guilds were identified for central hardwoods:

Heavy-seeded, advance-growth dependent, intermediates (Groups 6 and 7). The heavy-seeded oaks and hickories formed distinct groups in object space, separated by the difference in seed-stratification requirements (Figure 2). However, the hickories are similar to the white oaks: they are slow growing and more shade tolerant than red oaks, but their seeds germinate in the spring following a period of cold stratification. This guild combines these two groups because of their overall similarity in regeneration attributes.

Oaks and hickories develop and maintain 'advance growth' regeneration. New cohorts arise from established seedlings or sprouts that are released by canopy openings. Seeds germinate well in the understory, but seedlings have intermediate shade tolerance, so survival under a closed canopy is limited to several years. Seedlings persist as 'seedling sprouts' with repeated episodes of dieback and resprouting. Despite their large, gravity-dispersed seeds, the species in this guild often colonize new areas with seeds cached and then left by birds and rodents. Vigorous sprouts also develop from cut or damaged stems. Seedling sprouts or other sprout-origin stems exhibit fast height growth; thus, species in this guild are more competitive in canopy openings than the other persistent species (Group 4). Sprouting also gives these species an advantage where small-scale understory disturbances (e.g., surface fires) are common.

Slow growing, understory tolerant (Group 4). This is a highly versatile guild. It contains tolerant and very tolerant species that use seed banks, recurring seedling banks, sapling banks and stump sprouts to persist in the understory. Species are slow-growing and long-lived. Good seed crops are produced at regular intervals and a variety of seedbeds are suitable for germination. As small canopy gaps form, individuals are gradually recruited into the overstory. This guild is similar to the extremely shade-tolerant group defined by Barnes et al. (1998). These species exhibit many features of the conservative strategy (Bormann & Likens 1979) that allow them to reproduce even when disturbances are minor and infrequent.

Guild position and key attributes

The relationships among the regeneration guilds in object space are shown in Figure 4. The position of each guild reflects the importance of seed banking, tolerance, and seed dispersal in both the first and second dimensions. Also expressed are variables with high discrimination measures primarily in the first dimension (dispersal season and seedbed preference). For example, all pioneer guilds plot to the right of the origin, with the most widely dispersed and shade-intolerant species in the upper right quadrant (Figure 4A). Spring-dispersed species also have limited seed viability and establishment is restricted to mineral-soil seedbeds. The dry-site intolerants plot well below the origin; seeds of these conifers are not dispersed until fall and tend to remain viable for several years. This guild also was distinct when plotted in the third and fourth dimensions (not shown). Cohort origin (CORIG) discriminated well in the third dimension so that the conifers (their new cohorts arise almost exclusively from seed) were well separated from the hardwoods.

Opportunistic guilds (Figure 4B) are nearest the origin. Species in these guilds have attributes that are consistent with a variety of reproductive modes. Many are capable of wide-ranging seed dispersal, either by wind or birds, and most opportunists are moderately tolerant in the understory. Although growth rate was not included in our data set, these species all share the capacity for fast growth when gaps in the overstory are created. Species in opportunistic guilds also have flexible seedbed preferences and can germinate in a variety of post-disturbance environments. The dispersal-limited guild includes the most shade-intolerant opportunists. Some species plot well to the right of the origin and share many attributes with the pioneer guilds despite their large, poorly-dispersed seeds.

Persistent guilds plot to the left or below the origin in direct contrast to the pioneer guilds (Fig-

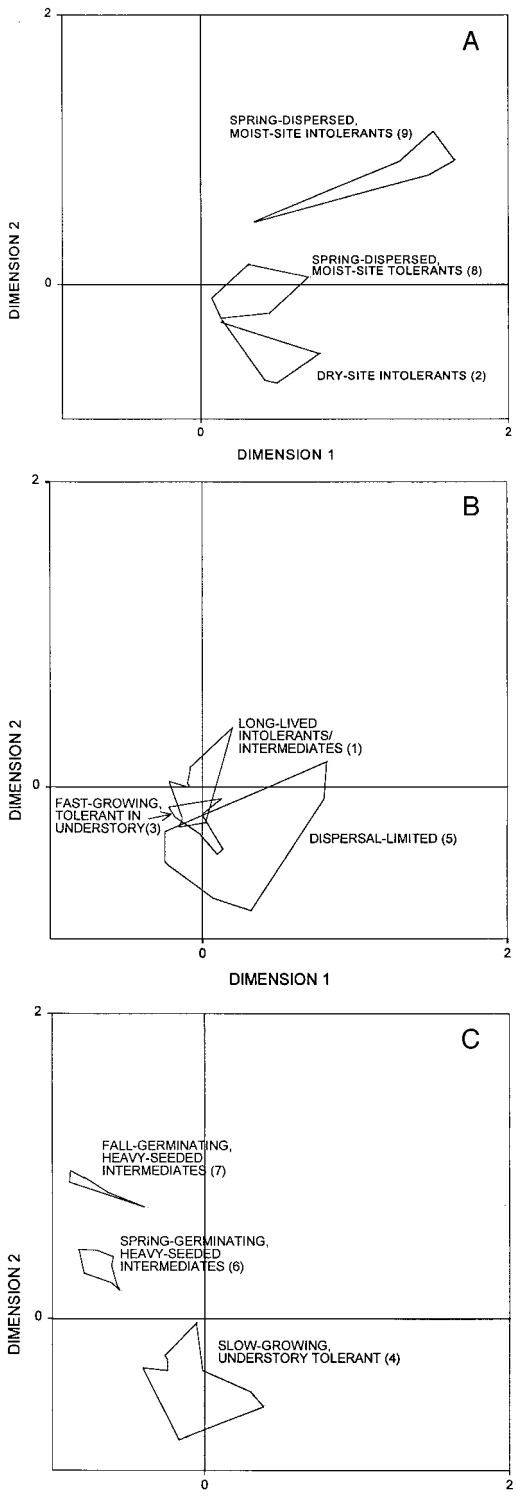

Figure 4. Regeneration guilds plotted in object space. (A) pioneer guilds; (B) opportunistic guilds; (C) persistent guilds. Group numbers corresponding to named guilds are given in parentheses.

ure 4C). Heavy-seeded, advance growth-dependent species (oaks and hickories) form two distinct groups in the upper left quadrant. The position of these groups reflects a preference for litter-covered seedbeds and intermediate shade tolerance along with limited dispersal potential and short seed viability. Species in the slow-growing, understory tolerant guild plot below the origin. Like the oaks and hickories, these species do not maintain seeds in the seed bank (there are several exceptions) and their lower position reflects a high level of understory tolerance.

Conclusions

Here we reduced the complexity of regeneration processes for a large and diverse group of species, the central hardwood forest type. In essence we have identified a set of plant functional types, specifically vegetation-dynamics types, that both reveal pattern and the essential dynamics of the system (Westoby & Leishman 1997). Our approach, which is objective and broad-based, utilizing available literature and not dependent on the collection of new data, is applicable to many vegetation types.

This research is particularly applicable to dynamic modeling efforts (e.g., Pacala et al. 1996). Forest dynamic modeling depends on reliable prediction of regeneration outcomes, and such predictions depend on a clear understanding of regeneration processes (Ribbens et al. 1994). Although a daunting task, the first step in characterizing regeneration processes should be the development of conceptual models that reflect a diverse set of reproductive pathways. These pathways should accommodate disturbance-mediated variables and be responsive to a variety of forest conditions and stages of stand development. The regeneration guilds that we have identified can be a starting point for such models because they separate species on the basis of their reproductive versatility. Models utilizing these guilds would be more realistic than those currently used in process-based models of forest dynamics (Liu & Ashton 1995), and more appropriate for simulating forest response to environmental variation such as climate change (see Yaussy et al. 1996; Westoby & Leishman 1997).

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See Appendix pages.

Appendix 1. Categorical values of regeneration attributes for central hardwood species.[a] See Table 1 for attribute codes, Appendix 2 for species abbreviations.

	Reproductive attributes:																			
	FLWR	FRST	POLL	SAGE	SPRO	SFREQ	SFALL	SBANK	SDISP	STRAT	GTIME	GLITE	GBED	GMIOS	GTEMP	TOL	ROOT	VSPR	RSCKR	CORIG
Species:																				
ACNE	2	2	1	1	1	1	2	2	5	1	1	2	3	2	2	4	2	1	2	2
ACNI	2	2	2	2	1	3	2	2	5	1	1	2	3	2	2	5	2	1	2	2
ACRU	1	2	1	1	1	2	1	3	5	2	1	2	3	2	2	4	2	1	2	2
ACSI	1	1	1	1	1	1	1	2	4	2	1	2	1	2	2	4	3	1	2	2
ACSA	2	2	2	2	1	4	2	2	5	1	1	2	3	2	1	5	2	1	2	2
AEGL	2	2	3	1	1	2	2	2	1	1	1	2	3	2	2	4	1	1	2	1
AEOC	2	2	3	1	1	2	2	2	1	1	1	2	3	2	2	4	1	1	2	1
BEAL	2	1	1	3	2	3	2	3	5	1	1	1	1	2	2	3	2	1	2	2
BELE	2	1	1	3	1	2	2	3	5	1	1	1	2	2	2	3	2	1	2	2
BENI	2	2	1	2	1	1	1	2	5	2	2	1	1	2	2	2	2	1	2	2
CACA	2	2	1	2	1	4	2	2	3	1	1	2	3	2	2	5	2	1	1	2
CACO	2	1	1	3	2	4	2	2	1	1	1	2	2	2	2	3	1	1	1	2
CAGL	2	1	1	3	3	2	2	2	1	1	1	2	2	2	2	3	1	1	1	2
CALA	2	1	1	3	3	2	2	2	1	1	1	2	2	2	2	5	1	1	1	2
CAOV	2	1	1	3	2	3	2	2	1	1	1	2	2	2	2	4	1	1	1	2
CATO	2	1	1	2	1	3	2	2	1	1	1	2	2	2	2	3	1	1	1	2
CEOC	2	2	1	1	1	1	2	3	3	1	1	2	3	2	2	4	2	1	2	2
CECA	1	2	3	1	1	2	3	3	1	1	1	2	1	2	2	4	1	2	2	1
COFL	2	2	1	1	1	1	2	3	3	1	1	2	3	2	2	5	3	1	1	2
DIVI	2	1	3	1	1	2	2	2	3	1	1	2	3	2	2	5	1	1	1	2
FAGR	2	1	1	3	1	4	3	2	2	1	1	2	3	2	2	5	1	1	1	2
FRAM	2	1	1	2	1	4	2	3	5	1	1	2	3	1	2	3	2	1	2	2
FRNI	2	1	1	2	1	4	2	3	5	1	1	2	3	1	2	2	3	1	2	2
FRPE	2	1	1	2	1	4	2	3	4	1	1	2	3	1	2	3	2	1	2	2
GLTR	3	2	3	1	1	2	3	3	1	1	1	2	3	2	2	2	2	1	1	2
JUCI	2	2	1	2	1	3	2	3	1	1	1	1	2	2	2	2	2	1	2	2
JUNI	3	2	1	1	1	4	2	3	1	1	1	1	2	2	2	2	1	1	2	2
JUVI	1	2	1	1	1	3	1	3	3	1	1	1	1	2	2	2	2	2	2	1
LIST	2	1	1	2	1	3	2	2	4	1	1	2	3	2	2	2	2	1	1	2
LITU	3	2	2	2	1	4	2	3	4	1	1	2	1	2	2	3	2	1	2	2
MAAC	3	2	2	2	2	4	2	3	3	1	1	2	2	2	2	3	2	1	2	2
MORU	2	2	1	1	1	3	1	2	3	1	1	2	2	2	2	4	2	1	2	2
NYSY	3	2	2	2	2	2	2	2	3	1	1	2	3	2	2	4	1	1	2	2
OSVI	2	2	1	2	1	2	2	3	4	1	1	2	1	2	2	5	2	1	2	2
OXAR	3	2	3	2	2	1	2	2	2	2	1	2	2	2	2	4	2	1	2	2
PIEC	2	2	1	2	1	4	3	2	4	1	1	1	1	2	2	2	1	1	2	1
PIRI	2	2	1	1	1	3	3	4	4	1	1	1	1	2	2	2	2	1	2	1
PIST	2	2	1	2	2	4	2	2	5	1	1	2	3	2	2	3	3	2	2	1
PIVI	2	2	1	1	2	3	3	3	4	1	1	1	3	2	2	2	3	2	2	1
PLOC	2	1	1	2	2	2	2	2	6	1	1	1	1	1	2	3	2	1	2	2
PODE	1	2	1	1	1	1	1	1	6	2	1	1	1	2	2	1	3	1	2	2
POGR	1	2	1	2	2	4	1	1	6	2	1	1	1	2	2	2	2	1	1	3
POTR	1	2	1	2	2	4	1	1	6	2	1	1	1	2	2	1	2	1	1	3
PRSE	2	1	1	1	1	1	1	3	3	1	1	2	2	2	2	3	2	1	2	2
QUAL	2	1	1	2	3	4	2	2	1	2	2	2	2	2	3	3	1	1	2	2
QUBI	2	2	1	3	3	4	2	2	1	2	2	2	2	2	2	3	1	1	2	2
QUCO	2	2	1	2	2	4	2	2	1	1	1	2	2	2	2	3	1	1	2	2
QUMA	2	2	1	3	3	3	2	2	1	2	2	2	2	2	2	3	1	1	2	2
QUPA	2	2	1	2	1	2	2	2	1	1	1	2	2	2	2	3	1	1	2	2
QUPR	2	1	1	2	2	4	2	2	1	2	2	2	2	3	2	3	1	1	2	2
QURU	2	2	1	2	2	3	2	2	1	1	1	2	2	2	2	3	1	1	2	2
QUST	2	1	1	2	2	3	2	2	1	2	2	1	2	2	2	2	1	1	2	2
QUVE	2	2	1	2	1	3	2	2	1	1	1	2	2	2	2	3	1	1	2	2
ROPS	2	2	3	1	1	2	2	3	1	2	1	1	1	2	2	1	3	1	1	3
SANI	2	1	2	1	1	1	1	1	6	2	1	1	1	1	2	1	3	1	1	2
SAAL	1	1	1	1	1	2	1	3	3	1	1	1	2	2	2	2	3	1	1	3
TIAM	3	2	2	1	1	2	2	3	2	1	1	2	1	2	3	4	2	1	2	3
TIHE	3	2	2	2	1	2	2	3	2	1	1	2	1	2	2	4	2	1	2	3
TSCA	2	2	1	3	1	3	3	2	4	1	1	2	3	2	3	5	2	2	2	1
ULAM	1	1	1	2	1	1	1	2	4	2	1	2	3	2	3	3	2	1	1	2
ULRU	2	1	1	2	1	3	1	2	4	2	1	2	3	2	2	4	2	1	2	2
ULTH	2	1	1	2	1	3	1	2	4	2	1	2	3	2	2	4	2	1	1	1

[a]See text for major sources. Additional sources include: Trimble (1975), Kelty (1988), Clark & Hutchinson (1989), Hornbeck & Leak (1992), and Smith (1993).

Appendix 2. Central hardwood forest tree species, name abbreviations for figures, and regeneration guilds. Nomenclature from *Silvics of North America* (Burns & Honkala 1990a, b).

Scientific name	Abbreviation	Regeneration guild
Acer negundo	ACNE	opportunistic, fast-growing understory tolerant
Acer nigrum	ACNI	persistent, slow-growing understory tolerant
Acer rubrum	ACRU	pioneer, spring-dispersed, moist-site tolerant
Acer saccharinum	ACSI	pioneer, spring-dispersed, moist-site tolerant
Acer saccharum	ACSA	persistent, slow-growing understory tolerant
Aesculus glabra	AEGL	opportunistic, dispersal limited
Aesculus octandra	AEOC	opportunistic, dispersal limited
Betula alleghaniensis	BEAL	opportunistic, long-lived intermediate
Betula lenta	BELE	opportunistic, long-lived intermediate
Betula nigra	BENI	pioneer, spring-dispersed, moist-site tolerant
Carpinus caroliniana	CACA	persistent, slow-growing understory tolerant
Carya cordiformis	CACO	persistent, large-seeded, advance growth dependent
Carya laciniosa	CALA	persistent, large-seeded, advance growth dependent
Carya glabra	CAGL	persistent, large-seeded, advance growth dependent
Carya ovata	CAOV	persistent, large-seeded, advance growth dependent
Carya tomentosa	CATO	persistent, large-seeded, advance growth dependent
Celtis occidentalis	CEOC	opportunistic, fast-growing understory tolerant
Cercis canadensis	CECA	opportunistic, dispersal limited
Cornus florida	COFL	opportunistic, fast-growing understory tolerant
Diospyros virginiana	DIVI	opportunistic, dispersal limited
Fagus grandifolia	FAGR	persistent, slow-growing understory tolerant
Fraxinus americana	FRAM	opportunistic, fast-growing understory tolerant
Fraxinus nigra	FRNI	opportunistic, fast-growing understory tolerant
Fraxinus pennsylvanica	FRPE	opportunistic, fast-growing understory tolerant
Gleditsia triacanthos	GLTR	opportunistic, dispersal limited (large-seeded)
Juglans cinerea	JUCI	opportunistic, long-lived intolerant
Juglans nigra	JUNI	opportunistic, long-lived intolerant
Juniperus virginiana	JUVI	pioneer, dry-site intolerant
Liquidambar styraciflua	LIST	opportunistic, long-lived intolerant
Liriodendron tulipifera	LITU	opportunistic, long-lived intermediate
Nyssa sylvatica var. *sylvatica*	NYSY	opportunistic, dispersal limited (large-seeded)
Ostrya virginiana	OSVI	persistent, slow-growing understory tolerant
Oxydendrum arboreum	OXAR	persistent, slow-growing understory tolerant
Pinus echinata	PIEC	pioneer, dry-site intolerant
Pinus rigida	PIRI	pioneer, dry-site intolerant
Pinus strobus	PIST	opportunistic, long-lived intermediate
Pinus virginiana	PIVI	pioneer, dry-site intolerant
Platanus occidentalis	PLOC	opportunistic, long-lived intermediate
Populus deltoides var. *deltoides*	PODE	pioneer, moist-site intolerant
Populus grandidentata	POGR	pioneer, moist-site intolerant
Populus tremuloides	POTR	pioneer, moist-site intolerant
Prunus serotina	PRSE	opportunistic, fast-growing understory tolerant
Quercus alba	QUAL	persistent, large-seeded, advance growth dependent
Quercus bicolor	QUBI	persistent, large-seeded, advance growth dependent
Quercus coccinea	QUCO	persistent, large-seeded, advance growth dependent
Quercus macrocarpa	QUMA	persistent, large-seeded, advance growth dependent
Quercus palustris	QUPA	persistent, large-seeded, advance growth dependent
Quercus prinus	QUPR	persistent, large-seeded, advance growth dependent
Quercus rubra	QURU	persistent, large-seeded, advance growth dependent
Quercus stellata	QUST	persistent, large-seeded, advance growth dependent
Quercus velutina	QUVE	persistent, large-seeded, advance growth dependent
Robinia pseudoacacia	ROPS	opportunistic, dispersal limited (sprout dependent)
Salix nigra	SANI	pioneer, moist-site intolerant
Sassafras albidum	SAAL	opportunistic, dispersal limited (sprout dependent)
Tilia americana	TIAM	persistent, slow-growing understory tolerant
Tilia heterophylla	TIHE	persistent, slow-growing understory tolerant
Tsuga canadensis	TSCA	persistent, slow-growing understory tolerant
Ulmus americana	ULAM	pioneer, spring-dispersed, moist-site tolerant
Ulmus rubra	ULRU	pioneer, spring-dispersed, moist-site tolerant
Ulmus thomasii	ULTH	pioneer, spring-dispersed, moist-site tolerant