Natural Disturbance-Based Silviculture for Restoration and Maintenance of Biological Diversity

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Executive Summary

Restoration and silvicultural approaches that most successfully sustain native biodiversity are those that integrate concepts of ecosystem responses to natural disturbances. A natural disturbance model for management assumes that species have evolved to local environmental conditions and a particular disturbance regime, such that there is a greater opportunity for sustaining biodiversity when the disparity between managed disturbances and natural disturbances is reduced.

This document synthesizes current understanding of natural forest disturbances, particularly biological legacies associated with the disturbances, which is key to sustaining biological diversity. First we provide a review of what is generally known about natural disturbances and how they influence biological legacies. Secondly, we contrast how managed disturbances in forests differ from the patterns and processes of natural disturbances, and how natural disturbance models may be implemented in silviculture for varied land objectives with a goal of conservation.

Because lands under management are characterized by specific site conditions, land-use histories, and a regional context, an understanding of the natural history of the particular system is vital for a land manager to be able to implement forestry from a conservation perspective. To illustrate this approach in actual places, we present case studies from the Southeast, Lake States, and Pacific Northwest where silvicultural management is conserving native biodiversity by using natural disturbance as a guide.

Introduction

Foresters have used an understanding of demographic and stand development patterns and processes in natural forests as models for development of silvicultural practices even though modern wood production is increasingly based on an agronomic model. Even-aged harvest prescriptions are often described as analogues for stand-replacement disturbance events, such as that of intense wildfire or windstorms. Individual tree and group selection practices are modeled on patterns of disturbance and mortality involving the death of individual or small groups of trees within otherwise intact stands. Hence, disturbance regimes are the conceptual foundation for the core of regeneration harvest silviculture.

Scientific understanding of the nature of disturbance events and successional or recovery processes in natural ecosystems has increased dramatically during the last several decades. The expansion in research on ecosystem structure, function, and composition began with the International Biological Program in the late 1960s and matured in subsequent efforts, such as the National Science Foundation's Long Term Ecological Research program. Several large and notable disturbances—the Mount St. Helens eruption of 1980 (Franklin et al. 1994; Franklin et al. 1996), the Yellowstone Fires of 1988 (Christensen et al. 1989), and Hurricanes Hugo (Walker

et al. 1991) and Andrew (Pimm et al. 1994)—provided irresistible opportunities for ecosystem research teams to extend their studies into recovery processes in intensely disturbed ecosystems. Concurrently, there has been a great expansion of efforts at understanding smaller-scale disturbance regimes and natural development processes in forest ecosystems (Frelich and Lorimer 1991, Coates and Burton 1997; Runkle 1981, 1998).

Research on natural disturbances has largely emphasized variables such as the type, size, frequency, intensity, and impact of the disturbances. In particular, effects of contrasting disturbance types—such as fire, wind, flood, insect pest, landslide, or snow avalanche—has received substantial attention and has progressed from observational studies to credible experimental (e.g., Foster et al. 1997). Disturbance scale has also received significant attention, with a scientific synthesis of the distinctive features and effects of large intense disturbances (Turner et al. 1988).

Predicting ecosystem responses to disturbance, however, are best understood not only through patterns of destruction or consumption, but by patterns and types of what remains following the disturbance, i.e., biological legacies. The concept of biological legacies emerged from studies of natural disturbances, beginning with research on the Mount St. Helens eruptions (Franklin et al. 1981. As with many ecological constructs, the notion of biological legacies is not really new; rather, it is a rediscovery and elaboration of Frederic Clement's concept of organic "residuals" proposed nearly 100 years ago. However, an increased understanding of the linkages between ecosystem structure and processes has highlighted the potential importance of organic legacies of pre-disturbance ecosystems in recovery processes. The net effect has been an increasing focus on organisms, organic matter and structures, and organically-derived patterns—collectively biological legacies--which survive a disturbance event.

In this paper we synthesize our current understanding of natural forest disturbances and stand development, particularly with reference to biological legacies, so as to provide a broad conceptual basis for designing silvicultural practices that will restore and maintain biological diversity and ecosystem processes. Comprehensive information on natural disturbance regimes is critical to guide forest management as society moves increasingly toward manipulation of forests to maintain biological diversity and critical ecosystem services. Achieving these types of ecological goals requires forest management practices that are based upon natural models, much more so than in the case of tree plantations managed to maximize wood production.

Biological Legacies

The concept of biological legacies emerges from our recent understanding that natural disturbances, even stand-replacement disturbances, rarely create the simple environment that is sometimes imagined (Figure 1). It is now clear that while many of these events disrupt the ecosystem and kill trees, usually relatively small amounts of organic matter are consumed or removed. Furthermore, much remaining organic matter is in the form of structures—such as standing dead trees (snags) and tree boles and other woody debris on the ground—that provide critical habitat and sustain other important functional roles in the ecosystem. Furthermore, many live mature trees, seedlings, and seeds persist through disturbances. The diversity and potential importance of surviving organisms and organically-derived structures and patterns is recognized in the concept of biological legacies. While this construct is not new, the extent and ecological role of such legacies, particularly structural legacies, have not been fully appreciated nor applied in forest management.

A) Understory plant communities, tree seedling banks, snags, and logs were legacies at some locations affected by the Mount St. Helens, Washington eruption of May 1980.

B) Understory plant communities, tree seedling and sapling banks, and large volumes of down tree boles are typical biological legacies of stand-replacement wind disturbances, as represented here on the Bull Run River drainage of the Mount Hood National Forest, Oregon.

C) Stand-replacement fire events generate extensive legacies of snags and associated woody debris, as seen here in a 6-year-old burn in Yosemite National Park, California.

Figure 1. Natural disturbances in forests leave behind significant biological legacies, including large amounts of organic matter in the form of large structures (snags and logs) that play important functional and habitat roles.

Biological legacies are defined as the organisms, organic matter (including structures), and biologically-created patterns that persist from the pre-disturbance ecosystem and influence recovery processes in the post-disturbance ecosystem (Franklin et al. 2003). Some types of biological legacies that typically occur in disturbed forest ecosystems include:

- Organisms – plant, animal, and microbial
  - Sexually mature and intact live trees
  - Tree reproduction (seedling and sapling banks)
  - Plant parts capable of vegetatively reproducing, such as root systems
  - Seed banks
  - Shrub, herb, and moss species
  - Sexually immature or mature animals
- Organic matter, including fine litter and particulate material
- Organically-derived structures
  - Standing dead trees (snags)
  - Downed tree boles (logs) and other coarse woody debris on forest floor
  - Root wads and holes from uprooted trees
- Organically-derived patterns
  - Patterns in soil chemical, physical, or microbiological properties
  - Forest understory compositional legacy

These are broad categories of legacies and occur in varied form and density, depending upon the nature of both the disturbance and the disrupted forest ecosystem.

Biological legacies play a wide array of important roles in ecosystem reorganization and recovery processes (Franklin and MacMahon 2000, Franklin et al. 2000, Franklin et al. 2003). A generalized function includes perpetuating genotypes and species on site. Thus, they have particular relevance to conservation of biological diversity within significantly disrupted forest ecosystems (Lindenmayer and Franklin 2002). Specific functional roles played by biological legacies include:

- Perpetuating plant species as surviving immature or mature individuals or as reproductive structures, such as seeds, spores, or vegetative parts with sprouting capability
- Perpetuating other biota by creating refugia for other species, a “lifeboating” function
- Providing habitat needed by re-colonizing organisms, primarily by “structurally enriching” the stand
- Improving connectivity in the landscape for some organisms by providing protective cover

These roles are particularly prominent where a large and intense (i.e., stand replacement) disturbance has taken place.

Given a stand replacement disturbance, the lifeboating function is typically provided by larger biological structures that persist following a disturbance, such as live trees, snags, and downed boles and their effects are both direct and indirect. These structures sustain organisms in the post-disturbance environment by providing necessary habitat (e.g., nesting sites and hiding cover) and energy, particularly immediately following the disturbance. Live green plants have particular importance in sustaining high-quality energy flows to below-ground organisms and food webs, as well as to above-ground herbivores. Residual structures also modify

microclimatic conditions, bringing them within the acceptable environmental range for organisms to survive that might otherwise be eliminated from the post-disturbance environment.

Following stand replacement disturbances, surviving large trees, snags, and downed boles also have long-term importance by structurally enriching the young forest ecosystem. Some species will be displaced from the disturbed ecosystem as a result of loss of suitable habitat conditions. The new tree cohort that develops typically will be even-aged and even-sized, limiting the opportunity for species requiring structures, such as large cavity-bearing trees and snags, unless there is a legacy of such structures from the pre-disturbance stand. With such structural legacies organisms such as the Northern Spotted Owl (*Strix occidentalis*) are able to return to much younger stands than would otherwise be the case. Hence, conceptually, biological legacies structurally enrich a new stand.

While we emphasize biological legacies associated with arboreal structures such as large live trees, snags, and downed boles in the following discussions, we do wish to emphasize that ***compositional legacies are as important as structural legacies*** with regards to many aspects of ecosystem function (Palik and Engstrom 1999). Compositional legacies include the variety of organisms that survive a disturbance including trees, but also non-arboreal plants, fungi, and animals. In forest ecosystems, arboreal structural legacies are important in facilitating survival of compositional legacies, but we must not forget that the organisms will, themselves, play important roles in re-establishing a diverse and functional forest ecosystem. Structural and compositional legacies may also play a role in sustaining required disturbance regimes, such as providing fuel for fire in systems that are disturbance-dependent, such as the longleaf pine (*Pinus palustris* Mill.) ecosystem.

Before proceeding we should note the effects of disturbances and their legacies on re-establishment of tree regeneration and, ultimately, dominance of forest cover. The initial stage of forest development following a major disturbance is regeneration of a cohort of trees, a stage sometimes referred to as "cohort establishment" and it is distinct from the disturbance and legacy creation event itself. However, the legacies of the disturbance can profoundly influence the rapidity with which forest cover develops. Establishment of a dense, cohort of tree regeneration may occur very rapidly where biological legacies include large seed or seedling banks or due to large numbers of sexually mature live trees. However, re-establishment of forest dominance may take decades or even centuries where large or repeated disturbances create areas lacking significant mature trees or seed or seedling banks. Severe environmental conditions (e.g., hot, dry or cold, snowy sites) or rapid development of competing vegetation will generally extend the "cohort establishment" periods.

Large, slowly regenerating disturbed areas were typical of many forests subjected to one or more major wildfires in the western United States. Portions of the Mount St. Helens devastated zone, which did not undergo salvage logging and tree planting and which had no seedling legacy, are undergoing an attenuated tree regeneration process. A slow recovery of a forest can also be the case for post-fire areas on drier, frostier, or snowier sites in other regions. Such large disturbed areas with slow recovery of forest cover may be important in providing concentrated habitat for species that thrive in structurally diverse, early successional habitats, such as many bird species. Note that these are ***not*** equivalent to large clearcuts but, rather, areas with legacies of plant and animal species as well as structural legacies, such as snags and logs, that persist for many decades.

General Disturbance Model for Forest Ecosystems

Ecological forestry can be defined as forest management that incorporates and maintains a wide range of ecological values, such as native forest biodiversity and ecosystem processes, along with timber production (Seymour and Hunter 1999). A general premise of ecological forestry is that silvicultural practices that most closely resemble the relevant natural disturbance regimes are most likely to achieve ecological objectives. While aspects of this hypothesis can be debated, a comprehensive understanding of natural disturbance regimes is clearly needed for implementation of the approach.

Prescriptions incorporating classical silvicultural systems provide a comprehensive plan for regeneration and tending of forest stands through time encompassing all stages of stand development from regeneration to harvest of mature trees. Systems for ecological forestry need to be similarly comprehensive. Hence, it is our view that the relevant disturbance regime includes both tree-regenerating disturbance events (defined here as those that result in mortality in the overstory and create potential for regenerating new cohorts of trees) and less intense disturbances, as well as competitive processes that help direct the development of the established stand. This is the perspective that we will ultimately adopt. However, we begin by first examining a model of tree-regenerating disturbances because these most closely parallel the classical regeneration harvest practices of individual tree selection, group selection, shelterwood, and clearcut, and allow the clearest contrast between these practices and natural disturbance regimes.

Our model of tree-regenerating disturbance incorporates scale (individual, gap, or stand level) of dominant tree mortality (x-axis) and disturbance type (y-axis) (Figure 2), which can be related, in turn, to a third dimension of biological legacies (Table 1).

Table 1. Some biological legacies associated with four disturbance agents (lightning, fire, wind, and bark beetle) operating at small (tree or gap) and stand scales.

Legacy	Wind Gap (A)	Ground Fire (B)	Beetle Gap (C)	Wind Stand Replacement (D)	Crown Fire (E)	Beetle Stand Replacement (F)	Clearcut/ Site Prep
Live, mature trees	Absent/Few	Yes	Species-dependent	Absent/Few	Absent/Few	Species-dependent	No
Seedling bank	Possible	No	Possible	Possible	No (except skips)	Possible	No
Intact understory	Yes	No	Yes	Yes	No (except skips)	Yes	No
Snags	Few	Few	Abundant	Few	Abundant	Abundant	No
Logs	Abundant	Few	No (initially)	Abundant	Common	No (initially)	No
Uproots	Abundant	No	No	Abundant	No	No	No
Mineral seedbed	Limited	Abundant	No	Limited	Abundant	No	Yes

<u>Effects of increasing opening size</u>

Microclimate	more modified at larger size
Light	increases with size to asymptote
Seed Supply	declines
Edge	initial increase

Tree-regenerating disturbances can be scaled from those involving individual or small groups of overstory trees to large-scale mortality events, commonly described as stand replacement disturbances (Figure 2). The gradient of scale portrayed in Figure 2 is also correlated with two other important variables—proportion of intact forest matrix after the disturbance and tendency for the disturbance to move stand structure toward heterogeneity or homogeneity. The first of these relationships is obvious. Tree and gap-level mortality events

leave forest cover largely intact and in control of the post-disturbance environment. Stand-level mortality events, on the other hand, destroy the dominant forest cover and create an open post-disturbance environment. Effects of disturbance scale on structural heterogeneity of post-disturbance forests are not as obvious. Stand-replacement events will generally homogenize the live tree structure by providing conditions for establishment or release of a new tree cohort; tree- and gap-scale events will, on the other hand, tend to create or perpetuate stand structural heterogeneity. These effects on structural heterogeneity will be discussed further in a later section.

Disturbance type is a second important disturbance variable in tree-regenerating disturbances (Figure 2). Fire, wind, and bark beetles are used to exemplify the effect of disturbance type since these are common agents and relate to disturbance regimes in well-known forest types. Clearly, any of these disturbance agents (as well as many others) can generate mortality across a range of spatial scales, from individual trees to entire stands. Also, lightning has dual roles in both killing individual dominant trees (such as in longleaf pine forests) and in initiating fires that may cause either gap-based or stand-replacement mortality (such as in ponderosa pine).

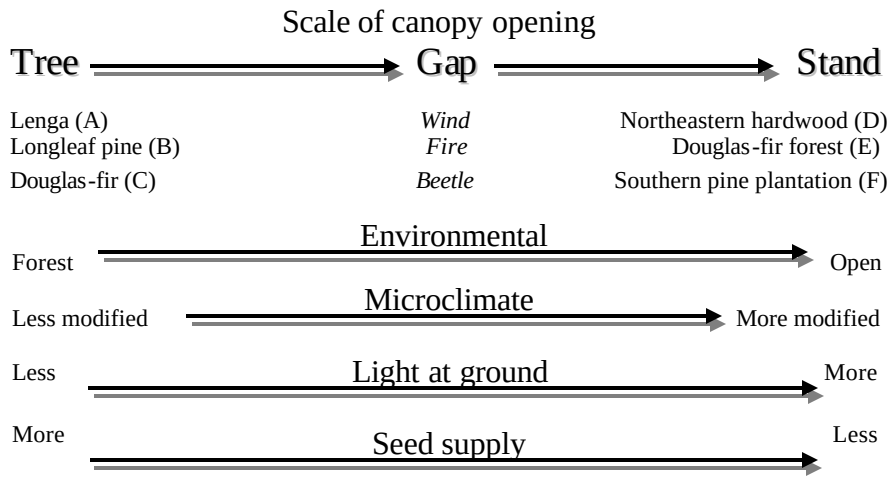

Figure 2. Disturbance gradient model based upon scale of mortality in overstory tree species and related disturbance attributes with three exemplary agents of mortality. Letters refer to columns of biological legacies in Table 1.

Disturbance types (fire, wind, and bark beetle) contrast greatly in their biological legacies, regardless of the scale of overstory tree mortality (Table 1). Generally wind and beetles tend to kill from "above", concentrating their impacts on the forest overstory and often leaving the understory essentially undisturbed, except for effects of uprooting and tree falls. On the other hand, fire tends to kill from "below", often heavily impacting the aboveground structure of smaller sized trees and other understory components disproportionately (stand-replacement fires will, of course, affect both understory and overstory). Of course, as we will see, some of these understory components may be well adapted to survive fire, particularly in forest types that were chronically perturbed by low- to moderate intensity wildfire.

Many forest types have a primary disturbance regime defined by wind created gaps; even more forests incorporate this as a "secondary" regime (see details below). Legacies within gaps typically include numerous boles on the forest floor and in larger gaps some large live trees and snags (Table 1). Cohorts of tree seedlings and saplings or "seedling banks" are often present and

sometimes in high densities; these regeneration banks are typically referred to as "advance regeneration" by foresters. Understory vegetation and seedbanks are typically left intact, except where there is uprooting. Areas of mineral soil seedbed are typically limited to areas influenced by uprooting in such gaps, i.e., tree-fall pits and mounds. The lenga (*Nothofagus pumilio*) forests of Tierra del Fuego provide an excellent example of a forest with a wind-gap disturbance regime (Arroyo et al. 1996, Rebertus et al. 1997); gap-based release from a dense understory seedling bank is characteristic of these forests.

Figure 3. Individual Douglas-fir and western larch (*Larix occidentalis*) trees survived this intense, stand-replacement fire on the Colville National Forest, Washington.

North American forest types dominated by a wind-gap disturbance regime include: Pacific Coast rainforests of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*) and Pacific silver fir (*Abies amabilis*) found in coastal British Columbia and Alaska (Lertzman et al. 1996); northern hardwood forests of the Great Lakes and New England regions (Frelich and Lorimer 1991); and mid-Atlantic and southern hardwood forest ecosystems (Runkle 1982).

Wind-generated disturbances at larger spatial scales (e.g., hurricanes, typhoons, and tornadoes) are similar to wind-gap disturbances in the nature of the biological legacies (Table 1). Structural legacies are primarily down boles with some snags and a few larger live trees (e.g., Palik and Robl 1999). Some larger snags often persist, probably because they have less surface area (i.e., a canopy), providing less purchase for winds. In many temperate and tropical hardwood forests, broken, bent, and partially uprooted trees have the capacity to re-sprout, even though they are no longer part of a dominant overstory (see, e.g., Foster et al. 1997 for temperate forests and Walker et al. 1991 for tropical forests). The understory of affected stands remains largely intact, except areas disrupted by uprooting or directly under boles; hence, seed and seedling banks and understory plants are a major legacy. In some ecosystems, seedling banks are an important legacy of large-scale wind disturbance, as exemplified by the western hemlock-dominated stands that developed from advanced regeneration following a large blowdown event on the western Olympic Peninsula, Washington in 1921.

Many forest types are subject to wind disturbances as either their primary or secondary regime. Intense wind events, including hurricanes, are a primary disturbance regime for temperate hardwood forests in eastern North America. Hurricanes are important in subtropical and tropical hardwood forests in the Caribbean region and, occasionally, in pine forests of the southeastern Coastal Plain. Intense windstorms also periodically blow down large areas of conifer forests along the Pacific Coast from Oregon to Alaska. Portions of the Pacific Northwest dominated by Douglas-fir forests are much better known for their stand-replacement fire regimes, but both large scale and more localized stand-replacement wind events do occur as evidenced by the 1962 Columbus Day windstorm and blowdowns in northern Oregon's Bull Run River drainage, respectively. Intense windstorms are also important in the Great Lakes region (Canham and Loucks 1984; Palik and Robl 1999).

Fire can generate overstory mortality at either small (tree and gap) or large (stand) scales but produces comparable legacies at all scales (Table 1). Typical biological legacies include a high density of snags and, sometimes, down boles on the forest floor but, by definition, relatively few large live trees if it is truly a stand-replacement disturbance. However, some large trees typically survive even intense fires as exemplified by such diverse types as jack pine (*Pinus banksiana*) in the Lake States (Abrams 1984) and Douglas-fir on the Pacific Coast (Figure 3). As with all events that kill overstory trees, the snags will eventually disintegrate to provide a diversity of coarse woody debris on the ground. Understory seedling and seed banks, understory plants, and organic layers on the soil surface are all affected by fire; however, some understory trees and plants typically survive either because of variable fire intensity or adaptations to fire or both (see below). Abundant mineral soil seedbeds are an important legacy of fire disturbances.

Gap-scale stand openings are often part of a frequent, low to moderate intensity fire regime, such as is characteristic of southeastern longleaf pine (*Pinus palustris*), some Great Lakes eastern white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) forests (Heinselman 1973), and many ponderosa pine (*Pinus ponderosa*) forests. Fire events may actually cover a large area but generate few gaps yet are critical for maintaining openings in the canopy. Many understory and ground cover plants are adapted to regular burning while many potential canopy species, such as oaks, survive fire, but are maintained in a low stature. Furthermore, in some of the forest types subject to this regime--particularly longleaf pine--overstory tree mortality is caused primarily by lightning or bark beetles rather than by surface fires (Figure 4, see Palik and Pederson 1996).

Figure 4. Dominant longleaf pine mortality is often associated with lightning rather than the effects of associated low to moderate intensity fires.

High intensity, stand-replacement fire is a common disturbance regime for many important forest types in North America. These include coastal Douglas-fir (*Pseudotsuga menziesii*), jack pine (*Pinus banksiana*) and red pine forests in the Great Lakes region (Van Wagner 1971, Heinselman 1973), lodgepole pine (*Pinus contorta*) forests throughout much of western North America, and subalpine and boreal spruce (*Picea* spp.) forests throughout North America. Highly variable fire intensities are characteristic of these large fire events; consequently, high levels of spatial heterogeneity in burn intensity and type and density of biological legacies are common. This heterogeneity is found at all spatial scales, from within stand to landscape, resulting in patches of varying burn intensity as well as unburned patches.

Bark beetle disturbances can occur at a variety of spatial scales, with specifics depending upon the beetle and host species. The Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) typically kills small groups of mature to old Douglas-firs, producing a gap-sized disturbance. Similarly, western pine beetle (*D. brevicomis*) kills individual or small patches of ponderosa pine in old-growth stands. Where extensive pure stands of host species exist, several other species of bark beetles are capable of large-scale, stand replacement disturbance events. Notable examples are: southern pine beetle (*D. frontalis*) in plantations of southern pines; mountain pine beetle (*D. ponderosae*) in young to mature stands of ponderosa pine and lodgepole pine as well as in extensive old-growth stands of

lodgepole pine; and spruce beetle (*D rufipennis*) in spruce (*Picea* spp.)-dominated forests throughout subalpine and boreal forest regions in North America. Snags and, eventually, boles and other coarse woody debris on the forest floor are primary biological legacies of beetle outbreaks. Intact understory communities, including seedling and seed banks and undisturbed forest floors are also legacies.

Biological legacies can be tabulated for other types of disturbance regimes and forest types. For example, general patterns of biological legacies are associated with such disturbance events as floods, snow avalanches, outbreaks of defoliating insects, and diseases of various types, such as root rots or foliar diseases. There are disturbances that leave few biological legacies, such as landslides or volcanic events that are dominated by lava flows or glowing avalanche deposits. Unusual species or life forms may also result in distinctive legacies; as one notable example, the presence of coast redwood (*Sequoia sempervirens*) in a stand adds a stump-sprouting, shade-tolerant coniferous species to coastal forests otherwise lacking in conifers with strong vegetative regeneration abilities.

Multi-Scale Disturbance Regimes

To illustrate key concepts we have considered primarily events at the extremes of the spatial scale (gap- and stand-level) but many disturbance events are actually spatially mixed. That is, many disturbances incorporate both gap-scale and stand-scale mortality of trees. Examples would include stand-replacement events in coastal Douglas-fir and Rocky Mountain lodgepole pine forests where fire mosaics leave unburned patches as well as substantial areas with moderate to large numbers of adult trees as a result of locally less intense fire. High levels of spatial heterogeneity are typical outcomes where variations in disturbance intensities result in highly variable levels of biological legacies within a single disturbance event.

Interactions among Disturbance Regimes (Gap & Stand Replacement)

Many interactions occur among disturbance regimes in terms of both scales and types. One of the most significant involves forest types that are characterized by stand-replacement disturbance regimes. Forest developmental sequences initiated by such disturbances are also invariably subject to gap-based disturbances processes that typically operate throughout the development of the stand; as will be seen, the longer the developmental time span the more profound the gap-based processes become.

Coastal Douglas-fir stands provide a good example of interacting disturbances. In these stands, time intervals between stand replacement wildfires may be 400 years or more (Hemstrom and Franklin 1982; Agee 1993; Franklin et al. 2002). Assuming that the sequence begins with destruction of an old-growth forest stand, the initiating event will result in replacement of a spatially patchy, multi-aged stand with a relatively even-aged cohort of trees. Insofar as live tree structures are concerned, the initiating disturbance can be viewed as a homogenizing event although it can create landscape-level heterogeneity. Density-dependent competitive mortality among the young conifer cohort contributes further to creation of homogeneity within the stand during the youthful competitive-exclusion stage of development; this is because the mortality is in smaller tree sizes and is most intense in densest portions of the stands (Franklin et al. 2002). As the Douglas-fir cohort matures, mortality shifts to such agents as wind, bark beetles, and root and bole diseases, which affects trees in the largest diameter classes and is typically spatially

aggregated. This shift in causes and patterns of mortality results in the development of canopy gaps within the stand and, consequently, regeneration and release of tree cohorts, albeit of the Douglas-fir's shade-tolerant associates, western hemlock and western redcedar. Hence, gap-based disturbance processes are now operating with the Douglas-fir sere and will do so with increasing frequency until the next stand replacement event erases this spatially complex stand structure. In effect, gap-based mortality in the overstory will eventually assert itself and move the stand toward a complex spatial structure.

Another similar example of interacting disturbances is found in Great Lakes aspen systems. Where aspen (*Populus grandidentata*, *P. tremuloides*) stands develop naturally, they are characterized by largely single-cohort structure, having initiated after intense stand replacing disturbance, particularly fire (Graham 1963). As the aspen-dominated stand matures, canopy gaps begin to open providing opportunities for establishment or release of later successional species, including tolerant northern hardwoods on better sites or white pine (*Pinus strobus*), white spruce (*Picea glauca*), and other conifers on poorer sites (Frelich and Reich 1995; Palik and Pregitzer 1993, 1994). In either case, multi-cohort, mixed-species stands develop

This pattern of gradual modification of homogenous even-aged stands by gap-level disturbance events--is repeated in most forest types subject to stand-replacement disturbances. Some of these types may not reach the level of spatial complexity that is characteristic of old-growth stands, due to either lack of longevity and growth potential or insufficient intervals between stand replacement disturbances or both. But the general pattern whereby gap-based disturbances gradually modify the homogenizing influence of the stand-replacement event can typically be observed.

It is instructive to contrast the structural conditions in stands and landscapes subject to stand-replacement versus gap-based disturbance regimes. Gap-based disturbance regimes result in stands with high levels of spatial complexity; stands are typically composed of mosaics of small structural units, each of which represents a different phase of stand development (Figure 5). Chronic gap-based disturbances--whether by wind, fire, or other agents--tend to perpetuate this complex structure; homogenizing, stand-replacement events are not a part of this disturbance regime. On the other hand, long-lived forest types that initiate with stand-replacement disturbance events do, ultimately, achieve similar complex structures but only after centuries of stand development. The end point in stand development in such a sere is a mosaic of small-scale structural units which collectively, incorporate all of the phases through which the stand evolved—disturbance, cohort establishment, canopy closure, competitive exclusion, vertical diversification, and horizontal diversification (Franklin et al. 2002) (Figure 6).

Chronic low-intensity disturbance regimes generate important biological legacies that shape stand development even though they do not necessarily kill overstory trees. Surface fire regimes associated with longleaf pine provide an excellent example (Kirkman et al. 2001, Palik et al. 2000). Such disturbances perpetuate the longleaf pine overstory and ground layers (e.g., wiregrass) that, in turn, provide the types and conditions of fuels that sustain this fire regime and prevent successional development of hardwood species (Williamson and Black 1981).

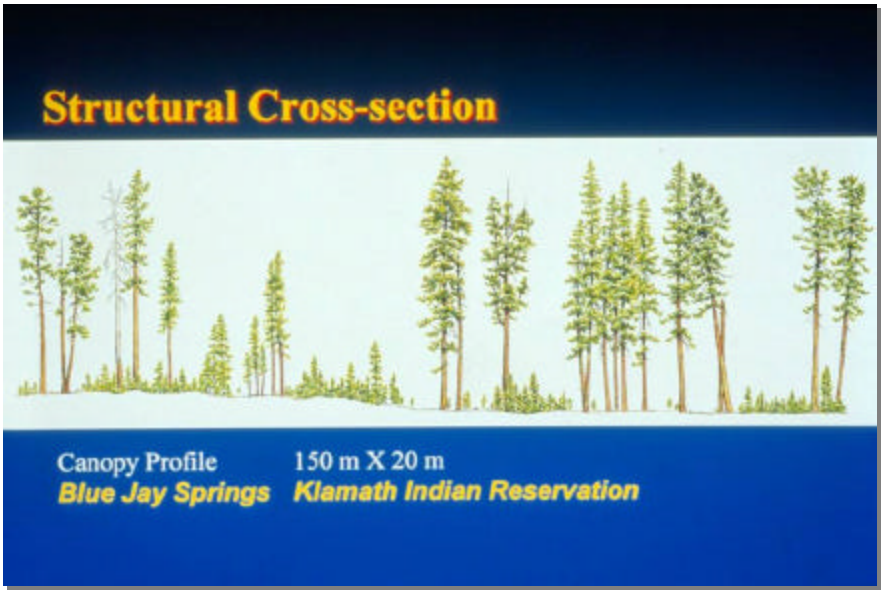

Figure 5. Cross-section of a ponderosa pine stand illustrating the complex mosaic of structural patches that is characteristic of forests that are subject to chronic light to moderate intensity disturbances, such as by wildfire or wind. Overstory mortality is in the form of individual tree or small gaps and shifting structural patchworks representing various stages in stand development are a consequence. (Bluejay Springs Natural Area, Winema National Forest, Oregon; drawing courtesy of Robert Van Pelt)

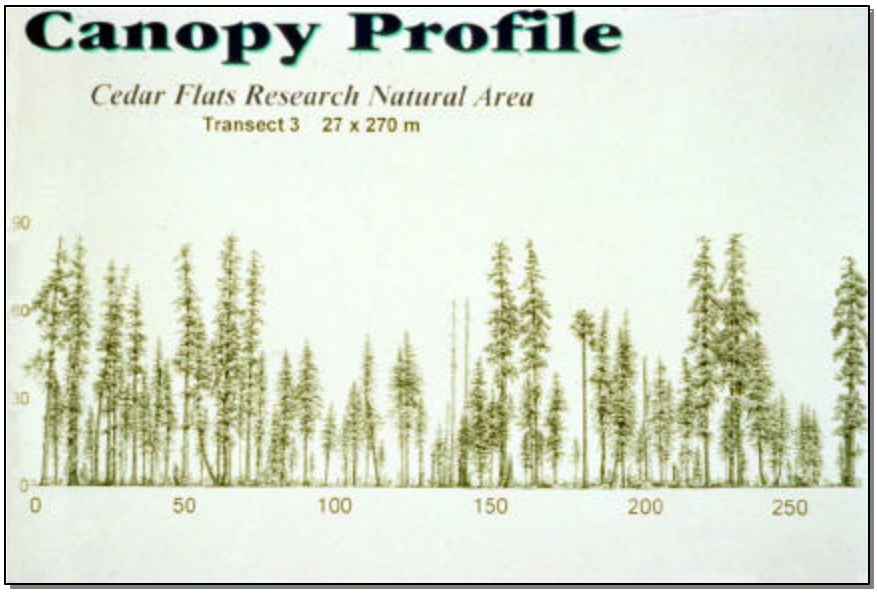

Figure 6. Cross-section of a 650-year-old stand of western redcedar, Douglas-fir, and western hemlock illustrating the mosaic of structural patches characteristic of old-growth stands in the Pacific Northwest. This mosaic is the consequence of centuries of development within a stand that was initially of even structure and age. The structural patches recapitulate all of the developmental stages through which the original stand evolved including disturbance, cohort regeneration, competitive exclusion, and maturation. (Cedar Flats Research Natural Area, Washington; drawing courtesy of Robert Van Pelt)

Contrasts between Natural Disturbance Regimes and Traditional Silvicultural Systems

Contrasts are large between traditional regeneration harvest techniques and conditions created by natural disturbance events and these are reflected primarily in the types of biological legacies that are left behind (Table 2). The contrasts are significant whether silviculture involves even- or uneven-aged regeneration harvesting techniques as will be discussed below.

Table 2. Biological legacies created by common regeneration harvest methods, as traditionally applied.

Legacy	Even-Aged			Uneven-Aged	
	Clearcut/Site Prep	Seedtree/Site Prep	Shelterwood/Site Prep*	Group Selection	Single-tree Selection
Live, mature trees	Absent	Absent to few	Absent	Absent (in group)	N/A
Seedling bank	Absent	Absent	Present	Possible	Possible
Intact understory	Absent	Absent	Absent	Possible	Possible
Snags	Absent	Absent	Absent	Absent (in group)	N/A
Logs	Few to Absent	Few to Absent	Few to Absent	Few/Absent (in group)	N/A
Uproots	Absent	Absent	Absent	Absent	N/A
Mineral seedbed**	Present	Present	Present	Present	N/A

* Following final removal of overstory
** Assuming ground-based harvest

There are also significant differences in the spatial and temporal patterns of natural disturbances and traditional regeneration harvest techniques. As noted above, natural disturbances that occur at the stand replacement scale typically generate substantial spatial heterogeneity in biological legacies. In contrast, harvested disturbances tend to homogenize and regularize the subsequent stand. This is particularly profound in the case of even-aged management regimes but is also true of many, if not most, uneven-aged management. For example, traditional selection systems for northern hardwood ecosystems in the Great Lakes region effectively drive overstory composition to sugar maple (*Acer saccharum*) dominance (Strong et al. 1997). In comparison, the canopy layer in unmanaged mature and old-growth northern hardwood stands often support 4 or 5 species in abundance and 10 or more species in total (Curtis 1959). Effectively, these approaches seek to create the idealized "regulated" condition at the landscape level and homogenize structural conditions at the stand level.

Even-Aged Management Regimes and Stand-Replacement Disturbances

Clearcut, seed tree, and shelterwood are the standard even-aged management regeneration approaches. In their basic form, clearcut and shelterwood regimes do not provide for any long-term structural legacies from the preceding stand. Overstory trees retained following the initial shelterwood harvest entries are eventually removed following successful establishment of regeneration. Only seed tree cutting provides an option to retain live trees, although retention

after regeneration of a new cohort of trees is typically done for economic rather than ecological reasons.

The lack of significant structural legacies is a major difference between these classical even-aged harvesting methods and natural stand replacement disturbances, whether by fire, wind or insects (Table 2). Most prominent among the missing legacies are remnant live trees and either abundant snags or down boles (with associated pit and mounds in the case of windthrow) or both.

Further contrasts between even-aged management regimes and natural stand-replacement disturbances relate to tree regeneration. Natural regeneration following wildfire is typically variable in time and space depending upon such variables as proximity of seed source and occurrence of large seed crops. Establishment of dense tree regeneration and subsequent tree canopy closure may take many years or even decades, particularly on sites with severe environmental conditions. Establishment of regeneration by planting--as is typical under many even-aged management regimes—or from advanced regeneration results in much more rapid and uniform re-establishment of forest cover.

Incorporating Natural Models into Stand-Replacement Systems

Incorporating structural legacies into traditional even-aged harvest practices is the most obvious way to better approximate the outcomes of natural disturbance regimes. Such legacies would include live trees, snags, and down boles. Size range of legacy structures is an important consideration. The sizes of retained live trees, snags, and logs on the ground should span a range of diameters including very large (in a relative sense) individuals

Modifying clearcut and shelterwood prescriptions to incorporate minimal levels of "wildlife" trees, snags, and logs is widely practiced today and represents a first step. Even-aged harvesting with "reserves" is a more formalized approach to incorporating some legacies into traditional harvest methods. However, a problem with this approach is that it rarely recognizes either the multiple ecological roles played by such "reserved" structures or the nearly infinite array of structural retention prescriptions that is possible. For example, these approaches rarely address spatially variable patterns of retention explicitly. An irregular shelterwood (Smith et al. 1997), for instance disperses residual trees uniformly across the stand (e.g., Boyer 1963, 1993 for longleaf pine), a pattern that is rare in nature.

Another problem is the confusion that can arise when significant structural legacies are retained but the prescription is still identified as a "clearcut" when it clearly (at least to all lay stakeholders) is not. Such confusing labeling is a semantic consequence of these structures being retained for ecological purposes rather than to assist in regeneration of a new tree crop! For example, it is misleading to use terms like reserve shelterwood or seed-tree prescription, when the primary goal for retaining large trees is sustainability of ecological services other than regeneration potential. Another problem with recent implementation of legacy tree approaches in even-aged management systems occurs when only poorly formed or small trees or non-commercial species are retained. While some of these trees may have ecological value, their selection is based primarily on economic factors and they certainly do not provide representative examples of the original forest nor of many of the most important structural features. An important question to ask, when judging the ecological success of retention, is whether examples of large, high quality stems and most valuable trees species are being retained at some level. If the answer to this question is no, then the ultimate success of the retention harvest is in doubt.

The conceptual development of variable retention harvesting provides both a philosophical and a practical basis for systematically incorporating structural legacies into harvesting prescriptions (Franklin et al. 1997; Lindenmayer and Franklin 2002). Silvicultural prescriptions using this approach consider the types, densities, and spatial arrangements of legacies that are needed to achieve management objectives. Variable retention harvesting is particularly relevant for forest systems subject to stand-replacement or mixed disturbance regimes and is more fully discussed later in this paper.

There are other important contrasts between stand-replacement disturbances and traditional even-aged silviculture that relate specifically to size and shape of the openings and frequency of the disturbance. Clearcuts are often smaller than the areas affected by stand-replacement disturbances; shapes are typically much simpler and uniform unless they have been specifically designed to minimize visual impacts. Rotation or regeneration harvest frequency is typically shorter, often much shorter, than the return interval of the natural disturbance.

Uneven-Aged Management Regimes and Gap-Creating Disturbances

Single tree selection and group selection are the traditional uneven-aged regeneration systems (Smith et al. 1997). Theoretically, selection practices are modeled closely on individual tree or gap-based natural disturbance regimes. In practice, these approaches can be highly formalized, such as where selection of trees is driven by efforts to create hypothetical stand diameter distributions based on *q* values (see below), even though most natural stands fail to exhibit such regularity. The most fundamental problem is that most selection prescriptions remove different trees and on different spatial patterns than small-scale natural disturbances, which clearly has consequences for biological diversity and ecosystem processes.

Individual tree selection

Typical individual tree selection contrasts significantly with natural disturbances in terms of the types of trees that are removed or, conversely, the nature of the biological legacies. For various reasons most selection systems involve the systematic removal of at least some, if not all, of the very large and old trees from the stand. Such trees are viewed as no longer contributing significant stand growth based on a general presumption that large, old trees are over-mature and likely to die in the near future. Ironically, these trees are often healthy and of exceptional form at the time of their removal. Thus their removal is driven as much by current economic considerations as by potential for impending mortality. Moreover, studies of tree demography in many forest types and for many tree species show that large trees actually have lower rates of mortality, i.e., greater probability of survival, than smaller trees.

Of course, traditional selection prescriptions do not recognize the importance of large decadent trees and their derivatives, large snags and large down boles, for biological diversity and many ecosystem processes (see Harmon et al. 1986 and Maser et al. 1988 for the numerous roles that such structures play). Consequently, most individual tree selection systems also involve the systematic removal of decadent, diseased, or poorly formed trees, although there are practitioners who explicitly retain trees of these types for ecological purposes, especially as wildlife habitat (Mitchell et al. 2000).

Use of gap-based canopy disturbance as a quantitative guide for multi-cohort silviculture contrasts in several significant ways to the traditional approach to selection based on the BD*q*

method. With the latter approach, a target residual basal area (B) and maximum diameter (D) are specified *a priori*, while the distribution of trees across diameter classes is determined by the diminution quotient (*q*), a value that reflects the ratio of the number of trees in diameter class a, to the number in diameter class a+*1* (Smith et al. 1997).

Specification of a target residual basal area is not necessarily in conflict with a gap-based approach to uneven-aged management. A forester can easily determine and justify a target residual basal area and then, using inventory data, calculate the number and size of canopy gaps needed to reach this target at a given harvest entry.

Selection of maximum tree diameters and *q* has the potential to move stands structurally in directions having little or no natural analogy, however, varying basal area targets based on variation found on bench mark sites may contribute to forest heterogeneity. The theoretical goal of the *q* quotient, which ranges from>1 to 2, is to create "balanced" all-aged stands that will sustain timber yield; that is, stands with uniform ratios between successive diameter distributions across the full range of diameters. Several conceptual difficulties arise with this approach. First, the system equates diameter with age, such that larger trees are assumed to be older. This often false assumption can have disastrous consequences. For example, smaller trees of a tolerant species may not respond to release if they are actually older than large trees. Second, there is little evidence that balanced all-aged stands occur with any regularity in nature. The sustainability of multi-aged stands is largely a function of mortality balancing new cohort establishment and growth over sufficiently long time periods. Over short time periods, mortality may greatly exceed in-growth or vice versa. Over a sufficient time perspective, there is no reason that diameter or age distributions need be balanced at any given time. Third, higher *q* values are more likely to result in sustained yield by allowing for greater numbers of smaller trees, relative to low *q* values. However, high *q* values also specify retention few larger diameter trees. In application, a poorly determined *q* value will greatly limit the number of old, large diameter trees in a stand, which are specifically those trees that have the great ecological value. For the same reason, specification of a maximum tree diameter, under the BD*q* methodology, makes no sense ecologically.

Finally, there is little reason why stands managed for multi-cohort structure need to conform to any expectations of sustained yield, based upon specific diameter distributions. The sustained yield concept is best applied to whole forests and regions. At the stand scale, the advantages of selection systems that produce multi-cohort structure have little to do with sustained yield, but are fundamentally issues of ecological sustainability as measured by structural complexity, compositional diversity, and occurrence of a wide range of habitat characteristics.

Group selection

Traditional group selection harvest practices contrast in structural legacies with multi-tree, gap-based natural disturbance regimes. Natural gap-based disturbances leave behind significant biological legacies, including snags or downed boles or both (Figure 7). Depending upon the disturbance agent there may be other living legacies, such as intact understory layers (including seedling banks) and uproot pits-and-mounds in the case of wind-created gaps. Few prescriptions based upon group selection have explicitly incorporated such structural legacies as large live trees, snags, downed boles, and soil disturbance, although they could do so.

Contrasts in opening size between gap-based natural disturbance regimes and traditional group selection harvest practices frequently arise. Group selection generally prescribes larger (sometimes several times larger) openings on average than the size of gaps created by natural disturbance processes. In many forests it is common for openings to exhibit a log-normal distribution of gap sizes, with the largest numbers of openings in the smallest size and rapidly declining numbers of gaps of increasingly larger gap sizes (see Figure 4 in Rebertus et al. 1997). For example, group selection is proposed as the primary harvest method in mixed-conifer types on national forests in the Sierra Nevada but 1-2 ha openings are prescribed. A "gap" this size is certainly much larger than size of natural gaps (typically 0.08-0.10 ha) that are typically found within these forests (see, e.g., Knight 1999). As noted earlier, natural gaps typically exhibit a range in sizes with the size distribution heavily skewed toward smaller openings. Factors influencing foresters to select larger than natural average opening sizes under group selection prescriptions almost certainly include concerns about: growth rates of reproduction; cost and operational difficulties associated with harvesting in small areas; and generation of greater revenues at one point in time.

Figure 7. Small disturbance gap with Sierran mixed-conifer forest in Yosemite National Park, California; note the biological legacies of snags and down boles as well as natural regeneration of ponderosa pine and associated species within the gap.

We would also argue that openings that are 1-2 ha in size are, in fact, small clearcuts rather than analogues to natural gaps. One can base this argument on the rule of thumb for defining minimum harvest sizes (Smith et al. 1997) that says the microclimate in the middle of a forest opening will be profoundly different from that of the surrounding forest if the opening has a radius greater than the height of the surrounding trees. (For a 20-m tall tree this equals 0.13 ha).

Incorporating natural models in selection systems

Selection silviculture can be modified easily to incorporate biological legacies, along with stand level goals that provide for compositional richness and structural complexity characteristic of natural gap-driven stands. Such an approach maintains the landscape in a forest-dominated condition, which is one of the most important environmental aspects of uneven-aged forestry. Marking guidelines can explicitly incorporate goals of maintaining old and large trees and their derivatives (large snags and downed boles) as part of the stand. There are examples of such approaches (Mitchell et al. 2000).

Similarly, prescriptions under group selection can (and we would argue, usually should) incorporate retention of snags, and downed boles explicitly in the gaps. Again, there are

examples of such prescriptions that have been applied to such diverse forest types as Coast Redwood (*Sequoia sempervirens*) and eastern hardwood forests. Group selection prescriptions proposed for mixed-conifer types on national forests in the Sierra Nevada provide for structural retention by requiring that all trees >30 inches diameter at breast height (dbh) be retained; the intention is to retain these structures in perpetuity.

Opening sizes and shapes prescribed under group selection should also vary to more closely match the sizes and shapes of gaps created by natural disturbances, rather than using a standard "cookie cutter" opening. Varying size in relationship to that observed in natural disturbance is likely to result in smaller average opening sizes as well as greater variability in opening size. Many, if not most, shade-intolerant species, such as many pines, appear to be very capable of successfully establishing themselves and growing within small openings (McGuire et al. 2002, Palik et al. 2003). Although survival and growth rates may be less than those achievable in clearcuts, reduced growth and survival is not a primary issue where timber production is not the dominant goal of management.

An additional issue to consider for individual tree and small group selection systems is the incorporation of multiple structural objectives within individual stands. As a specific example, silvicultural systems that create (if not already present) and maintain a population of large, old trees should be considered for many forest types subject to gap- or tree-based disturbance regimes. Western North American mixed conifer forests naturally subject to frequent, low- to moderate intensity disturbance regimes are an example. Large, old trees and their derivative structures (large snags and downed boles) were constant and important structural elements of such forests. One management goal would be to maintain some minimum population level—say 10 large, old trees/ha--with flexibility to achieve this goal on larger spatial scales. In other words, in a large stand, an area based target for large, old tree could be met by retaining, for example, 25 trees/ha in some parts of the stand, but none in other parts of the stand. The latter part of the stand could be managed as either an even- or uneven-aged stand to achieve a variety of goals, including acceptable fuel levels and production of wood products; of course, it would have to also be managed to provide replacement trees for the population of large, old trees.

Two-Cohort Management and Heavy Partial Disturbances

One can view the previous discussions on even-aged and uneven-aged management as two endpoints along a gradient of structural complexity and retention of legacies. Consider the middle ground along this gradient, that is, heavy partial disturbances that create largely two- or three-cohort stands can be instructive (Palik et al. 2002). Retention harvesting, as an analog to stand replacing natural disturbance (see above), also creates two-cohort stands, but the outcome may be a fairly low level of retention, such that the new cohort is the dominant structural feature of the stand. In contrast, heavy partial disturbances result in higher levels of retention than is characteristic of stand replacement disturbance, but also remove more of the overstory in any one event than individual tree or gap disturbances. A useful way to characterize heavy partial disturbance, relative to gap or stand replacement disturbance, is through consideration of simultaneous responses of regeneration and residual tree growth. Gap-scale disturbances provide regeneration opportunities in only a limited area of a stand after any single event. Similarly, gap disturbances increase growing space for only a limited number of residual trees. In contrast, stand replacement disturbance provide substantial regeneration opportunities throughout most of

the stand, but by definition, few overstory trees remain to capitalize on increased growing space. Heavy partial canopy disturbances provide substantial opportunities for new establishment along with increased growth of residual canopy trees, the latter because many trees escape the disturbance and growing space for these trees is opened throughout much of the stand (Fajvan and Seymour 1993). Heavy partial disturbances are characteristic of a wide array of forest types including Acadian mixed conifer forests (Fajvan and Seymour 1993, Seymour and Hunter 1999) and the Great Lakes red-white pine forests (Heinselman 1981). In the nomenclature of traditional silviculture, an irregular shelterwood, with retention levels exceeding 20% but less than 60%, may be a good silvicultural analogue in such systems (Seymour and Hunter 1999, Palik and Zasada 2002).

Applying Principles from Natural Disturbance Regimes to Ecological Silviculture

Principles and constructs from natural disturbance and stand development regimes provide the conceptual basis for designing complete silvicultural systems to achieve the goals of ecological forestry, which include restoration and maintenance of biological diversity and ecosystem functions, along with wood production. There are three basic approaches or classes of activity that must be incorporated into ecological silviculture:

- Incorporating the concept of legacies into harvesting prescriptions, such as:
  - Structural legacies (e.g., trees, snags, logs, and uproots);
  - Compositional legacies (e.g., seed and seedling banks, trees, shrubs, and herbs representing different species or functional capabilities);
  - Physical legacies (e.g., mineral soil seedbeds or opening sizes).
- Incorporating natural stand development processes, including small-scale disturbances, into silvicultural treatments of established stands, such as:
  - Variability density thinning;
  - Decadence creation; and
  - Prescribed burning
- Allowing for appropriate recovery periods between regeneration harvests Whether in stand-, gap-, or individual tree-replacement forest types.

We discuss each of these categories of activity in more detail below.

An essential first step in applying principles from natural disturbance regimes and stand development to ecological silviculture is to understand that creating and perpetuating appropriate structural, functional, and compositional attributes in stands is the primary goal. “Appropriate” here means attributes that will achieve our defined goals, which under restoration forestry always include ecological objectives. Our purpose is ***not*** development of silvicultural systems that are precisely modeled on natural disturbances and stand development regimes, even if that were possible, which it almost never is (e.g., see Palik et al. 2002). Rather, the objective is to understand natural processes and draw upon them in designing a management regime that will achieve ecological and other management goals. This issue is discussed further in a following section, “Realities of restoring diversity and complexity in managed forests”.

Adopting a mind-set of forest continuity rather than forest termination is helpful in opening oneself to the possibilities inherent in ecological forestry. It is useful to put aside the

notion *that all forest stands must be terminated and new ones regenerated at some point in the future*! This appears to be a fundamental assumption of even-aged management, at least wherever forest types with stand-replacement disturbance regimes are being considered. We have learned that at least some structural elements of the stand are continuously maintained even under stand-replacement regimes and that such stands can often be managed with sufficient levels of retention so as to maintain at least some level of continuous forest influence over the site. Of course, where tree- and gap-based disturbance regimes are characteristic of the forest type or site, natural stands are rarely, if ever, terminated. In a very real sense, ***natural situations in which forest stands are completely terminated and totally replaced by a new stand are rare rather than common,*** however common we have made even-aged stands in a production-oriented landscapes

Incorporating Legacies into Harvesting Prescriptions

Incorporating the concept of biological legacies into regeneration harvest prescriptions is one of the important principles of ecological forestry. We know from our earlier discussions that these include important structural legacies from the existing stands, such as large and decadent trees, snags, and boles and other coarse woody debris on the forest floor. Such structures typically: persist as legacies even through the most intense stand-replacement disturbances; they play critical roles as habitat, modifiers of the physical environment, and participants in physical (e.g., geomorphological and hydrological) processes; and they are difficult or impossible to re-create in managed stands, hence the need to carry them over from the predisturbance stand. Directly and indirectly, such structural legacies lifeboat many elements of biodiversity and, where a stand-replacement disturbance regime prevails, structurally enrich the new stand.

Structural retention is being increasingly incorporated into harvest prescriptions throughout the temperate forest regions of the world (Franklin et al. 1997, Vanha-Majamaa and Jalonen 2001, Lindenmayer and Franklin 2002). This approach has been labeled "variable retention harvesting" (VRH) and defined as:

> ". . . an approach to harvesting based on the retention of structural elements or biological legacies (trees, snags, logs, etc.) from the harvested stand for integration into the new stand to achieve various ecological objectives. . . Major variables are types, densities, and spatial arrangements of retained structures" (Helms 1998)".

In Canada the approach has been formalized as the "Variable Retention Harvest System" and defined as:

> "Retention system means a silvicultural system that is designed to: (a) retain individual trees to maintain the structural diversity over the area of the cut block for at least one rotation, and (b) leave more than half of the total area of the cut block within one tree height from the base of a tree or group of trees, whether or not the tree or group of trees is within the cut block" (Mitchell and Beese 2002)".

VRH prescription must address the three issues including which structures to retain, how much of each to retain, and the spatial pattern of retention—e.g., dispersed or spatially aggregated in the harvest unit. Decisions on these three variables obviously must be related to the specific management goals for the harvested stand and priorities among those goals; consequently, a broad spectrum of specific prescriptions is possible (Figure 8) (Franklin et al. 1997; Lindenmayer and Franklin 2002).

VRH has most often been applied to forest types and sites characterized by stand-replacement disturbances and used to modify traditional even-aged management regimes. Legacies typically selected for retention are large structures--including large old and often decadent trees, snags, and downed boles--that fulfill many important ecological functions but are

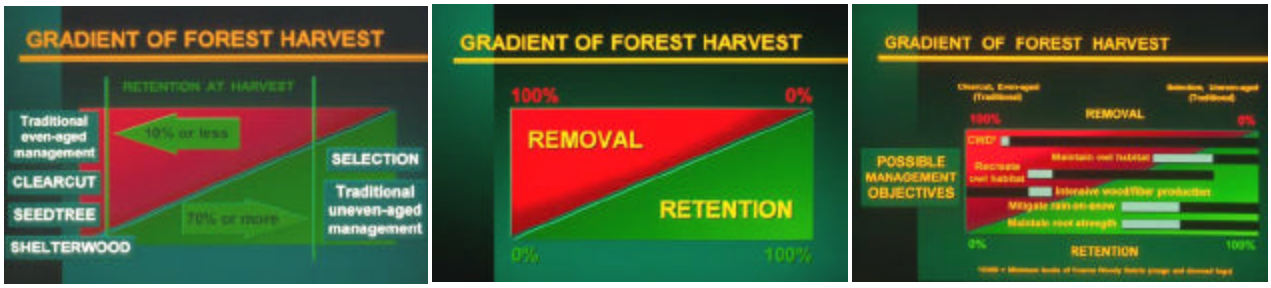

Figure 8. Variable retention harvesting represents a continuum of possibilities (a) which traditional forest harvest systems have only partially exploited (b) but which can be exploited to respond to a range of management goals (c).

Figure 9. Typical structures retained on a harvest unit on public lands in the Douglas-fir region include large, decadent live trees, large snags, and large downed boles, all of which are impossible to re-create in stands managed under even moderate (e.g., 100-year) rotations.

difficult to recreate under typical management regimes (Figure 9). The issue of spatially variable retention is a particularly interesting one, since some ecological objectives are best sustained by dispersing the structures over the harvest unit while other objectives are best served by aggregating the structures (Table 3). Similarly, spatial pattern of retention may lead to profound differences in growth and productivity of tree species (Palik et al. 2003).

Compositional legacies can be very important considerations in VRH even though we have emphasized structural legacies up to this point. For example, retention of specific species can be an explicit element of a VRH prescription. Sometimes this will actually be done in order to retain structures or structural conditions of a specific type, such as with retention of a hardwood component in an otherwise conifer-dominated stand. Retention should incorporate both commercial and non-commercial species. Historically, the latter often are removed despite their ecological value, such as the deliberate removal of non-commercial hardwood species in boreal conifer forests (see Palik and Engstrom 1999). Sometimes retention may be prescribed in order to maintain species with special functional capabilities, such as in nutrient cycling. Of course, as noted earlier, one of the major purposes of structural retention is to lifeboat many elements of biological diversity, whether these elements are explicitly identified or not.

Table 3. Comparison of effectiveness of spatially dispersed and aggregated structural retention for different ecological objectives, including conserving biological diversity.

OBJECTIVE ON HARVEST UNIT	PATTERN OF RETENTION	
	Dispersed	***Aggregated***
Microclimate modification	Less, but generalized over harvest area	More, but on localized portions of harvest area
Influence on geohydrological processes	Same as above	Same as above
Maintenance of root strength	Same as above	Same as above
Retain diversity of tree sizes, species, and conditions	Low probability	High probability
Retain large-diameter trees	More emphasis	Less emphasis
Retain multiple vegetation (including tree) canopy layers	Low probability	High probability
Retain snags	Difficult, especially for soft snags	Readily accomplished, even for soft snags
Retain areas of undisturbed forest floor and intact understory community	Limited possibilities	Yes; can be as extensive as Aggregates
Retain structurally intact forest habitat patches	Not possible	Possible
Distributed sources of coarse woody debris (snags and logs)	Yes	No
Distributed source of arboreal energy to maintain below-ground processes and organisms	Yes	No
Carrying capacity for territorial snag- and/or log-dwelling species	More	Less
Windthrow hazard for residual trees	Average wind firmness greater (strong dominants), but trees are isolated	Average wind firmness less, but trees have mutual support
Impacts on growth of regenerated stand	More; generalized over harvest area	Less; impacts are localized

Structural and compositional retention is also relevant to silvicultural prescriptions for uneven-aged or multi-aged stands, i.e., for forest types subject to tree- or gap-based or mixed disturbance regimes. For example, it is often appropriate to retain structures as a part of gap-based harvest prescriptions, i.e., within harvested gaps or "groups". This can be augmented by permanently reserving a certain percentage of the stand from any future harvest, thereby insuring that such structures will persist in some part of the stand.

Perhaps even more broadly relevant is the notion of managing stands to sustain some desired population level of large old trees and the derivative large snags and large downed boles they provide. This is certainly one of the goals implicit in most VRH prescriptions, whether in even-, multi-, or uneven-aged stands. However, perpetuating a specific tree population

obviously goes beyond the immediate goal of lifeboating organisms and processes and makes explicit the need to manage the remainder of the stand so as to provide for replacement trees.

Incorporating Natural Stand Development Processes in Tending Stands

Managing established stands for structural and compositional heterogeneity is a second important category of potential silvicultural activity. This category is comparable to intermediate stand-level treatments in traditional silviculture, such as thinning and pruning, and may actually include such practices. However, the goal in ecological forestry is typically to create structural and compositional diversity throughout the harvested stand, rather than to concentrate growth on selected trees and create spatially uniform stands, which is the case with most traditional stand tending applications.

Intermediate stand-level treatments are generally modeled on natural stand development processes, such as:

- Competitive (density dependent) tree mortality, which stimulates development of large diameter trees and associated features, such as large branches and extensive heartwood;
- Disturbance-based tree mortality (e.g., from root rots, wind, and bark beetles), which generates gaps and large CWD;
- Disturbance-based impacts on understory conditions from low intensity fire with varied species-specific consequences (retardation to stimulation) and effects on fuel loadings;
- Development of multi-layered canopies and ground-layer vegetation in response to reduced stand densities and development of gaps; and
- Development of decadence in living trees, such as brooms, decay pockets, and cavities.

Note that many of these stand development processes are actually tree- or gap-scale disturbance events or their consequences!

The importance of small-scale disturbance processes in influencing stand development processes is apparent, particularly after the initial period of exponential stand growth and competitive mortality have been completed (Franklin et al. 2002). Hence, we should be specifically planning for intermediate stand-level treatments that replicate the small-scale disturbance or gap-forming processes, such as variable density thinning. If this conclusion seems obvious we need to remember that traditional timber management foresters specifically seek to avoid ***any*** disturbance based mortality, especially when it kills dominant trees and tends to be spatially aggregated, i.e., creates canopy gaps. Such mortality is typically ***not*** viewed as a part of natural or, at least, acceptable stand development processes! So, stand management practices that attempt to emulate such gap-creating disturbances are a major deviation from practices used in traditional timber production.

Specific intermediate stand-level treatments that can be carried out to create and maintain structural and compositional complexity and heterogeneity in established stands include:

- Thinning to stimulate development of larger trees;
- Variable density thinning to stimulate development of spatial heterogeneity;
- Decadence creation in living trees and in the form of snags and down boles;
- Introduction and conservation of compositional diversity; and
- Control of undesirable plant and animal species.

Intermediate stand-level treatments are usually carried out using mechanical approaches (e.g., axe and saw) or prescribed fire or combinations of the two approaches, although other methods, such as use of chemical or biological agents, are possible. Mechanical treatments and prescribed fire are clearly not equivalent in all of their effects on the treated forest, even though they may produce comparable reductions in stand density. For example, fire results in the consumption of fine organic matter and release of nutrients. Insofar as thinning is concerned, effects of prescribed fire tend to be less predictable and more varied than mechanical thinning; indeed, one of the benefits of prescribed fire is that it is likely to produce a 'variable density" mosaic.

Incorporating Appropriate Recovery Periods

Allowing appropriate recovery periods for the development of a rich array of biological legacies, as well as significant structural and compositional heterogeneity within stands, is the third key principle of ecological forestry. Too often, forests are terminated before significant complexity has developed (Figure 10). Consequently, most commercially managed stands are lacking trees of large diameter, significant amounts of large dead wood, and trees with unique structures (cavities, large limbs, large amounts of heartwood). Moreover, they are compositional depauperate, particularly in the canopy, because not enough time has passed for tolerant species to recruit from the understory into gaps opened by small disturbance. This problem is compounded further if the stand was deliberately or inadvertently simplified during establishment, e.g., no legacies retained, single-species planting with uniform spacing.

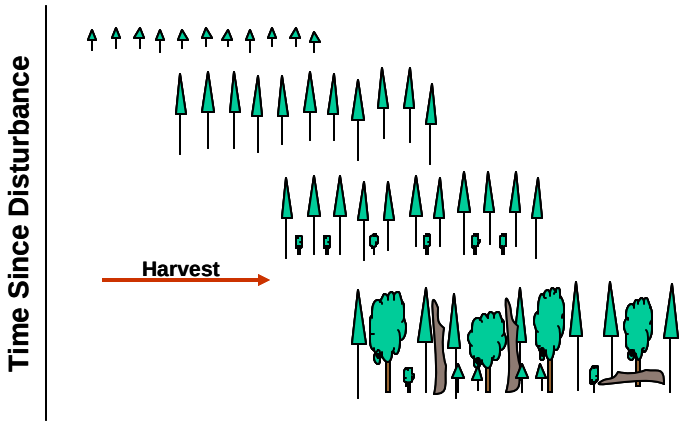

Figure 10. Conceptual representation of the development of structural complexity over time. In this example, the young post-disturbance stand is managed for simplified structure and composition (first frame). In many traditional forestry approaches, the stand is harvested before significant compositional diversity and structural complexity has had time to develop (last frame).

In such a case, a stand largely devoid of legacies is harvested before significant amounts of structural and compositional complexity has developed. A good example of this is seen in Great Lakes aspen forests. The majority of this forest type initiated in the early part of the last century after widespread logging was followed by intense slash fires (Graham et al. 1963). Historically, managed aspen stands in the great lakes landscape, are devoid of significant amounts of biological legacies, or of spatial heterogeneity in structure (Figure 11).

Figure 11. A regenerating aspen stand in Michigan. Note: older eastern white pine is the only significant ecological legacy from the previous stand. Photo: Kurt Pregitzer.

Moreover, the traditional management prescription calls for clearcut harvesting by 60 to 80 years of age, often before significant amounts of structural and compositional complexity have developed in the stand.

The motivation for terminating stands before development of complexity is driven by the prevailing practice among production foresters of linking rotation age to the growth trajectory of crop trees; so called culmination of mean annual increment. Specifically, rotation age is set around the point where the trajectory of periodic annual increment intersects the trajectory of mean annual increment. It is at this age where the rate of growth for crop trees in a stand has declined to a level that is no longer considered acceptable economically. In stands that are not thinned, time to culmination of annual increment can be quite short, relative to tree life spans. For instance, volume growth of site index 170 Douglas-fir culminates at around 65 years (as cited in Daniel et al 1979). Obviously, for such a long-lived species, this is well before much structural complexity will have developed in managed stands.

Another issue is the fact that culmination of annual increment can be delayed or reversed through periodic thinnings. For example, the mean annual volume increment curve for red pine in extended rotation stands in northern Minnesota intersect the periodic annual increment curve at an advanced age, due to growth increases after repeated thinning beginning at age 85 (Figure 12). The traditional rotation age for red pine on industry lands in the region is 50-70 years. This dynamic suggests that setting a rotation age on growth increment alone is problematic from even an economic standpoint, let alone from an ecological standpoint. In short, for ecological forestry, there is little reason to set a rotation age of a stand based solely on growth and economic factors. Rather, the primary determination of harvest age should be the development of acceptable levels of structural complexity, compositional diversity, and within stand heterogeneity of these factors.

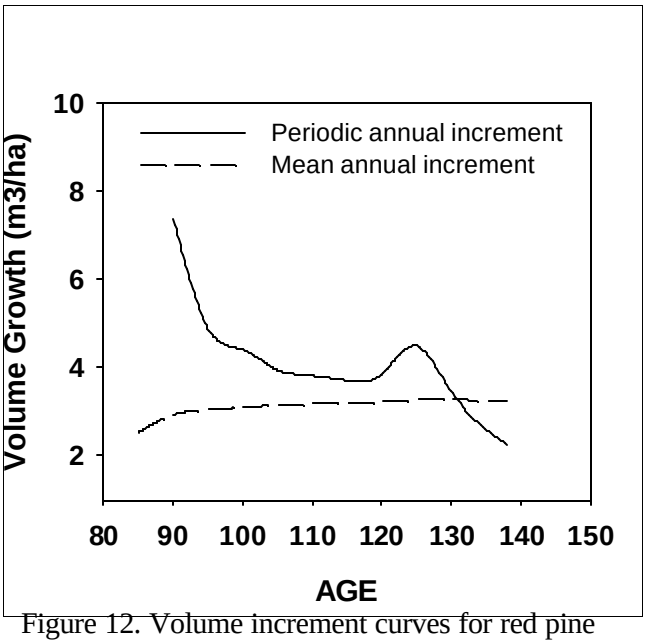

Figure 12. Volume increment curves for red pine in the Cutfoot Experimental Forest, northern Minnesota. The forest was thinned seven times, to a target basal area of 25 m^2/ha since stand age 85. Dashed line is mean annual increment; solid line is periodic annual increment (B. Palik unpublished data).

Realities of Restoring Diversity and Complexity in Managed Forests: How Close to the Natural Model?

Silviculturally mimicking natural disturbance regimes to restore ecological complexity is a challenge if for no other reason than the conditions created by natural disturbances can never be fully achieved in forests that are also managed for wood production (Palik et al. 2002). However, failure to precisely duplicate these conditions is not a shortfall of the approach but, rather, a consequence of the desire to produce timber and harvest wood from managed forests as well to maintain ecological values.

The challenge is the need for approaches that lead to restoration and maintenance of ecological complexity, along with opportunities to meet certain timber management goals. The balance may shift towards one goal or the other at different times and different locations, depending upon priorities among management objectives. In many cases, the ultimate objective is to facilitate implementation of silviculture based upon natural disturbance and stand development models without ignoring the economic goals.

A useful framework for addressing issues of ecological complexity in forests managed for wood is a conceptual model that arrays stands along gradients of i) management objectives, ii) time or age since disturbance, and iii) among stand variability of complexity (Figure 10). In this model the area in gray represents the domain of natural variability of the system (Landres et al. 1999) as defined by combinations of time since disturbance and degree of structural and compositional complexity. This domain represents the array of benchmark conditions for the system.

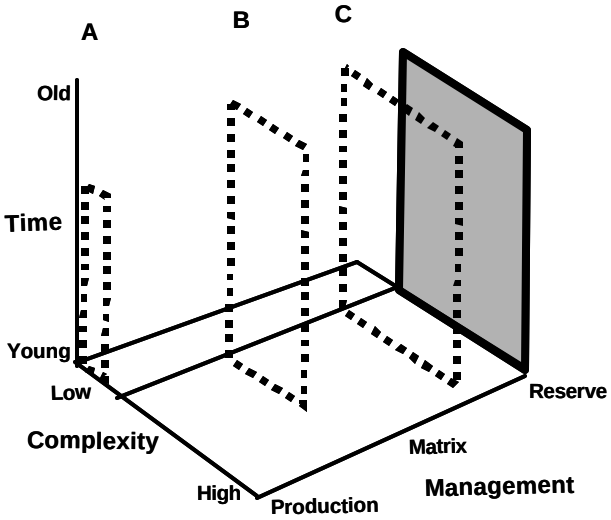

Figure 13. Multi-dimensional conceptual model for judging disparity in ecological complexity between managed forests and benchmark conditions. The area in gray represents the domain of natural variation in complexity of the benchmark condition, as a function of time since disturbance. The dashed rectangles represent domains of variability in complexity, as a function of time since disturbance, for a variety of management scenarios. See text for details.

The nature of the benchmark condition is constantly debated (Hunter 1996). Presettlement forests represent one potential benchmark, but restoration to a strict presettlement reference is unrealistic for most landscapes because of changing climates, altered potential for use of fire in management, and uncertainty as to what presettlement conditions actually entailed, particularly at the stand scale. An alternative approach--"designing by nature"—places less emphasis on the exact characteristics of the benchmark condition but, rather, assumes that use of natural disturbance-based silviculture will move forest ecosystems toward desired future conditions. The extent that that assumption can be tested is the degree that rarity, both in terms of rare ecosystems with their characteristic biotic richness and rare organisms are sustained in robust ways in the landscape.

Regardless of the exact nature of the benchmark condition, it is important to recognize that the domain of natural variability includes young post-natural disturbance ecosystems and that these young stands often contain high levels structural and compositional complexity, even immediately after a stand-replacement disturbance (Franklin et al. 1997).

In the model, the dashed rectangles are domains of variability in age structure and composition for management scenarios differing in the degree to which they achieve multiple objectives of wood production and sustainability of ecological complexity. Domain A might represent a plantation of an exotic species managed intensively for fiber; note that the range of variability in complexity is not only narrow but also lies outside the range of natural variability. Domain B might include systems managed for large-diameter saw logs and structural complexity by developing two-cohort stands. Notice that the range of variability is narrow, relative to the benchmark condition, but still within the domain of natural variability. Domain C might represent a system managed for maximum similarity to a benchmark condition, such as with limited harvesting of lightning or wind-killed trees.

When considering this model, managers should determine how similar to the benchmark conditions are needed to achieve the management goals. The answer is objective driven. When managing ecological reserves, the goal probably will be to get as close to the benchmark condition as possible. When managing for maximum fiber yield, reducing the disparity with the benchmark condition is probably not a consideration. When managing for outcomes within the region of matrix management, reducing the disparity to the benchmark condition is an important consideration, but in many instances it will be done in ways that are constrained by meeting other objectives. The goal often will be to model the benchmark condition, within the real-world constraints of managing for wood production. In this case, the objective is to shift stands to the right on the management axis (Figure 13) through innovative incorporation of complexity, while still maintaining some level timber production as one objective.

Simberloff (1999) suggests that any proposed silvicultural system designed to maintain biodiversity and produce timber should be treated as a hypothesis, due to the limited number of empirical studies to support or refute the approach. Our model can be used to pose such hypotheses and than design silvicultural experiments to test them. For instance, one might hypothesize that as managed systems move closer to the benchmark condition, productivity of bole wood declines linearly, exponentially, or not at all. Alternative, one could test the hypothesis that the amount of complexity in managed stands can be increased while maintaining a fixed level of wood production.

Natural Disturbance-Based Silviculture and the Restoration and Sustaining of biodiversity: Case Studies from Three Regions

General principles, as previously presented, that conceptually link natural disturbances, forest structure, and maintenance of biodiversity with silvicultural is necessary but not sufficient to restore or sustain native biodiversity. Managers deal with a specific property, each of which is managed for specific objectives and is found in a specific condition. Application of the general principals developed in the literature review requires that managers integrate concepts with a thorough knowledge of the natural history and ecology of the system that they manage and an appreciation for how the specific objectives of the land in question fits into broader regional goals of conservation biology.

To illustrate how concept and practice can be developed into silvicultural approaches that have conservation of biodiversity as a direct goal we review efforts in the southeastern U.S., the Lake States, and Pacific Northwest. Each case study is intended to describe the implementation of silviculture that restores and sustains monitors and adapts through time.

Southeastern Case Studies

Introduction

The fire-maintained longleaf pine savannas of the southeastern Coastal Plain are not only among the most species-rich communities in North America (Walker and Peet 1983, Kirkman et al. 2001) but also home to large numbers of rare and threatened endemic flora and fauna (Hardin and White 1989, Walker 1993). Moreover, they are among the most threatened ecosystems having experienced one of the most precipitous declines since European settlement (Noss et al. 1995). This upland forest type is also important in the maintenance of regional biodiversity because it serves as a vector for fire to spread into associated wetland communities, maintaining habitat for unique assemblages of plants (Kirkman et al. 1998, 2000; Figure 14) and animals particularly amphibians and reptiles (Duellmann and Sweet 1999). The diminishing nature of these habitats have been due to multitude of factors including fire suppression, intensive site conversion to other timber species, and conversion of land to agricultural and urban land uses (Landers et al. 1995).

Figure 14. The longleaf pine-wiregrass ecosystem has evolved under a number of stochastic disturbances of various intensities. The most important of these disturbances is frequent fire, which maintains the open-canopy structure and high groundcover biodiversity. Photo by Stephen Pecot.

The longleaf pine ecosystem evolved as a result of frequent lightning- and human-ignited fires, similar to other fire-dominated ecosystems (Bird and Cali 1998, Loope and Aderton 1998). As a result, sustaining longleaf pine forests is dependent on frequent fire (Christensen 1981), which in the present day landscape necessitates prescribed fire (Leach and Givnish 1996). In the absence of fire, hardwoods encroach and compete with fire-dependent vegetation, ultimately altering the composition and structure of the forest (Lemon 1949). Natural regeneration of longleaf pine is dependent on fire and its processes for several reasons, including the regulation of competing ground vegetation, the effects of lightning on canopy gaps, and maintenance of open canopy conditions (Grace and Platt 1995). Two biological indicators of past land management with frequent fire and minimal impacts on biodiversity are the presence of wiregrass as a dominant ground cover species (Grace and Hedman 2000, Kirkman et al., in review) and the occurrence of the federally endangered Red-Cockaded Woodpecker (*Picoides borealis*, or RCW) (Engstrom et al. 1996). The presence of wiregrass indicates a disturbance history lacking agricultural alterations or intensive site preparation resulting in extirpation of much of the diversity found in the understory (Clewell 1989). Wiregrass also provides a functionally important role as a fine fuel (Noss 1989). Because of its dependence on old-growth

trees for cavities and on frequent fire to maintain open foraging stands, the RCW has been suggested to represent an umbrella species for southeastern costal plain ecosystem diversity. In other words, landscape-scale management that encourages RCW habitat maintains structural features needed for late successional obligates and is likely to facilitate high biological diversity that is characteristic of the fire-dependent species of the ecosystem.

To illustrate how restoration silviculture can be used to enhance and sustain biodiversity, we present the management philosophy and approaches at three locations with remnant stands of longleaf pine forests in which RCW colonies have been maintained in high numbers. These areas also have sites with intact ground cover (e.g. wiregrass dominates the ground cover and high species richness of fire-dependent species, Figure 15). We use these examples to transcend various scales of management from the individual tree to the landscape as well as encompass private and public land management. Because the historical, social and economic contexts of these sites oppose the prevailing trends that represent much of the regional landscape, they are factors that have been integral to conservation of biodiversity. Our primary example is a group of large, privately owned properties collectively known as the Red Hills. These properties are located in southern Georgia and northern Florida and have been managed for game bird and timber extraction. In this region, a conservation-oriented forest management philosophy has evolved through the forest practices of Herbert L. Stoddard, Sr. and Leon Neel. The other two examples are in public ownership (Eglin Air Force Base and Apalachicola National Forest), both in the western Panhandle of Florida. These two sites are located on relatively poor soils for agriculture (extremely xeric and extremely wet sites) and thus, were minimally cultivated prior to federal acquisition. Currently, both of these public lands must be managed in compliance with the Endangered Species Act, particularly in regard to the RCW. We present lessons learned from the management of these two publicly owned tracts.

Figure 15. Fire-maintained longleaf pine-wiregrass ecosystems with intact groundcover are among the most floristically diverse forests in North America. Photo by Stephen Pecot.

We contrast the histories of these sites with those of traditional forest management in the Southeast, specifically timber and pulpwood production of slash pine and loblolly pine, which has dominated industrial and private forest land management. A standard silvicultural prescription in production forestry calls for highly stocked, even-aged plantations with rotation intervals of approximately 25-30 years to maximize fiber and monetary return. The closed canopy structure of these forests and the intensive site preparation that is often associated with traditional silviculture including herbicide use to control competitors and mechanical means such as bedding can result in reducing the diversity of native ground flora. In contrast, the common perspective of the management programs examined in the following case studies is recognition

of the importance of retention of old canopy trees, the application of frequent fire, and the conservation value of maintaining the complexity of biological communities.

The Red Hills

The greater Red Hills physiographic area occurs in a 240 km strip with a maximum width of approximately 40 km (a total of 960,000 ha) along the border of Georgia and Florida within the lower coastal plain. The area (hereinafter, the Red Hills) is a subsection of the larger physiographic area that is roughly defined by the Ochlockonee River to the west, the Aucilla River to the east, and the Cody Escarpment to the south. The Cody Escarpment is a sharp division between Miocene-age sediments within the Red Hills and Pleistocene-age carbonate sediments to the south (Paisley 1989; Gatewood et al. 1994). The Miocene sediments, ranging in thickness from 30 to 60 m, overlie permeable Oligocene limestones and dolostones that form the substrate for the Floridan aquifer (Gatewood et al. 1994). This karst topography is riddled with sink holes and three large lakes (Miccosukee, Iamonia, and Jackson) that periodically drain through sink holes during drought conditions. Thomasville, Georgia, lies at the northern edge and Tallahassee, Florida, at the southern edge of the Red Hills. The characteristic red clay of the Red Hills was derived from parent materials in the Appalachian Mountains approximately 20 million years ago (Paisley 1989). Subsequent erosion of the region generated the rolling hills of the region.

The Red Hills region is composed of 27 natural communities (Gatewood et al. 1994). Two of these communities, xeric sandhills and mesic upland pine forest, were believed to be dominated by longleaf pine before extensive European settlement. Some researchers have suggested that mixed *Carya-Quercus-Pinus echinata* woodlands may have been common in northern Leon County, Florida (Harper 1914), but longleaf pine clearly dominated much of the uplands in Thomas County, Georgia, because some of the best examples of old-growth longleaf pine in existence occur there (Means 1996).

Paleo-Indians (12,000 to 9,500 years before present) left remains in the rivers of north Florida and likely occupied parts of southern Georgia (Gatewood et al. 1994). Artifacts from this period have been found around Lake Iamonia in Leon County, Florida (Tesar 1980). Successive Native American cultures, including the mound-building Mississippian, occurred in the Red Hills until the arrival of the Apalachee tribe in the early 1500s (Paisley 1989). The Apalachees had a large population in the Tallahassee area at the time of the earliest European explorers Pánfilo de Narváez (1528) and Hernando de Soto (1539-40). Both the Apalachees and the mound-building culture that preceded them had agricultural fields, particularly on alluvial river bottoms.

From the arrival of Spanish explorers, the Tallahassee area of the Red Hills was inhabited by Spaniards and Indians until English possession in 1763. The timing of human settlement and cultivation of land for agriculture from the 16th to 19th centuries was crucial in determining the forest conditions that are present in the Red Hills today. The Florida portion of the Red Hills (primarily Leon County) has a much older history of extensive human use of land for agriculture than the Georgia Red Hills. As Rogers (1963; pg. 4) noted: "Apparently, a land dotted with pine barrens and wiregrass was not considered to have much agricultural potential. The presence of hostile Indians on the western side of the Chattahoochee River and rumors of malaria and bad water were other retarding factors." Thomas County was established in 1825, and thus the Georgia portion of the Red Hills was developed for only 40 years before the Civil War and the

collapse of the large-scale, intensive, cotton economy. The close timing of Anglo settlement of southwestern Georgia and the effective end of a strong agricultural economy prevented the conversion to agriculture of some of the extensive areas of undisturbed longleaf pine-wiregrass (*Aristida stricta*). After the Civil War, the cotton economy faltered, recovered briefly, and then slowly declined as other crops emerged, cotton prices fell, labor supplies became less certain, and weather deposed "King Cotton." Approximately 12,000 hectares of apparently unplowed land out of an estimated 223,000 hectares of land that likely was upland pine forest remain in the Red Hills today (Ambrose 2001). Almost all of the unplowed land is in Thomas County.

The emergence of Thomasville as a resort and a destination for wealthy northerners in the late 19th and early 20th centuries further slowed the growth of agriculture in the southern portion of Thomas County (Rogers 1973). Purchase of large estates for the purpose of sport hunting marked a decline in the need for landowners to earn income from productions of the land (Stoddard 1931). In fact, many of the landowners "preferred the stands of original growth and second growth timber to remain for aesthetic reasons, rather than sell them for the small income the forests would have brought at that time" (Neel 1967). As the value of timber and the costs of land management for hunting increased, interest in deriving income from timber rose. In 1941 Herbert L. Stoddard, Sr. initiated a forestry consultant business to address the particular needs of the hunting estate owners. Selective cutting and long rotations were keys to management of these "recreation forests." The selection centered on removal of "poorer quality, deformed, and cull trees [to develop] a forest of high grade poles and piling-type timber" (Komarek 1976). Stoddard's background as an ornithologist and self-taught ecologist provided an unusual vantage for a forester. He was knowledgeable about the natural history of the dominant upland pines (*Pinus palustris, P. echinata, P. taeda, and P. elliottii*), but he was also aware of how forest management practices affected habitat of the primary game species, the northern bobwhite (*Colinus virginiana*), and the bird species that is arguably the most closely tied to fire-maintained pine forests in the Southeast, the RCW. Stoddard hired Leon Neel in 1950 as an assistant, and the "Stoddard-Neel" style of forestry developed through time. Management goals of the Stoddard-Neel approach placed high value on the aesthetic and wildlife values of the forest in addition to economic values.

Apalachicola National Forest

The Apalachicola National Forest (ANF) is comprised of 228,639 ha on gently rolling to flat terrain, and is the largest National Forest in Florida. It is located southwest of Tallahassee, Florida in Liberty, Franklin, Wakulla and Leon Counties, Florida. Two major geologic regions divide the property into east-west sections: the Woodville Karst Plain and the Apalachicola Coastal Lowlands. The eastern region, the Woodville Karst Plain, is characterized by surface sand approximately 6 meters thick, which resides above a layer of limestone. The western region, the Apalachicola Coastal Lowlands, is also known as the "Apalachicola Flat Woods". The surface of the Apalachicola Coastal Lowlands is generally flat and sandy surface soils with a thick layer of sandy clay and peat above the underlying layer of limestone. The region has a high water table and much of the surface areas are characteristically wet.

Structurally, the natural condition of the pine forests of ANF was estimated to be "an open, airy pine forest with an understory of grasses, herbs, and subshrubs" (Estill 1999) based on a composite of descriptions provided by Bartram (1791), Nash (1895), Schwarz (1907), Harper (1911), Chapman (1923), and Wahlenberg (1946). Schwarz's (1907; p. 9) description of a virgin

longleaf pine forest was quoted in Estill (1999) to help define the spatial characteristics of a natural mature forest. In particular, "…dense groves of poles and tall saplings, though of constant occurrence in the virgin longleaf pine forest, are usually not over 0.2 ha in extent, and in the aggregate form but a small part of the total area" was used to characterize gap-phase regeneration.

The entire area was deeded to John Forbes and Company by the Seminole Indians in 1803-04, and remained in private ownership until about 1930 when the federal government acquired and managed it under the Resettlement Administration. ANF was officially established on 31 May 1936 (Clewell 1971). From the time of the purchase by the Forbes Company and acquisition by the federal government, many small farms were established, but they were located mainly near roads and rivers. Extensive agricultural development never occurred on the land that became ANF because of the poor soil types.

On the Apalachicola Ranger District, localized logging began in the 1830's, but between 1913 and 1927 the Graves Brothers Lumber Company essentially clear-cut the entire district. Enough trees were retained to regenerate the second forest that occurs on the District today. The flatwoods of the Wakulla Ranger District were logged between 1910 and 1920. In both districts, widely scattered, stunted, flat-topped trees were apparently avoided during the original timber harvests (Clewell 1971). These "leave trees" may have become a critical seed source for the second-growth forest, and they certainly were important for RCW as den, nest, and forage trees when the first extensive harvest occurred in the early 20th century until forest regrowth (see below).

Changes to the ANF that occurred as a result of forest management include: (1) conversion of approximately 25% of the area that would have been dominated by fire-tolerant longleaf pine to native, but less fire-tolerant slash pine (*P. elliottii*), (2) a radical shift in understory structure from open and "park-like" to a midstory dominated by small trees (e.g., turkey oak [*Quercus laevis*]) and shrubs (e.g., titi [*Cliftonia*]) caused by fire suppression, primarily in the Wakulla Ranger District; (3) a shift in understory composition where the soil was disturbed mechanically for firebreaks and site preparation for slash pine planting; (4) a constricted age class distribution; and (5) spatial distribution of the trees that differs from the historical forest (Estill 1999).

Eglin Air Force Base

The largest remaining contiguous tract of longleaf pine forest in the Southeast is under federal ownership, located on Eglin Air Force Base (AFB) in the western Panhandle of Florida. Eglin AFB extends for 82 km in an east-west direction through Santa Rosa, Okaloosa, and Walton Counties. Over 80% of the 187,500 ha property is forested on upland xeric sites. This forest land includes 90% of the remaining old-growth longleaf pine forest (Kush and Varner 1990) and supports the fourth-largest population of RCW. In addition, sixty federal and state rare plant species are documented on this site (Chafin and Schotz 1995).

Much of Eglin AFB was within the Choctawhatchee National Forest, prior to being transferred to the U.S. Air Force (Army Air Corps) in 1947. These holdings, as well as properties previously in private ownership were extensively managed for turpentine production and grazing. Both land uses included frequent burning of the woods (annual burning in most cases). However, the U.S. Forest Service, followed by the Army Air Corps, instituted site-wide management polices of fire suppression in the 1940s. Since that time, and prior to 1988, large-

scale logging and conversion of natural longleaf pine stands to sand pine (*Pinus clausa*) or slash plantations has occurred. These plantations (over 20% of the property) are concentrated in the geographic center of the Base due to the ease of access for timber harvest operations and the location of an Eglin-owned mill near the present-day community of Niceville, Florida. Presently, consumptive resources at Eglin include timber extraction, firewood extraction, hunting and fishing. RCW habitat at Eglin AFB was not considered in forest management operations until the U.S. Fish and Wildlife Service issued a Jeopardy Opinion in 1988. In 1994, the Department of Defense (DOD) issued official policy that requires the implementation of ecosystem management practices on all military lands.

Since 1988, Eglin AFB natural resource management and funding has been driven by habitat recovery and protection of the RCW in compliance with the Endangered Species Act (50CFR 17.11-12). While funding and management directives within the Department of Defense have remained oriented primarily towards endangered species management, Eglin AFB has effectively used the RCW as an umbrella species to manage and protect the longleaf pine sandhill ecosystem as a whole. The extensiveness of the property has required a management effort to protect the ecosystem at the landscape scale. In turn, this ecosystem approach also has supported rapid growth of the RCW population and protection of other rare species.

Xeric longleaf pine sandhills compose nearly three-quarters of the ecological communities on Eglin AFB and are dependent on frequent fire to maintain ecosystem integrity. In the absence of frequent fire, hardwood encroachment occurs, litter and duff fuel accumulation presents hazards to longleaf pine survival with eventual re-introduction of fire (prescribed or wildfire), and rapid sand pine invasion takes place. Thus, in addition to maintenance of the desired ecological condition with frequent fire, substantial restoration challenges include reduction of sand pine and reintroduction of fire to fire-suppressed stands.

Stand Management in Gap Replacement Forests (Longleaf Pine-Grassland Ecosystems)

Natural Disturbances in Longleaf Pine Ecosystems

Historically, fire was the dominant disturbance influencing structure and regulating function in longleaf pine grasslands of the southeast. Early descriptions of Pre-European settlement forests of the southeastern coastal plain speak of vast areas of savannas that were dominated by a matrix of open canopy, multi-aged longleaf pine in which even-aged cohorts of regeneration would be found in the larger openings (Schwarz 1907). While the most common regeneration patches were relatively small in scale (0.1 ha), large even-aged patches could be found suggesting large-scale disturbances from hurricane or tornadoes (Wahlenberg 1946). The ground flora was described as grass-dominated but rich in herbaceous species. Later work suggested that longleaf pine overstory mortality was predominately a result of small-scale, single-tree mortality events or few trees dying from a variety of disturbances including lightning, beetles, wind, and disease (Palik and Pederson 1996) along with infrequent but large-scale wind disturbance events (Doren et al. 1993).

The dominance of longleaf pine savanna structure indicates that fire frequency was most often 1-3 years and, less frequently, 3-5 year return intervals in areas with limited ignition sources or where topography protected areas from burning (Frost 1990). In the latter sites, longleaf pine would be a co-dominant with other southern pines and/or hardwoods. This high

frequency of burning allows for diversity in understory flora to reach levels of species richness that are as high as is recorded in the literature for North American vegetation (Walker and Peet 1983, Kirkman et al. 2001). While early work has suggested that plant response to fire is strongly based on season of burn considerations (Platt et al. 1988), recent work suggests that season of burn may not be a strong selection force that is general to the flora (Hiers et al. 2000). Moreover, Glitzenstein et al. (2002) showed that diversity was strongly affected by frequency, with the greatest species richness occurring with annual winter burning. They suggest that varying the season without extending fire return interval is the preferred way of restoring and sustaining native diversity.

Maintaining perpetual forests as those created in gap-replacement dynamic aid in sustaining frequent fire. The long needles of longleaf pine are intercepted by bunchgrass crowns such that more than half are elevated above the forest floor (Hendricks et al. 2002). This results in loosely packed, fully aerated fuels that dry quickly after rain and ignite easily. Fuel structure combined with high concentrations of terpenes and other volatile high carbon, low nitrogen compounds make longleaf pine needles high quality fuels for use in prescribed burning operations. Sustaining overstory through time allows fuels to maintain a high frequency of burning needed to maintain structure and diverse composition.

The Stoddard/Neel Silvicultural Approach to Stand Management with Gap Replacement Forests

The single-tree selection silvicultural system developed by Herbert L. Stoddard, Sr. and modified through time by Leon Neel for the past 60 years on private properties of the Red Hills has conserved biodiversity with a consistency that is unmatched in the region (see later section on forest management and biodiversity). The Stoddard/Neel approach (SNA) to management differs in basic philosophy from that of the type of silviculture commonly practiced in the southeast. Most commercial silvicultural approaches view forest management from an agricultural perspective of growing and tending a crop. For example, this is typically achieved by 1) initiating a forest, 2) tending the forests by thinning or other mid-rotation silvicultural activity, 3) liquidating the forest when the trees have reached rotation age, and 4) preparing sites for the beginning of a new forest. The time required for forest initiation to liquidation is viewed as an economic factor compounding costs and, thus, this period is minimized. Similarly, uneven-aged management, which is much less commonly practiced in the Southeast, has a central objective of cutting that simplifies forest structure. Specifically, cutting is prescribed by formulas that regulate diameter distribution, stocking (basal area, or volume), and/or liquidation of trees once they reach a maximum size (see BDq discussion in previous review). Regulated forests in either of these scenarios can be less variable in structure (e.g., fewer age classes, less dead wood of various stages of decay) and result in sustaining much lower levels of biotic diversity than found in native forests of the coastal plain region (Hedman and Grace 2000). While some populations of the native biota thrive with this type of forest turnover (e.g., young loblolly pines, slash pines, early successional ruderal plants, deer and turkey), many other important components of biodiversity in the Southeast are diminished. Nearly 30 faunal species (Means and Grow 1985) and at least 187 plants associated with Coastal Plain grassland ecosystems of the southeastern Coastal Plain are considered to be of concern at state, national or global scales with respect to their long-term viability (Walker 1993). Across the southeastern landscape, species such as the red-cockaded woodpecker, Bachman's sparrow, flatwood salamander, gopher tortoise, and

gopher frogs are rare; yet, habitat for these species occur abundantly in the Red Hills managed with the Stoddard/Neel Approach (SNA).

The uniqueness of the SNA is to maintain a perpetual forest with all its components while extracting timber of considerable economic value. By emulating natural disturbance processes that retain variation in the forest, the SNA promotes a forest with no beginning or end, in contrast to large-scale clear cutting. The SNA treats the timber base of a property in an analogous way to that of an endowment that is allowed to grow to a threshold before any resources are removed. Once the timber threshold is obtained, then a portion of the growth can be removed. Thus the standing crop is treated as the principal in an annuity; growing through time so that it is never intentionally reduced. The SNA recognizes time as an important ecological feature of land that is always factored into management. Forests are viewed as more than the wood they produce or the game that can be harvested from them. They are viewed as ecosystems rich in organisms and sustained through interacting disturbances that provide complexity in structure, variation in time, and heterogeneity in function. This variation in structure and function is critical to sustaining the myriad of plants and animals that are native to these ecosystems. While disturbance takes many forms in these forests, the most important to management is frequently applied and controlled fire.

Sustained management of the pine grassland ecosystems of the SE coastal plain is dependent on the use of frequent controlled fire and the retention of fuel to carry frequent fire. Fire is to the coastal plain what rain is to rain forests in that fire regulates the structure and controls ecosystem function. Fire is the primary tool that maintains the open canopy pine structure, sustains understory regeneration, encourages diversity of plant life, regulates the flow of energy and materials through the ecosystem, and maintains fine fuels. In addition to the ecological imperative of fire in these systems, fire remains the most cost effective tool of vegetation management in the reduction of hardwoods. Reintroduction of fire and the conditions needed to permit burning in places where fire has been lacking is critical to restoring native biodiversity.

Frequent fire is most simply applied to stands of longleaf pine with virgin ground cover dominated by wiregrass that has been frequently burned in the past. This ground cover provides the most flexibility in the conditions under which burning can be conducted. Thus, any management in these areas should take into account the maintenance of native ground cover (through frequent burning, avoiding soil disturbances that disrupt root systems of perennial ground cover species, avoidance of dense, closed-canopy overstory structure, and parsimonious use of herbicides if ever used), and the continued production of fuels from longleaf pine needles (through maintenance of overstory). In areas where the ground cover has been disrupted or the forests have been disturbed so that fuel production by grasses is compromised, the challenge of keeping areas from invasion of woody shrubs is much more formidable.

Maintaining the diversity of longleaf pine grassland ecosystems of the southeast is in large part an exercise in discouraging the dominance of hardwood vegetation that invades in the absence of fire. Regulating hardwoods to small stature within the upland matrix is most effectively done by sustaining pine overstory through time. Maintaining a pine overstory throughout time is the goal of the SNA in throughout the upland landscape; as sites become more extreme along hydrologic or productivity gradients the importance of the overstory in maintaining fire and competition becomes increasingly important.

Hardwood species distribution, their abundance, and their stature reflect the interactions between site resources, and past disturbance histories. Sandhill sites tend to be the least

productive of all longleaf pine sites (Mitchell et al. 1999) due to their low water-holding capacity, low organic matter content, and cation exchange capacity. Harvesting the forest reduces pine fuels such that burning is likely to be much patchier after timber harvest, allowing oaks to become established and grow to sizes that are much fire-tolerant. As oaks grow, their litter is less flammable than grass or pine needle litter providing a feedback that helps them persistence in fire-dominated ecosystems (Williamson and Black 1981). Fire on these low productivity sites regulates but does not eliminate scrub oak populations.

Hardwoods are also found in dominant or co-dominant crown positions at the opposite range of the hydrologic gradient (drains and depressions in the landscape). Hardwood development on these sites represents an interaction of resource gradients and disturbance. Fire is less frequent on wet sites due in part to the moist conditions being less conducive to fire during typical hydro-periods. Also, the high NPP of these sites (Mitchell et al. 1999) allows for large amounts of hardwood litter to be produced in relatively short periods of time once hardwoods have become established. This drastically reduces the propensity for drains to burn and increases the propensity for hardwoods to survive between fires and rapidly establish on these sites. Once entrenched, they gradually establish toward the uplands. No demarcation in the landscape exists to delineate where the drains that support hardwoods stop and where upland, fire-dominated savannas should begin. Rather than a static point in the landscape, if managed well the ecotone between the upland and wetland is a dynamic part of the landscape moving as a function of prescribed fire and time since burning. The ecotone between the uplands and wetlands is particularly rich in species (Kirkman et al.1998b). Thus, managing this dynamic portion of the landscape and associated wetlands is disproportionately important to conserving the biodiversity of the region. The SNA recognizes the importance of the pine canopy in maintaining fire in this ecologically sensitive portion of the landscape.

Although valuable timber is harvested in this system of management, harvests are considered only after the standing crop of timber is sufficient to maintain the forest for perpetuity. Extraction is done with care to enhance the ecosystem (e.g. increasing the age structure of pine, converting from one species of pine to longleaf pine on upland sites, or removal of undesirable hardwoods to encourage grass and pine fuels to sustain frequent controlled burns) or when harvesting is benign to the sustenance of ecosystems (removal of trees of low vigor or economic defect in stands of fully stocked multi-aged longleaf pine). This not only requires that each stand and property be viewed biased on its unique condition and setting in the landscape, but that each tree is individually evaluated for removal. This system precludes simple rules or equations, however, principles can be identified to guide the selection of trees that are harvested, and even more importantly, to determine which trees are left standing after a harvest (see Mitchell et al. 2000 for a more full description of SNA).

Marking trees for harvest requires the retention of trees that may be extremely marketable but have significant value in the long-term health of the forests. For example, in the SNA, tree harvest in upland sites retains longleaf pine preferentially in the stand. Longleaf pine, the dominant upland tree species in pine grassland forest, is the longest lived southern pine species, the most preferable for providing habitat for endangered species such as RCW (Engstrom 1996), and provides superior fuels for frequent and flexible burning (Christensen 1981). However, as site moisture increases, slash pine becomes a common associate (Christensen 1988) and eventually the dominant tree species. Therefore, in wetter sites, the canopy retention criterion will be adjusted to account for the change in species dominance.

Older (live) trees are favored to be left over younger trees because they provide structure associated with heartwood. Heartwood tends to be less susceptible to decay and fire (Wahlenberg 1946) and is a major source of coarse standing and fallen woody debris (Harmon et al. 1986). Decay organisms such as red heart disease provide unique habitat for cavity nesters in live trees, but red heart only occurs in older pines. Thus, slash, loblolly and shortleaf pine greater than 100 years old and longleaf pine 120+ years provide habitat that is rare, and becoming rarer as older trees and stands disappear from the region (Conner et al. 1994).

Preferentially removing crowns with low vigor (sparse crowns with chlorotic needles) helps maintain vigor in remaining trees; however, all trees in decline are not removed at any particular harvest. Defective trees (e.g., forked, crooked, or diseased such as trees with fusiform cankers) are preferentially harvested, provided that all defects selected for removal are not eliminated from the stand. For example, some defects in terms of wood quality and value, such as witch's brooms, are retained in the forest due to their intrinsic value as habitat to some faunal species as dense refugia high in the canopy. This practice provides variation in the forest. The presence of dead trees is a structural feature of a healthy pine grassland ecosystem, whether standing or on the forest floor. Old, dead trees are of ecological value because of the rarity of heartwood in the landscape as well as their resistance to fire and biological decay. On the other hand, these old trees are quite valuable economically and are not producing fine needle for fuels; thus, harvesting some of these trees for their heartwood is preferred over harvest of live trees. Nonetheless, removal decisions must be made with conservation of maintaining the overall habitat in mind.

Tree selection for harvest is also based on their spatial distribution within the stand, with the goal of maintaining heterogeneity of pine grasslands ranging from nearly closed canopy to widely scattered trees. Cutting can be done to release seedlings present in the grass stage or enhance openings in the forest to encourage new regeneration to be established, but opening size and total area should be restricted to maintain the canopy cover needed to contribute to litter. Contrary to the fact that longleaf pines are considered shade-intolerant trees, seedlings develop well in gaps as small as 0.1 ha; thus, cutting should not frequently exceed 0.25 ha for the purpose of encouraging regeneration (McGuire et al. 2001). Cutting single trees in one cutting cycle may start the process of regeneration that continues through several cutting cycles, gradually enlarging openings and releasing seedlings. Cutting incorporates time into regeneration considerations, incrementally recruiting new individuals to replace those that are slowly removed from the stand through time.

The SNA to silviculture recognizes the central role that maintaining forest aesthetic has in all management activities. Management of the timber in this way allows for natural cycles to be expressed and woods to move more gradually toward a desired future condition. After a property reaches that desired condition it is maintained in a fluid stability, always changing at smaller spatial scales with trees regenerating and growing, but the forest is stable over larger spatial scales (Figure 16). The beauty of the savannas of the southeast is often the connection that landowners, or those concerned with public land

Figure 16. The product of the SNA is a perpetual forest with all natural components present and functioning. Photo by Stephen Pecot.

management, have with conservation, and the aesthetic value is often the motivation that allows them to forego the shorter term income that can be derived from liquidating the timber base. While aesthetics was well recognized by early conservationists like Leopold and Stoddard, it is often ignored in both the contemporary silviculture community and scientific community concerned with land management.

Uneven-aged Management Using the BDq Approach at Apalachicola National Forest

Natural longleaf pine regeneration is being encouraged under the BDq method as implemented on the Apalachicola National Forest (ANF) by creating gaps that range in size from (0.1 to 0.8) hectares (Estill 1999; 2-19). This range is based on an analysis of gaps created in the wake of Hurricane Kate in 1985 (Estill 1999). Seedlings should be established in clusters beneath sparse overstory or in gaps before timber harvest. Farrar (1996) emphasizes the importance of obtaining reproduction before overstory is removed, because of the dynamic nature of competition between pines and hardwoods. According to Farrar (1996), "The reproduction patch should be enlarged as feasible at subsequent cuts by removing perimeter larger timber or thinning the larger timber to promote regeneration beneath it." Other than this general instruction and a prohibition from "cutting holes" in the forest, little guidance is provided for creating and managing overstory conditions to promote regeneration. Gap management is a facet of BDq method that would benefit from the ecological tenets of the Stoddard-Neel approach to silviculture.

Longleaf pine woodlands in the ANF are in the process of being shifted from even-aged to uneven-aged silviculture. The uneven-aged technique that is being implemented is a variation of the basal area/maximum dbh/q method (BDq method; Farrar 1984, Farrar and Boyer 1991). The BDq method involves comparison of the actual size class structure (trees per unit area vs. DBH size classes) to a desired size class structure (BDq residual stand size class distribution). The BDq distribution is determined by a target residual total basal area, a maximum DBH, and a variable "q" that defines the relationship between the numbers of stems in neighboring size classes (Farrar 1996). Superimposing these two size class distributions (actual and BDq residual) provides targets for the number of trees available for harvest in each size class, where the actual number of trees in a given size class exceeds the number of trees in the same size class in the BDq distribution. The BDq distribution approximates a negative exponential distribution that is the hypothesized distribution of old-growth stands.

Theoretically, a forest managed under the BDq method will never leave any sizeable area without forest cover, and, if the requirement for a maximum DBH is relaxed, it could include trees that are large and old—a necessary legacy to provide habitat for the RCW (Engstrom et al. 1996). Shortcomings of the method are that an extensive inventory is needed to establish the actual size class structure, multiple entries are required for harvests through time (as opposed to even aged management with no thinning), and very little guidance is provided for marking trees to be removed within a diameter class other than "cut the worst and leave the best" (Farrar 1996).

Landscape Management of Fire – Eglin Air Force Base

Recent management of the longleaf pine forest landscape at Eglin Air Force Base (AFB) has been largely an exercise in expanding its prescribed burning program and thus encouraging

regeneration and sustaining diversity of fire-dependent biota. Management at this scale and from the perspective of urban interface has presented challenges that differ from that of smaller, privately-owned forests. From 1992 to present, Eglin AFB has pioneered the use of integrated natural resource management plans (INRMP) in management of military lands. Through a modification of The Nature Conservancy's site conservation planning process, spatially explicit goals for RCW recovery were identified to maximize overlap with other conservation targets, or those species and communities identified as having priority conservation value. The most valuable product from this planning process is the spatial conceptualization of RCW management goals for resource managers through GIS tools. This effort required identification of important features for RCW habitat and a method for prioritization of prescribed fire.

The size of the landholding, urban interface issues, resource limitations (particularly the lack of prescribed fire personnel) and constraints of prescribed burning imposed by the Air Force Mission have significantly reduced the portion of the landscape that can be managed or restored to meet RCW recovery and other conservation goals. On average, less than 21,000 ha have been burned annually, resulting in a 7-yr+ fire return interval, falling far short of the projected 2-3 yr return interval. Without objective criteria for assessing burn prioritization, the Eglin AFB landscape was simply too large for managers to objectively assess how to effectively distribute limited resources across that landscape. To target prescribed fire application on the site, GIS modeling tools were utilized. Evidence provided by a state and transition model of stand condition demonstrated that the current prescribed fire return interval would likely result in the gradual degradation of the entire landscape, while meeting none of the Eglin AFB management objectives (Peterson & Hardesty 1999). Therefore, a spatially explicit burn prioritization model was developed that incorporated resource managers' experience in the identification of criteria used to rank sites according to the need to burn (Hiers et al. in press).

First, managers and biologists identified 11 key conservation criteria and landscape management objectives that drive the application of prescribed fire to a particular site. These criteria included factors such as the time since restoration harvest, site productivity, vegetation characteristics, total number of burns, and presence of endangered species. Secondly, a dynamic map of site rankings was produced. For this task, a GIS or remotely sensed data layer was developed for each criterion and management objective. Next, each criterion variable was assigned a weight according to its relative contribution to overall burn prioritization and each variable value was ranked as to its influence using Arcview Spatial Analyst Model Builder™. Variable rankings were determined by applying simple sub-model routines (e.g., regressions) that represent correlative relationships between conditions and goals. The model offers flexibility for modification as management objectives and landscape condition change. Critical to the success of this approach is the transparency of coupling the goals, rationale, and site conditions into a user friendly prioritization tool. Modeling allows managers to incorporate existing monitoring and research data into their model of ecosystem condition, while explicitly stating assumptions and uncertainties and gaps in knowledge.

Converting established stands of undesirable composition and/or structure (including fuel structure): Lessons from ANF and EAFB and inferences from Stoddard-Neel

Pine timber management is integrally related to how fire can be used as a management tool. All silviculture in upland pine grasslands that is geared to conservation of native biodiversity should

emphasize the maintenance of frequent fire regimes. "Off-site" pines such as slash pine or loblolly plantations can play a valuable role in providing forest structure, and fuels needed to sustain that structure, even during a conversion to longleaf pine forests. Often, as a restoration approach, stands of loblolly, slash or shortleaf are clear-cut and longleaf pines are planted in even-aged stands. This large-scale canopy removal encourages development of hardwood midstory, which often has to be reduced through herbicides or mechanical means to remove competition and permit use of fire. Restoration of pine grassland is best accomplished when restoration is undertaken incrementally with a long-term perspective. By retaining pine forests perpetually through time, even in situations where pine canopy species may be less desirable than longleaf pine, both competition and fuel production of canopy pines allow for hardwood control to be accomplished primarily by fire. A slow conversion of off-site pine stands to those of all-aged longleaf pine results not only in lower management costs, but helps sustain the richness of the herbaceous ground cover.

While longleaf pine as a species is favored in upland management due to its long-lived nature and superior fuel characteristics, restoration of pine grassland should not be exclusively species driven. Restoration is best accomplished when a long-term view is taken. Overstory pines restrict hardwood development through competition for resources which slows growth of hardwoods and makes them more venerable to fire. They also add fine fuels that allow for frequent fire to maintain hardwoods in low stature (McGuire et al.2001). Thus both competitive intensity and fuel distribution (and fire intensity) declines curvilinearly with distance from overstory pines. Increasing opening size encourages development of a hardwood midstory that often has to be controlled through herbicides or mechanical means if allowed to establish in earnest. By maintaining pine forests perpetually through time, even in situations of species may be less desirable than longleaf pine, both competition and fuel production of older pines allow for hardwood control to be accomplished primarily by fire resulting in lower management costs (thus requiring less timber harvests to pay for management costs) and much a greater ability to sustain the richness of the plant understory. Slowly converting off-site pine stands to those of all-aged longleaf pine by cutting practices that favor any overstory longleaf pine present, fire regimes that encourage longleaf pine regeneration while suppressing other tree regeneration, and supplemental planting or seeding of longleaf pine in gaps created by harvesting off-site pine according to the SNA approach described above, allows for stands to gradually move from off-site pine to a multi-aged longleaf pine forest. This modification of the SNA (conversion of slash pine plantations to multi-aged longleaf forests) is being documented in experiments that are on-going at the J.W. Jones Ecological Research Center in cooperation with Leon Neel (see supplemental studies Kirkman et al. 2003).

Forests develop through time. While some redundancy exists among species, there are few, if any, ecological substitutes for time. The previous example of pine species conversion gives an example of taking time into account in management. A 40-year-old slash pine stand can provide some of the structural features needed to sustain pine grasslands. Fuels are provided that can support frequent burning to suppress the size and population of oaks, and 40 years of forest structure can be used as foraging areas for RCW. The period of time for stands to reach ages that support red heart disease and RCW is reduced as compared to clearing the pines and planting longleaf pine. Thus, even when management objectives may be to create habitat for endangered species such as RCW, and longleaf pine is a much preferred species for such an objective, the SNA recognizes that time is a critical factor that needs to be incorporated into restoration.

The Revised Land and Resource Management Plan for the Apalachicola National Forest calls for approximately 20,200 hectares of off-site slash pine to be clear-cut and replanted with longleaf pine during the next 50 years (Estill 1999). This is one of the most intensive methods of restoration. The long-term alternative method of restoration, in which the off-site slash is allowed to mature and then longleaf pine is slowly replanted as natural gaps develop in the forest, was deemed to be to slow and costly. Clear-cutting and re-planting has the additional benefit of providing some income to local communities that depend in part on payment in lieu of taxes (PILT) derived from timber harvest on the national forest. Clearing sand pine that has developed through fire suppression as well as off-site slash and planting of longleaf pine with heavy site preparation is common. Both Eglin and Apalachicola would benefit from determining how and when conversion of the forest could be accomplished without its liquidation.

In addition to species conversion, reintroduction of fire at Eglin Air Force Base has been a priority for restoration guided by the state and transition model previously discussed. Removal of fire from fire-dependent systems leads to many alterations in ecosystem properties (Agee 1998). Longleaf pine needles are extremely slow in decomposition (Hendricks et al. 2002) and will accumulate thick layers of duff with fire suppression. However, litter from long suppressed stands has significant components other than pine needles (such as bark, partially decomposed oak litter etc.) that promote smoldering fires. These smoldering fires cause significant increases in soil temperature because of long residence times, increasing the opportunity for injury to roots and cambium at the tree base. Smoldering fires also cause problems in smoke management. Given sufficient time, litter layers differentiate into: an Oi or L horizon of recently fallen and only slightly decomposed foliage, bark, and twigs; an Oe or F horizon of decomposed litter with abundant hyphae and plant roots; an Oa or H horizon of decomposed plant litter mixed with mineral soil; and an A1 mineral horizon. The structure of litter influences fire and regulates the mortality observed after fire is re-introduced to a stand.

Upon burning longleaf pine stands that have been fire suppressed, mortality is often observed, sometimes delayed from a month to as much as three years post-fire (Kush and Varner 1999). Mortality has been hypothesized to involve direct effects of fire, such as root damage (Ryan and Frandsen 1991, Swezy and Agee 1991), girdling of the stem (Martin 1963, Ryan 2000), leaf scorch (Ryan 2000, Menges and Deyrup 2001), and meristem damage (Menges and Deyrup 2001). Indirect effects may be due to insect or pathogen induced injury after fire (Bauman et al. 2001, Menges and Deyrup 2001). Older trees may be more susceptible to fire mortality, either due to heavier litter accumulation under large crowns of older trees, or less ability to cope with carbon strain associated with damage from fire and greater susceptibility to insect attack (Raffa and Berryman 1983, Dunn and Lorio 1992).

Reintroduction of fire into longleaf pine systems while avoiding excessive pine mortality requires a careful and conservative approach. Mounds of pine litter accumulate near the stem, particularly around large, old trees with expansive crowns. For the most valuable trees (e.g. an old growth tree with a RCW cavity), careful raking of litter away from trees may be useful to avoid damage. However raking litter is expensive and time-consuming, and becomes impractical at large scales. Only reintroduction of fire can restore these ecosystems at large scales. Although some hardwood control may be achieved in the fuel reduction burns, the main purpose of the first reintroduction of fire is fuel reduction, and fire intensity must be controlled so that pine mortality is minimized. Reintroduction of fire in a site with prolonged fire suppression should be conducted in winter months, under conditions when the litter is nearly too moist to burn. The fire in such conditions will result in only a modest amount of surface litter reduction.

All smoldering embers should be extinguished to avoid damage to pine. The subsequent burns should be conducted in the cool season as well, under moderate fuel moisture conditions such that layer after layer of duff are consumed with each fire event. This will gradually encourage grass abundance as fine fuel, and greater percentage of the land area will receive fire, expanding from those places that burned in the last burn. After the fuel reduction phase, burning during conditions (low humidity, lower fuel moisture) that increase fire intensity for hardwood control can be implemented.

Repeated fire in the uplands will help delineate the upland area that will be managed with frequent fire and identify the drains that will require infrequent but intense fire to keep them at bay. Between burn events, hardwoods establish, or those established, grow in size. The rate of growth of hardwoods is greater in wetter sites such as drains. As fire frequency decreases, the hardwood dominance in the landscape moves further upslope. Periodically pushing controlled burns into the bottoms helps allow the bottomland forest and the ecotone between the hardwood drains and the uplands to be a dynamic property of the landscape that is defined by fire.

Forest Structure and Biodiversity

The influence on red-cockaded woodpeckers of the Stoddard-Neel approach to forestry in the Red Hills

The RCW population in the Red Hills physiographic region persisted when other populations on private lands throughout the Southeast declined precipitously because of a fortuitous combination of chance historical events and purposeful management. This combination resulted in the anomaly of a large population of this endangered species on private land (180 active clusters and the seventh largest population), although the population was spread across 27 different land ownerships (Engstrom and Baker 1995; Cox et al. 2002). We briefly describe the historical reasons that contributed to persistence of the woodpecker and examine in more detail the forest management approach (an ecologically-based single-tree selection as practiced by Herbert Stoddard and Leon Neel) that sustained most of the population.

The history of the Red Hills quail hunting estates, as described earlier, provided an unusual combination of features that favored persistence of a large population of RCW. First, the primary game species, the northern bobwhite quail, needed habitat that was largely compatible with the habitat needs of the woodpecker (Engstrom and Palmer *in press*). The most important element of bobwhite management that benefited the woodpecker and other species of the upland pinewoods was the use of fire. Use of fire that maintained dominance of pines with a diverse groundcover was used pervasively throughout the Red Hills, even when use of fire was discouraged on a national level (Komarek 1964). Second, the relatively contiguous patches of mature upland pine forest on the hunting estates in the Red Hills were especially important for the woodpecker, because of the crucial role of demographic exchange in the life history of the species. The Red Hills suffered relatively little habitat fragmentation that has played an important role in decline of the species throughout its range. Third, the quail hunting estates in the Red Hills have been in existence for over 100 years during the period of the extensive loss of the longleaf pine ecosystem. Wealth of the Red Hills estate owners obviated the need for substantial income from the natural resources, particularly timber. Retention of extensive stands of old timber was precisely what provided the essential habitat for the woodpecker.

Intentional management for the benefit of the RCW has largely been attributed to a forest management approach developed by Herbert Stoddard, Sr. and his associate Leon Neel, although a local style of uneven-aged silviculture was also developed and practiced by others in the Red Hills, such as R.C. Balfour. Ten years ago, Leon Neel managed lands that contained about 90% of the active red-cockaded woodpecker clusters in the Red Hills (W.W. Baker, pers. comm.)

Herbert Stoddard had the unusual distinction, from a modern perspective, of being a practicing consulting forester who was foremost a self-taught professional ornithologist and keen observer of natural history. Stoddard approached forest management with an understanding of the life history of many bird species, including the RCW, and field knowledge of the life history of the dominant upland tree species, the longleaf pine. He purposefully and successfully blended management for the woodpecker with land management objectives that were more important to the landowners: production of northern bobwhite, aesthetically pleasing woodlands, and revenue generated from timber harvest. If anything, his management for the RCW ran counter to the prevailing attitude toward the species and could be characterized now as progressive and holistic for the time.

Forest management practiced by Stoddard and continued by Neel had several ecological characteristics that clearly benefited the RCW. First, Stoddard and Neel identified and worked tirelessly to conserve known patches of old-growth longleaf pine in the Red Hills. The Wade Tract and the Greenwood Big Woods are the stellar examples, but additional scattered patches are also important. Old-growth longleaf pine in the Red Hills supports a high density of RCW that is apparently highly persistent (Engstrom and Sanders 1997; Engstrom and Mikusinski 1998). Studies of these patches of old growth have provided important insights into foraging habitat quality (Engstrom and Sanders 1997), cavity tree dynamics (Engstrom and Evans 1990), and longleaf pine population dynamics (Platt et al. 1988). Second, Stoddard and Neel made a point during timber inventories to note RCW cavity trees—both active and inactive—and to protect them from harvest. Again, this ran counter to the regional trend of purposefully harvesting these "diseased" trees. Cavity trees are a critical resource in the life history of the species (Walters et al. 1988). Third, identifying and protecting potential cavity trees within the cluster area and scattered throughout the landscape was also an explicit goal of the Stoddard-Neel approach (L. Neel pers. comm.). Observation of start trees (trees selected for cavities by the woodpeckers) over time gave important insights into what was needed for the species to persist. Fourth, the Stoddard-Neel approach was deliberately multi-age and took advantage of many opportunities for longleaf pine regeneration. Crucially, many relatively old trees (>100 years) were retained throughout the landscape for aesthetic and ecological reasons. These trees are the preferred foraging locations for RCW (Engstrom and Sanders 1997). Fifth, the SNA typically advocates high stocking levels of mature trees, which also provided high quality foraging habitat. Finally, L. Neel, in particular, became a strong advocate for conservation and restoration of longleaf pine where appropriate on the landscape. RCW will readily use other species of upland pine *(P. taeda, P. echinata, P. elliottii*), but longleaf pine appears to be the preferred species. In a recent analysis, Cox and Engstrom (2002) found that the percentage of longleaf pine in the cluster trees was the best predictor of whether a cluster would remain active over a 10-year period (Cox and Engstrom 2001).

Frequent fire and the savanna structure of longleaf pine forests that sustains RCW also provide critical habitat for the gopher tortoise (*Gopherus polyphemus*) (Guyer and Bailey 1993), a species of concern in the southeastern US. Gopher tortoises excavate extensive subterranean burrows in open-canopy forests with abundant herbaceous ground cover for forage. In

traditionally managed forests, intensive site preparation (particularly on short rotation) can eliminate herbaceous food plants of the gopher tortoise (Landers and Speake 1980, Diemer 1986). High tree densities lead to a closed canopy, which ultimately causes tortoises to abandon their burrows and migrate toward forest edges and roadsides (Aresco and Guyer 1999). A similar pattern occurs in fire-suppressed longleaf pine forests where encroachment with oaks results in a closed canopy. Furthermore, studies of tortoise populations in the Red Hills region have revealed demographic differences between populations on old-growth versus younger, forested sites (Hermann et al. 2002).

Gopher tortoise burrows (both active and abandoned) provide shelter from thermal extremes as well as predators and are used by more than 60 vertebrate and 300 invertebrate species (Jackson and Milstrey 1989). Thus, tortoises add an important structural component to longleaf pine forests. One species that relies almost exclusively on the tortoise burrow is the Florida gopher frog (*Rana capito*). This frog spends most of its life in and around tortoise burrows, leaving only to breed in seasonally inundated wetlands during winter months. It requires both an open-canopy pine forest suitable to tortoises as well as access to suitable wetlands. The species deposits its eggs on emergent vegetation, which is present in fire-maintained wetlands that experience growing season fire. Fire suppression or changes in the hydrologic regime of wetlands can render wetlands unsuitable for this species to breed successfully. Alterations to the ecotone, such as the incursion of oaks in the absence of fire, may alter the hydroperiod within the pond such that larvae may be unable to fully develop. Oak thickets also may support large numbers of mammalian predators (Chamberlain et al. 2003), which might impact migrating adults or juveniles.

Even-aged silvicultural forests also lack much of the structural diversity necessary to support other species of reptiles and amphibians. Standing dead snags, fallen logs, and stump holes that develop following fire and decomposition offer refuge to a number of reptiles. Stump holes, in particular, provide critical refuge to species such as the rare eastern indigo snake (*Drymarchon corais*) and eastern diamondback rattlesnake (*Crotalus adamanteus*).

One major problem in determining the impacts of different management regimes on herpetofaunal diversity is a lack of empirical data on diversity in undisturbed forests herpetofaunal richness (O'Neill 1995, Phelps and Lancia 1995; Russell et al. 2002). One of the shortcomings of these studies is that they are typically of short duration and more importantly, they were conducted in systems that were already disturbed. For example, in the Russell et al. (2002) study, a comparison was made of amphibian and reptile diversity at isolated wetlands in 18-25 year old stands of loblolly pine. The treatments included clearcuts and clearcuts with site preparation and replanting. One might expect that the fauna in these wetlands reflected the legacies of past forestry practices, such that species tolerant of silvicultural practices were all that remained. In fact, Phelps and Lancia (1995) found fewer salamanders in clearcuts as compared to control sites and that among anurans, generalist species such as southern toads and leopard frogs were more common in clearcuts. A better test would have been to examine differences in faunal richness and diversity at undisturbed sites, old-growth sites or at least at sites with longer rotation silviculture and/or a more natural management regime.

Regulated forest management, either even-aged or uneven-aged management with adherence to cutting formulas can be less variable in structure (e.g., fewer age classes, less dead wood of various stages of decay) and result in sustaining much lower levels of floral diversity than found in frequently burned native longleaf pine forests of the coastal plain region (Hedman, Grace and King 2000). The resulting loss of floral diversity is due primarily to the soil

disturbances that destroy the root systems of perennial species and to decreased or suppressed fire regimes. The native flora is composed of species with adaptations to frequent disturbances, with rapid re-sprouting capability following above-ground disturbances, such as fire. However, some species are particularly vulnerable to disruption of roots and rhizomes, and become re-established to pre-disturbance abundances in young forest stands very slowly, if ever (Clewell 1971). These species are vulnerable to fire suppression and will rapidly decline in the absence of fire (Lemon 1949). Because of the sensitivity of many ground cover species to soil disturbance, the disturbance history of a site as well as landscape context will influence the rate and degree of recolonization. Thus, protection of the existing ground cover or reintroduction of fine fuels coupled with pine canopy litter is essential for providing the fuel necessary to sustain the source of plant diversity. Forest management with restoration goals or sawtimber management of longleaf pine forests where a perpetual forest structure is maintained over time is key to the perpetuation of the floral diversity of the ecosystem.

Great Lakes Case Study: Eastern White Pine Restoration Using Overstory Retention

Introduction

This case study examines the results of over 25 years of silvicultural fieldwork in the restoration of eastern white pine (*Pinus strobus*), and associated tree species, in the forests of north-central Minnesota. The restoration program described is based on work by Rajala Companies, a fourth-generation, family-owned group of small sawmills and forest product manufacturing plants that collectively manage about 12,000 hectares. Their primary objective is to maximize the quantity and quality of sawtimber (hardwood and pine species) grown under a sustained-yield management program. To quote Jack Rajala, the CEO of Rajala Companies, "the company seeks to restore and sustain forests that will provide high quality, high value sawtimber for … great, great grandchildren and beyond". For Rajala Co., economic drivers have lead to the development of non-traditional silvicultural approaches to produce commercially valuable and sustainable white pine forests, while at the same time, restoring compositional diversity and structural complexity to managed stands.

Rajala Co. uses primarily native, local species in their effort to build an economically sustainable business; integral to this plan is the development of valuable, sustainable forests. All company lands are managed to produce veneer and high-grade lumber products whenever possible, regardless of species. The companies call this "big-tree management". Rajala Co. seeks to restore white pine to their lands for a variety of reasons, but an important impetus is to capitalize on the high value of white pine for both lumber and veneer products.

Rajala Co. favors growing a diversity of native species on a site for as long as the trees are healthy and vigorous, rather than harvesting based on merchantable size criteria alone. Healthy trees are considered "money in the bank", with the value of a veneer quality tree potentially growing exponentially once a minimum sawtimber size is achieved. Healthy, large (sawtimber size), high quality and high value trees of any species are retained whenever possible.

The companies' pine silvicultural program focuses on white pine, but also includes red pine (*Pinus resinosa*). While, red pine is considered a much lower maintenance species, i.e., easier and more economical to establish (artificially) and grow, white pine is a more desirable species because of its ability to grow across a range of site conditions, it's moderate shade tolerance, and it's "millability", i.e. the physical and mechanical properties of the wood which make it easier to work with than red pine wood and less demanding to mill equipment.

Natural Disturbances and White Pine

The natural disturbance regime under which white pine was maintained was characterized by a repeating, cyclic sequence of catastrophic fires with light surface fires occurring at shorter intervals (Frelich 1992). White pine occurred most abundantly in areas where catastrophic fire intervals were about 150 to 300 years. More frequent fires, towards the 100-150 year interval, tended to favor red pine while intervals greater than 300 years tended to succeed to northern hardwoods. White pine occurred most frequently with red pine and most often followed jack pine (Frelich 1992).

White pine is considered to be a mid-successional species. White pine responds favorably to mineral soil seedbeds and high sunlight after fires and yet does not have serotinous cones, vegetative sprouts, or wide-spread abundant seeds – all traits classically associated with fire dependence. Furthermore, white pine has relatively slow growth rates during early, critical establishment years following germination which allow faster growing pioneer species to dominate young post-fire stands. However, white pine naturally persists in stands due to its long life span (up to 450 years), ability to survive surface fires, and moderate tolerance of shade.

Seedling establishment of white pine following fire occurs over 20-40 years under faster-growing pioneer species such as aspen, birch, or oak species (Frelich 1992). More shade-tolerant tree species (especially sugar maple) did not usually survive to compete with white pine after a stand-initiating fire. During understory re-initiation stages and older, multi-aged stages white pine diameter distributions become bimodal (Frelich 1992). Non-catastrophic disturbances affect white pine in forests between 100 and 200 years. Surface fires occurred at 20–40 years (Frissel 1973 as cited in Frelich 1992) and tended to kill hardwoods invading the understory. Gaps created by winds and surface fires created multi-modal diameter distributions and formed increasingly multi-aged stands. White pine stands may have been maintained in the old-multi-aged stage for one to several centuries (Heinselman 1981 as cited in Frelich 1992), until the occurrence of another catastrophic occurrence.

The current landscape of northern Minnesota and the upper Great Lakes Region in general, is largely comprised of second growth forests strongly shaped by a variety of human disturbances. These include initial harvesting of white pine followed by other species; large-scale slash-fueled wildfires, followed by near total fire exclusion. While there is great regional variation in secondary forest characteristics, a common element is greatly reduced white pine and red pine abundance across the range of sites that these species once occupied.

Management Concerns for Eastern White pine in North-Central Minnesota

There are five main impediments to restoring white pine in this setting: *1)* landscape-wide reduction of viable seed trees; *2)* the broad invasion of sugar maple (*Acer saccharum*), other northern hardwoods, and woody brush species, primarily hazel (*Corylus cornuta*), following fire exclusion; *3)* the proliferation of white tail deer (*Odocoileus virginianus*) populations, which preferentially browse white pine in northern Minnesota; *4)* the introduction of exotic white pine blister rust (*Cronartium ribicola*); and *5)* white pine tip weevil (*Pissodes strobi*) which kills terminal leaders of white pine.

1. The region-wide reduction in white pine and red pine forests in Minnesota, from an estimated 1.4 million hectares prior to settlement to about 0.2 million ha currently, has greatly reduced the presence of white pine seed sources in the landscape. This has been widely recognized as one factor influencing the drastic loss of white pine in the regional landscape over the last 100 years. The desire to contribute towards re-establishing viable seed trees in the landscape is one motivation for Rajala Co. efforts to plant white pine on suitable sites (particularly when white pine stumps are evident). Rajala Co. seedlings are grown in local and regional nurseries using the most local seed sources possible. In good seed crop years, Rajala Co. collects large amounts of cones for future use. Recently, Rajala Co. started a bare root nursery to better control all aspects of seedling production and to reduce seedling costs. In addition to planting, Rajala Co. actively and systematically seeks out any naturally occurring white pine regeneration whenever

possible. Existing mature white pine are noted in all management units and are retained as future seed sources in every harvest area unless other canopy, or potential canopy (established seedlings and saplings and larger stems) white pine trees are present.
2. In the absence of fire, more shade-tolerant deciduous species dominate pine sites, including sugar maple, aspen (*Populus tremuloides* and *P. grandidentata*), paper birch (*Betula papyrifera*), basswood (*Tilia americana*) northern red oak (*Quercus rubra*), and hazel. The company estimates that over a million planted seedlings were lost in the first decade of their program while they experimented with economical methods to control competition (and deer browsing).

3. Deer browsing. Deer populations in Minnesota are vastly larger than in presettlement forests. In northern Minnesota, deer prefer white pine buds to other conifer species due to lower resin content. Early plantings of white pine (estimates of about 1 million) by Rajala Co. were lost to deer browsing (and overwhelming competition in the understory).

4. White pine blister rust, introduced in 1916, is a fungal disease that requires two hosts, alternating between white pine and *Ribes* species. Blister rust requires live needles, moisture in the understory (spores enter through the stomata in solution), and consistent cool temperatures. North-central Minnesota holds one of the highest hazard ratings for white pine blister rust in the Lake States region. Large-scale efforts in the 1970s to eliminate *Ribes* species, in hopes of reducing infection of white pine, were an abject failure, and counter-productive to goals of maintaining native plant diversity.

5. White pine tip weevil tunnels into terminal leaders of seedlings, causing death of the leader, growth loss, and poor form, all of which reduce the potential value of an individual tree. Weevil damage occurs primarily on saplings that are at least 1.5 m tall growing in open conditions.

Working against the Odds

The challenges of managing for white pine in the northern Minnesota landscape seem insurmountable to some. By the mid-1980's, most foresters concluded that the economic risk and costs of restoring white pine were too high. The outlook was so extreme that the Minnesota Department of Natural Resources sought to have references to the species removed from sections of public law. Specifically, earlier reforestation acts had called for restoration of white pine and attempts were made to have these references removed. Forestry professionals actively discouraged Rajala Co. from pursuing restoration of white pine, as they themselves abandoned most efforts at white pine management in the state.

In spite of the difficulties, and at great cost, Rajala Co. persevered to develop a successful white pine restoration program. A key element in this success has been recognition of the role of natural disturbance in regeneration of white pine and the need for silviculture approaches that provide conditions similar to those generated by natural disturbance, particularly fire. This realization was developed using a monitoring and adaptive management framework that explored a range silvicultural approaches, including regeneration harvests, methods of seedbed preparation, and vegetation control. Every approach has been assessed financially for cost and benefits, which were measured by success in seedling survival and vigor of growth.

Overstory retention and restoration of eastern white pine

The Rajala Co. approach differs from conventional pine management in the region in that live, mature trees are retained during harvest in either dispersed or aggregate patterns (i.e., variable retention *sensu* Franklin et al. 1997; Figure 17). Moreover, snags are intentionally retained on all harvest sites, downed logs are common, and a mineral seedbed is intentionally generated at abundant levels. The Rajala system may be described as a modified irregular shelterwood method; however the range and variability of harvest (and retention) patterns defy conventional description.

Figure 17. Overstory retention of large pine after harvest in a managed Great Lakes mixed-pine system. Photo by Elizabeth Jacqmain.

Rajala Co. white pine forests are managed on extended rotations that will generally exceed 100 to 200 years and include two to several commercial thinnings. White pine is underplanted following variable retention harvests, or variable density thinnings, using combinations of dispersed and aggregate residuals. Residual canopy trees function as nurse trees, but are also retained as crop trees whenever possible, to accrue value as future veneer and high grade lumber products.

White pine is the species of choice for retention, but preference is given to other commercially valuable species including red oak, paper birch, basswood, and balsam fir. If no crop trees are present, then the least merchantable trees are retained strictly as nurse trees. On dry sites where non-merchantable paper birch trees are selected as nurse trees, higher densities of trees are retained in anticipation of mortality from Post-Logging Decline phenomenon. Post-Logging Decline in paper birch has become a widely recognized phenomenon characterized by extensive crown dieback following harvests, quickly followed by mortality. This dieback has been attributed primarily to increases in soil temperature occurring in the upper soil layers.

Nurse trees, whether crop trees or not, function to ameliorate frost pockets by retaining heat and, thus, reducing condensation resulting from rising pockets of air. Moisture is a key factor in the ability of blister rust to infect white pine needles, by controlling moisture managers and decrease the probabilities of blister rust infection. Overstory shade also helps reduce tip weevil infestation by keeping the terminal leaders below a threshold size.

Another key to success of the Rajala Co. approach includes close contact with and the training of loggers. The company largely uses its own employees for white pine harvesting operations. These personnel have been trained to understand the ecological requirements of white pine regeneration. The loggers make decisions at the micro-site scale to create optimal white pine habitat. For example, riparian edges in non-white pine operations are typically left unharvested, or lightly harvested, to reduce operational costs associated with minimizing

compaction. However, for white pine underplanting, the loggers tie planting areas to the edges of swamps and lakes to take advantage of later sunlight, taking great care to avoid rutting. Also, loggers minimize damage to residual nurse trees, even when they are not commercially valuable crop trees, in recognition of their ecological importance to underplanted white pine.

Contrary to still common silvicultural approaches, Rajala Co. leaves individual canopy trees and aggregates (patches) when individuals are vigorous and have the potential to accrue greater value. The result is, generally, more complex harvest operations (i.e., greater costs). However, when spatially variable combinations of dispersed and aggregate trees are retained the result is greater canopy species diversity and structural complexity than is typical of both managed and unmanaged secondary forests in the surrounding landscape.

White pine management sites generally range from 1 to 24 hectares in area. The general white pine management cycle is as follows: 1) stands are assessed and regeneration goals are developed; 2) harvest plans are made for white pine underplanting and trees are marked for harvest or leave; 3) harvest completed; 4) site preparation activities are completed including mechanical scarification (raking) and herbicide application; 5) site is planted; 6) intermediate treatments are applied including protection, pruning, and commercial thinnings; and 7) final harvest (shelterwood removal).

Rajala Co. has gone through two stages in the development of their white pine restoration program. The first stage was experimental where white pine was used in a large variety of sites under variable harvesting and site preparation treatments. Restoration sites were generally selected by soil characteristics rather than characteristics of competing vegetation or deer populations. Each year evaluations and assessments were made to determine which treatment combinations were most successful and cost-effective. The second stage has been greater selectivity of sites incorporating not only characteristics of competing vegetation but also those of deer populations.

Pre-harvest basal area is not the basis for determining harvest levels; rather, the amount of harvest is generally determined using crown closure management, guided by tree species architectural characteristics and predictions of crown responses to thinning. For example, sugar maple crowns are expected to respond aggressively (within 2-5 years) to thinnings. For this reason, in stands containing abundant sugar maple the post-harvest crown closure range is (20 to 30) percent. In contrast, stands dominated by species with much narrower and thinner crowns, such as trembling and bigtooth aspen, paper birch, balsam fir, or red pine, the crown closure target is 40% to 60%.

Current harvests are followed by intensive site preparation and a variety of intermediate silvicultural treatments designed to provide optimal conditions for the establishment of white pine. Underplantings were attempted following site preparation with herbicides only and mechanical scarification only – both approaches were generally not successful. Establishment of white pine was only successful once site preparation included exposure of a mineral seedbed through mechanical scarification (rake) in combination with herbicide treatments that reduced woody brush and herbaceous vegetation for a 3-5 years period. Exposure of mineral soil and the reduction of competition in the understory were important effects of periodic natural surface fires in Great Lakes pine systems. In the absence of natural or prescribed disturbances, surrogates that provide some of the same outcomes are key to a successful white pine regeneration program.

A variety of herbicide combinations were investigated. Some herbicides widely favored by forest industry were designed for use in open areas and were found to damage residual canopy trees in Rajala Co. operations. In particular, residual basswood (*Tilia americana)* and paper

birch were vulnerable to several commercial herbicides (such as triclopyr and hexazinone). The current combination of broadcast herbicides used (translocated from leaves to roots) is designed to reduce both herbaceous and woody competition while remaining on the site for the shortest time possible (half-life of 6 days). The active ingredients used include low concentrations of glyphosate and sulfometuron methyl along with adjuvants, other surfactants, water softener, and defoaming agents.

Intermediate silvicultural treatments include improvement and protection activities. Cultural pruning of crop trees will take place starting after seedlings reach a sapling size of (1.75 to 2.5) meters (after the majority of mortality has occurred - over 50%) and saplings are above most deer browse height. Crop trees will be pruned to a final height of about 5 meters to increase the amount of knot-free, clear wood for high value lumber and veneer products.

Protective treatments include manual release of white pine from woody competition and protection from deer browsing. Although chemical release from vegetative competition is considered less expensive (both materials and labor) than manual activities, white pine is much less resistant to chemical damage than most pine species. Other intermediate, protective treatments include protection from deer browsing and pruning to remove blister rust infection sites and to prevent future infections (so-called pathological pruning).

Rajala Co. exhaustively investigated various methods of deterring deer browsing, including Tooley tubes and commercial deer repellents (such as Deer-Away, Plantskydd, and garlic). The most cost-effective technique for the company is budcapping of terminal leaders each fall before deer browsing begins. An additional benefit of budcapping is that each planting site is visited annually, allowing detailed observations of restoration success and the identification of current and potential problems (e.g. blister rust).

These frequent observations, along with direct communications between all operational units of the restoration program (harvesting, site preparation, planting and protection) have led to a streamlined adaptive management approach that has been crucial to the success of the program.

Strategies for Restoring Eastern White pine – Three Examples

The following examples illustrate the manner that a natural disturbance model, specifically fire, has been applied in a near-boreal landscape managed under commercial production objectives. By understanding current land conditions and likely successional trajectories, Rajala Co. used knowledge of local natural history to develop silvicultural techniques to meet management goals that, although driven by economics, includes conserving an important native tree species.

Example 1. Restoration of structural complexity in a red pine plantation: variable retention with white pine underplanting

This example is a 75-year-old plantation covering 32 hectares. It is dominated by red pine with occasional white pine, trembling aspen, and paper birch. The plantation includes about 8 hectares of scattered patches of 30-year-old trembling aspen clones initiated in gaps following the removal of canopy aspen. Red pine was planted at unusually high initial densities (greater than 283 per hectare.) and produced greater than expected volumes. About one-third of the volume was removed - over 250 cords of pine and 50 cords of other species, including paper birch, aspen and balsam fir. Short-term objectives were to remove all but the most vigorous trees

in the canopy, reducing crown closure to about 40%, and underplant with white pine. Rajala Co. has begun targeting red pine sites for underplanting with white pine for both ecological and economic reasons. Red pine was often planted on old farm fields, which often are have better soils than non-farmed sites, and woody competition is more easily controlled. Ecologically, white pine typically invaded sites that were dominated by red and jack pine (Frelich 1992).

The plantation was summer-thinned in 1999, leaving both dispersed and aggregate residuals of mostly red pine, along with scattered, mature white pine (Figure 18). The white pines present in the canopy are derived from natural regeneration. Summer harvest was used to insure adequate scarification of the site and to help eliminate woody competition. The harvest removed all individuals of poor form and those with low wood value. In areas where no crop trees were present, lower value individuals were retained as nurse trees. Patches of healthy red pine saplings and small poles were retained. These stems had naturally regenerated in and around small openings in the canopy. Scattered healthy individuals of other commercially valuable species were retained as well, including paper birch and trembling aspen. The majority of residual red and white pines were crop trees, that is, those with the potential to become high quality, large sawtimber. These were pruned to a height of 5 meters in the winter following harvest. The site was raked in early spring 2000 and sprayed in the fall using broadcast herbicides. Planting occurred the following spring, using seedlings grown from naturally occurring local groves of mature white pine.

Figure 18. Overstory retention to restore structural complexity and compositional diversity in a red pine plantation. Note "bud-capped", planted eastern white pine seedlings in foreground.

The intermediate objectives for the site are to create a two-aged forest (white pine under red) allowing the underplanted white pine to reach 30 – 50 years of age before removal of the overstory (canopy at 105 to 125 years). The long-term plan is to convert the site to a mixed-pine, multi-cohort forest trending towards an uneven-aged management system that relies on natural regeneration. Rajala Cos.' experiments with seed tree cuts indicate that by continuing to provide disturbance outcomes (canopy removal, soil scarification, and control of vegetative competition) along with protection from impediments (blister rust, tip weevil, and deer browsing) we can provide continuous natural regeneration.

Example 2. Restoration of mixed white pine and paper birch stand: partial canopy disturbance to release natural white pine regeneration

This north facing lakeshore was dominated historically by a grove of eastern white pine that was logged in the 1890's. After this logging, the stand was dominated by remnant sugar maple, paper birch and a few scattered super-dominant white pines. Abundant sugar maple developed in the lower canopy in the years after logging. In 1995, most of the remnant white pine was removed due to extensive damage by blister rust. Only a few healthy and lightly infected individuals were retained. Additionally, logging removed canopy birch possessing weak crowns (less than 30% of bole) and poor form. Winter harvest was used to minimize scarification to the forest floor believed to contribute to Post-Logging Decline in paper birch. This also served to protect existing white pine regeneration.

In the 8 years since harvest, sugar maple has steadily increased its dominance in all strata. Growth rates of paper birch indicated that another release might be beneficial. At the same time, there was concern that natural white pine regeneration may fail due to the dense sugar maple canopy. Consequently, mid- and over-story sugar maple were killed in the summer of 2000 through girdling (a hypo-hatchet was used to inject a triclopyr herbicide), primarily to release paper birch crop trees. Girdling was followed by manual release of the white pine seedlings to remove seedlings and saplings of competing sugar maple.

The silvicultural plan for this site is to initially develop a two-aged stand (white pine under birch) carrying the paper birch as long as possible before harvest. Following harvest of paper birch the stand will be converted to a white pine type while regenerating and maintaining paper birch on the site in both natural and harvest gaps.

Example 3. Restoration of white pine in a simplified northern hardwood stand

This example is a site which is typed as a northern hardwood stand that historically contained a substantial white pine component (as indicated by numerous, scattered white pine stumps). After removal of mature white pine in the 1920's, and the subsequent exclusion of fire, the forest succeeded to mostly sugar maple, with occasional patches and scattered individuals of basswood, balsam fir (*Abies balsamea)*, paper birch, trembling aspen, red oak, and bigtooth aspen and a few residual super-dominant white spruce (*Picea glauca* (Moench) Voss) in the canopy. The groundstory was dominated by well-established balsam fir and it was determined that without disturbance, the site would succeed to domination by balsam fir and sugar maple.

One half of the site was summer harvested in 1988 to salvage red oak killed by Armallaria (*Armillaria* spp.) root rot. Mature white pines were retained whenever possible, along with high quality, healthy canopy trees of red oak, basswood, and paper birch (Figure 19). Some patches of healthy advanced regeneration were also retained and included red oak, basswood, paper birch and balsam fir.

Advance regeneration of balsam fir, birch and basswood, regeneration was low enough in patches that other artificial regeneration (planting) options were considered to supplement natural regeneration. However, the presences of dispersed advanced regeneration of hardwoods in the understory precluded the use of mechanical raking and herbicide application.

Figure 19. Post-harvest overstory retention of large pines (top) and hardwoods (bottom).

In 1988, Rajala Co. was still experimenting with restoring white pine on a variety of sites and this site was selected to test underplanting white pine. There was no raking or herbicide application. Following harvest and planting, growth by sugar maple in the mid-story was aggressive. Crown closure had increased to over 80% wherever sugar maple was abundant. In 1991 a brush saw was used to release white pine seedlings with care to protect all existing red oak and basswood seedlings. In 1998 overstory and mid-story sugar maple were girdled and white pine seedlings were hand released. Subsequent crown closure was estimated to be about 40%. Seedlings were again hand released in 2000. The result was 90% survival of white pine plus abundant natural regeneration of red oak.

Red oak regeneration developed primarily along the edges of this stand. Red oak is one of the most commercially valuable species in the Lake States Region. Fortuitously, the stand-level disturbance which created optimal habitat for white pine seedlings, including mineral soil exposure, also resulted in the successful regeneration of red oak, another fire dependent species. This same phenomenon has been observed on sites where paper birch was retained as a seed source. Finally, in 2002, the lower 1/3 of all white pine crop tree crowns were pruned to prevent infection by blister rust.

The remaining portion of this stand was harvested in the winter of 1997. Initial harvest decreased canopy closure to 30% in the matrix dominated by sugar maple. Canopy paper birch was preferentially retained, but at a higher canopy closure (60%) than other species in anticipation of mortality due to Post-Logging Decline. As in the earlier harvest (1988), mature white pines were retained whenever possible, as were high quality red oak, basswood, and aspen. Effort was make to protect healthy advanced reproduction of these species, along with balsam fir. Herbicides were applied following raking and white pine was underplanted in 1999.

In this case study, red oak has successfully reproduced within the interior of the second harvest area. Additionally, paper birch regenerated abundantly whenever seed source was available. By creating conditions similar to those resulting from a natural fire regime, Rajala Co. has been successful at restoring white pine in this site, and also other fire-dependent species. Moreover, variable retention harvest has lead to greater structural complexity and canopy species diversity than that occurring in the surrounding managed landscape.

Pacific Northwest Case Study: Restoring and Maintaining Biodiversity and Ecosystem Function in Pacific Coast Forests

Introduction

Restoration and maintenance of biological diversity and ecosystem function in Pacific Coast forests is the subject of this case study. Pacific Coast forests are defined primarily as those found in the wet, maritime region west of the Cascade Range and, in Canada, the Coast Ranges from the coast redwood region of northern California to southern British Columbia, including Vancouver Island. Although similar forests extend north to the Gulf of Alaska they are not included in this case study because they contrast substantially in both natural and social history with those further south, most notably in patterns of natural disturbance (no fire) and stand development.

This case study begins with brief reviews of the natural and socio-economic histories of the forests found in region of North America. As noted earlier in this report appropriate programs for restoration and maintenance of forest biodiversity and function must consider the unique environment, species, and disturbance patterns of a region; hence, these are the primary variables of the natural history review. Incorporation of both the history and the social and economic structures of a region are also critical in developing appropriate restorative approaches; hence, a review of the diverse land ownerships and history of exploitation and modification of the forest resources is appropriate.

The bulk of the case study is an overview of programs for restoration and maintenance of forest biodiversity and function that are underway within the region. These are based on an expanded understanding of natural disturbance regimes and stand development patterns within this region that has developed in the last 30 years. These build on the broad principles developed earlier in this report but reflect the need to adapt those to the ecological and social conditions found within a specific region.

The case study is directed to two contrasting but highly compatible approaches: 1) Maintaining biodiversity and functionality by providing for structural retention during regeneration harvests; and 2) Restoring biodiversity and ecosystem functions in structurally simplified stands by utilizing principles from small-scale disturbance and other stand development processes. The first approach—structural retention at harvest—has received much emphasis in the region due to continuing harvest of natural forest stands on many ownerships; the issue has been how to better model such harvests on natural stand-replacement disturbance regimes, so that biodiversity and functionality are sustained or quickly restored. The second approach—managing stands to restore structural complexity and, thereby, native biodiversity—has received major emphasis from the need to restore diversity and functionality to large areas of simplified young stands that have been created by clearcutting and planting, especially during the last 50 years.

Applications of these two approaches to biodiversity maintenance and restoration on forests of varied land ownerships and objectives will be reviewed along with the outcomes of these approaches as currently documented or predicted. The goal is to make clear how and why we arrived at the current situation, which requires restoration and maintenance of biodiversity as

a goal and to document what is being done and its relationship to natural disturbance and stand development regimes.

Natural History of Pacific Coast Forests

Environmental Conditions

Globally distinctive temperate forests are found in the wet to moist, mild maritime climate region along the Pacific Coast of North America in the wet to moist, mild maritime climate regions. These are located west of the major coastal mountain ranges, which consist primarily of the Cascade Range in the United States and the Coast Range in British Columbia (Franklin and Dyrness 1988; Franklin and Halpern 2000). Annual precipitation is typically high (1270 to 3810 mm) but is highly seasonal with little rainfall during the summer growing season (June through September). Consequently, dry warm summers are characteristic with important implications for wildfire. Winter temperatures are mild so that significant photosynthesis and other important processes are active year-around. Winter storm systems with high winds are common and there are occasional extreme wind events within the region, usually at intervals of several decades.

Species Composition

Massive coniferous forests dominated this region prior to settlement (Figure 20). The old-growth forests found here provide the largest accumulations of organic matter of any forested ecosystems in the world (Waring and Franklin 1979; Franklin and Dyrness 1988; Franklin and Halpern 2000). While high levels of forest productivity contribute to this phenomenon, the high biomass accumulations are clearly due to the presence of dominant tree species that have very long life spans and the capacity to grow for many centuries and to very large sizes. Many of the genera represented here find their largest and longest-lived representatives within the Pacific Coastal forest including *Pseudotsuga, Pinus, Tsuga, Abies, Picea, Thuja, Chamaecyparis,* and *Sequoia*.

Tree species typical of the Pacific Coast temperate forests include the evergreen conifers: Douglas-fir, western hemlock, western redcedar, Sitka spruce, western white pine, noble fir, Pacific silver fir, and Port-Orford-cedar and, at higher elevations, mountain hemlock and Alaska-cedar. Coast redwood is an important and distinctive species in northwestern California and extreme southwestern Oregon. Locally, deciduous hardwood species are also important stand components and include bigleaf maple, black cottonwood, and red alder, which incorporate nitrogen-fixing bacteria in nodules on its roots. In southwestern Oregon and northwestern California evergreen hardwoods, such as tanoak, Pacific madrone, Canyon live oak, and California laurel may be common stand components. Deciduous oaks, primarily

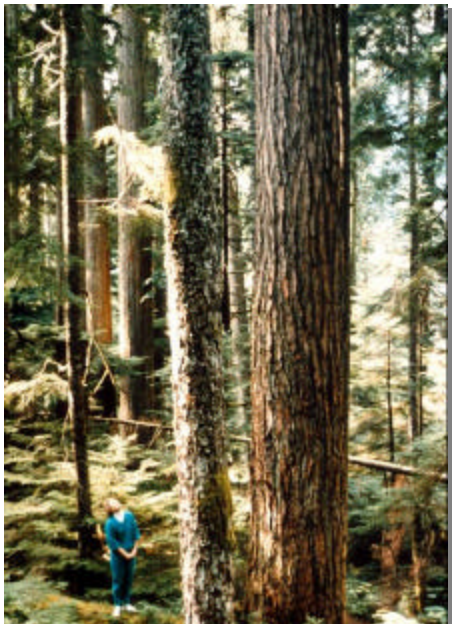

Figure 20. Massive coniferous forests were characteristic of the pre-settlement Pacific Coastal forest landscape. These reflect both high productivity and the dominance of species with long life spans and the capacity to grow to large sizes.

Oregon white oak and California black oak, can also be important species, particularly in ecotones with valley grasslands.

Disturbance Regimes

Stand-replacement disturbance regimes are general through the Pacific Coastal forest region, although the specifics of these regimes are quite variable. The dominant disturbance regime is characterized by intense, very large scale, stand-replacement fires on return intervals of several centuries (Franklin and Hemstrom 1981; Franklin and Dyrness 1988; Franklin and Halpern 2000). For example, a fire return interval of 465 years was calculated for the forests of Mount Rainier National Park on the west side of the Washington Cascade Range (Hemstrom and Franklin 1982). These fires are a result of the large accumulations of fuels that are a constant feature of these forests coupled with the warm, dry summer periods; synoptic weather patterns that produce strong flows of hot, dry air from continental regions are invariably associated with major fire events. Regional variations in fire regimes are associated with latitude, with decreasing fire return intervals in the south (see Agee 1993) and with proximity to the ocean (i.e., coastal Sitka spruce-western hemlock forests have much lower probabilities of fire).

Wind is important in disturbing forests at both the gap and the stand level in Pacific Coast forests. Wind, rather than fire, is the primary stand-replacement disturbance in many coastal areas, such as the coastal plain of the Olympic Peninsula (Henderson 1994) and in wetter portions of coastal British Columbia. Intense windstorms can also produce large scale stand-replacement disturbance events elsewhere. A notable example is the Columbus Day Windstorm of 1962, which affected several million hectares of forest in western Washington and Oregon.

Volcanic events have clearly been important disturbance phenomena in the Pacific Coast forests as demonstrated by the 1980 eruptions of Mount St. Helens, a stand-replacement event that affected over 50,000 ha of forest. This was a seminal event in the development of the biological legacies concept, as noted earlier (Franklin et al. 1995).

Stand Development and Succession

Patterns of compositional and structural change with stand development are well understood for the Pacific Coast Douglas-fir-dominated forests. The classic successional sequence begins with initial dominance of stands developed following a stand-replacement disturbance by the hardy, shade-intolerant pioneer species, Douglas-fir (Franklin and Hemstrom 1982; Franklin and Dyrness 1988). Shade-tolerant species, such as western hemlock and western redcedar gradually become established in the stand and grow into the upper canopy, a process that can take several centuries. The shade-tolerant associates gradually replace the Douglas-fir, which generally fails to successfully reproduce in gaps that develop within the stand. There are, of course, many variations and exceptions to this general pattern. For example, shade-tolerant species are often also part of the initial cohort established following stand replacement disturbances and may even dominate early in sere. Douglas-fir does occasionally reproduce and grow successfully in established stands. Furthermore, stand replacement disturbance events typically return to stands long before the long-lived Douglas-fir, which can survive for 800 to 1500 years, completely disappear.

A comprehensive conceptual model of Douglas-fir stand development has been published recently, which incorporates numerous developmental processes and structures and provides the

best basis for ecological forestry (Franklin et al. 2002). Eight developmental stages are recognized: (1) Disturbance and legacy creation; (2) Cohort Establishment; (3) Canopy Closure; (4) Competitive Exclusion; (5) Maturation; (6) Vertical Diversification; (7) Horizontal Diversification; and (8) Pioneer Cohort Loss. Substantial emphasis is placed upon the initiating disturbance and the type of biological legacies that are generated for incorporation into stand recovery processes. However, many other stand development processes are recognized (Table PNW-1), including small, gap-scale disturbance processes, which make major contributions to biodiversity and other ecosystem functions.

Table 4. Processes contributing to structural development of coniferous forest stands in the Pacific Coastal forest (from Franklin et al. 2002).

DISTURBANCES AND LEGACY CREATION
Establishment of new cohort of trees or other organisms
Canopy closure by tree layer
Competitive exclusion (by shading) of ground flora
Lower tree canopy loss
Death and pruning of lower branch systems
Biomass accumulation
Density-dependent tree mortality (due to competition among tree life form)
Density independent tree mortality (due to such agents as disease, insects, and wind)
Canopy gap initiation and expansion
Generation of snags, downed boles, and other coarse woody debris
Uprooting
Understory redevelopment (shrub and herb layers)
Establishment of shade-tolerant tree species
Shade patch ("anti-gap") development
Maturation of pioneer tree cohort (attainment of maximum height and crown spread)
Canopy elaboration (development of multi-layered or continuous tree canopy)
Growth of shade-tolerant trees into overstory
Redevelopment of lower branch systems on dominant trees (epicormic branches)
Development of live tree decadence (multiple tops, stem and top rots, cavities, brooms)
Development of large-diameter branches
Development of epiphytic communities
Pioneer cohort loss

This stand-development model can be generalized to forest types other than those dominated by Douglas-fir or by stand-replacement fire. Hence, a general model of structural and compositional change exists for this region that can provide the natural model for both retention harvest and intermediate stand level treatments.

Socio-Economic History of Pacific Coast Forests

When western settlement of the Pacific Coastal forests began in the early 19th century, old-growth forests (>200 years in age) probably accounted for two-thirds of the forest cover. Indeed,

the percentage of old-growth forests was probably near the maximum for the millennium as a consequence of extensive stand-replacement fires around 1490-1500 AD. Effects of Native Americans on forest conditions are believed to have been minimal, except in localized areas (Agee 1993).

These forests represented both a challenge and an opportunity for settlers. The challenge was the difficult task of clearing these forests for agriculture and development of communities, although there were a few areas, such as Oregon's Willamette Valley, where extensive grasslands existed. The opportunity was utilizing these forests as sources of raw material, initially providing wood for construction of homes, settlements, railroads, etc. and, ultimately, as the basis for a major industry. Harvesting and milling of trees began early with the first sawmill established at Fort Vancouver in the mid-19th century.

Major cutting of native forests and production and export of wood products was well underway by the late 19th century. Early commercial developments were tied to waterways and ocean ports. Hence, an early geographic concentration was in the Puget Sound region; the center of harvest and wood production gradually shifted south ultimately reaching western Oregon in the mid-20th century.

Land Ownership

Land ownership was and is an important factor influencing management and use of the forest lands and the basic patterns of ownership were largely completed by the early 20th century. The bulk of the low-elevation and accessible forest lands, which included most of the highly productive sites and high timber volumes, were already in the hands of private interests by the time establishment of the federal Forest Reserves had begun to occur in the 1890s. The transfer of the public domain took place as a result of a variety of transactions, legal and illegal. Much of the transfer occurred as a result of such legislation as the Homestead and Timber and Stone Acts. Large land grants were used to encourage or subsidize construction of railroads and wagon roads.

Trust lands were also acquired by states with the intent that these properties would be managed to provide income for secondary schools and universities, roads, and other public services; these lands are sometimes, inappropriately, viewed as "public lands" because they are administered by state government agencies. The largest block of trust lands were transfers from federal government to the newly admitted states of Oregon and Washington. States were also allowed to select additional *"in lieu"* lands, in place of sections of land that they would normally have received but which were already in private hands. Washington State acquired an extraordinarily heavily timbered and highly productive tract on the western Olympic Peninsula as an *"in lieu"* selection. Local and state governments acquired additional trust lands as a result of land abandonment and unpaid taxes, particularly the Great Depression and as a result of several large wildfires (the Tillamook and Yacholt Burns).

A large block of Pacific Coastal forest was retained in public ownership as forest reserves or, as they were renamed in 1905, the national forests. Timber harvest was viewed as an appropriate use of these lands and was aggressively pursued as an agency agenda by the administering Forest Service. Areas of federal forest reserve were ultimately were transferred from national forest to national park status, as in the case of Olympic and Mount Rainier National Parks, removing them from consideration for timber harvest. The federal government

also retained trust responsibility for Indian reservation lands, through the Bureau of Indian Affairs.

Ownership patterns developed very differently in British Columbia than in the United States. The provincial government retained ownership of the bulk of the provincial forest lands as "crown lands", rather than transferring them to private hands. Some forest lands were sold or granted to private individuals, such as the railroad grant made on Vancouver Island. Forests on crown lands have been made available for timber harvest and industrial development, primarily through a program of long-term tree farm licensing. At various times government foresters have played either managerial or regulatory roles in attempting to assure that sound silvicultural practices are utilized in management of the crown lands by private entities.

Land ownership patterns are important in understanding why and how forest policy developed and our current needs for forest restoration. To summarize, essentially all of the most productive, accessible, and heavily timbered Pacific Coastal forests had been transferred to the private sector (individuals, companies, and corporations) or to trusts by the early 20th century in the United States. The majority of forest lands were retained as publicly owned "crown lands" in British Columbia but with large blocks leased to private companies and corporations for timber harvest.

History of Forest Harvest and Silviculture

The development of timber harvesting technologies and of silvicultural practices occurred very rapidly during the first few decades of the 20th century. R. A. Rajala (1998) documents these changes very well in his book, *"Clearcutting the Pacific rain forest: production, science, and regulation"*.

Early History. Utilization of Pacific Coastal forests began with inefficient and often destructive logging of forest stands using teams of oxen or horses to move huge logs relatively short distances to streams and rivers for long distance movement. Development of railroads, steam donkeys, and cable-yarding systems resulted in increasingly efficient and profitable harvesting of these forests. Utilization improved but often was still confined to the most valuable components of the stand, particularly the old-growth Douglas-fir trees. Rapid expansion of timber harvesting—clearing of old-growth forests—was a consequence of these developments. However, large expanses of logging slash were left behind, which often resulted in devastating wildfires on and adjacent to logged areas. In the 1920s forest logging techniques began to shift from the capital- and labor-intensive railroad logging to techniques that utilized tractors and trucks. With this change came substantial pressure for selective logging of Douglas-fir stands.

Large wildfires were critically important in influencing forestry policy and programs during the early 20th century in Pacific Coastal forests. While large forest fires occurred regularly during the period of land clearing and settlement throughout the 19th century, the 20th century was ushered in by several million hectares of wildfires in the fall of 1902. The most notable of these 1902 fires was the Yacholt Burn, which burned nearly 100,000 hectares in southwestern Washington and killed many people. Large wildfires continued to be a recurring problem in Pacific Coastal forest lands throughout the first 3 decades, often being ignited by logging activity. Oregon's Tillamook Burn covered approximately 111,000 hectares in 1933 and large portions were subsequently re-burned two or more times, as was the case with the Yacholt Burn.

One consequence of the extensive wildfires was that private landowners were unwilling to actually manage their forest stands according to silvicultural principles, until effective forest fire suppression programs began to emerge in the 1920s. The commitment of private landowners to reforestation and other silvicultural management of private forest lands followed the development of fire control programs. The emergence of the tree farm movement in 1940 signaled arrival of fire suppression programs that were at least viewed as credible.

Post-World War II Period. Major changes occurred in management of federal and trust timberlands following World War II. Timber harvest had been concentrated on private forest lands during the first half century; indeed, industrial forest owners had actively lobbied to keep federal timber off of the market during the depression. Although there had been active timber sales from national forests from the time of their establishment, timber harvest activity had been confined to the most accessible and heavily timbered areas. The immense demand for wood products in the post WWII period provided the opportunity that the Forest Service had been seeking to bring the Pacific Coastal national forests under intensive timber management—including the necessary congressional appropriations.

The last half of the 20th century saw increasingly intensive management practices on Pacific Coast timberlands. Clearcutting and even-aged management were adopted on both private and public lands. Clearcutting was usually justified on the basis of the ecological requirements of the favored commercial species—i.e., a purported need for large open cutovers to successfully regenerate and grow the shade intolerant Douglas-fir. Clearcuts were described as being equivalent ecologically to the stand-replacement fires that characterized the region. Clearcut sizes did differ between private and public lands; large continuous clearcuts covering hundreds of hectares were characteristic of private lands and while dispersed small (2.5 to 5.6 hectare) clearcuts were characteristic of federal lands (Franklin and Forman 1987).

Management on federal lands and trust lands increasingly followed the tree farm or high yield forestry models developed initially for corporate forest lands. Regeneration shifted from an emphasis on natural regeneration to a nearly exclusive reliance on planting. Utilization standards increased to high levels, leaving little organic material behind. On federal lands standard treatments of logging slash reduced this even more. Both utilization and fuel objectives contributed to requirements for yarding and piling cull logs--called YUM (yard unmerchantable material) and PUM (pile unmerchantable material)—on all clearcuts. Removal of slash and all woody debris was extended to streamside areas by the 1960s. Pre-commercial thinning of young stands was viewed as a standard practice critical to proper development of the dense young plantations.

The consequences of intensified management for forest biodiversity and ecosystem function received little attention during this run-up of management intensity on federal lands. Wildlife considerations were confined to game species, which were presumed to flourish with development of additional edge habitat, such as by clearcutting. Effects on ecosystem functions, such as regulation of nutrient and hydrologic regimes, generally did not receive much attention; it was assumed that conditions that were favorable to wood production would be favorable to other forest values. Concerns did begin to emerge in the scientific community about effects of intensive, even-aged management and associated roads on ecosystem functions, such as soil stability, sedimentation, and stream temperature by the mid-1960s.

Public concern about developing conditions on Pacific Coast forest lands—especially the federal lands—developed in pace with the extension and intensification of forest management. Much of this was fueled by concerns about environmental values, although aesthetic issues

loomed very large in popularizing the issues. These concerns, which were often initially intuitive, were fueled by an increasing volume of scientific study on ecosystem processes and biodiversity, as exemplified by research at Hubbard Brook in New Hampshire, Coweeta Hydrologic Laboratory in North Carolina, and the Andrews Experimental Forest in Oregon.

A series of environmental laws passed in the 1960s and 1970s provided the bases for legal challenges to forestry practices on federal and, to a lesser degree, private and trust lands. These include the National Environmental Policy Act (NEPA), National Forest Management Act of 1976 (NFMA), and Endangered Species Act (ESA). Extensive litigation by environmental organizations ultimately forced major changes in management emphasis on all regional forest lands.

Circumstances at the End of the 20th Century. At the end of the 20th century we found ourselves with the majority of the Pacific Coast forests converted from structurally and compositionally complex ecosystems to highly simplified plantations and landscapes with limited capacity to provide for many elements of native biodiversity, especially biodiversity related to late-successional forests. Such organisms as the Northern Spotted Owl, Marbled Murrelet, Bull Trout, and many populations of salmonids were identified as legally threatened or endangered species and provided powerful flagships in generating public awareness. Societal goals for federal forest management had shifted substantially as a result of successful litigation, with greatly increased concerns for biological diversity and critical ecosystem functions, such as regulation of hydrologic processes.

The societal paradigm shift has had the earliest and greatest impacts on the federal lands. Forest plans for the federal lands have been dramatically modified under the terms of the Northwest Forest Plan (Forest Ecosystem Management Assessment Team 1993). One result is that management priorities on federal lands are now directed to maintenance of native biodiversity and key ecosystem processes, even at the expense of dramatically reduced timber harvest. Trust lands and private forest lands have not escaped consequences of the shift, however, since aspects of the Endangered Species Act are applicable to these lands. The need to maintain and restore aquatic biodiversity has had the greatest impact on forest lands in private and trust ownership.

Current societal goals for Pacific Coastal forests require restoration of upland and riparian forests to conditions that are more functional with regards to sustaining native biodiversity and critical ecosystem functions. Achievement of these goals also requires development and application of forest harvest prescriptions that will sustain native biodiversity. Hence, the development of the ecological forestry approaches to harvest and management of forest stands described in the following section.

Development of Ecological Forestry—What Is Being Done and Why?

In Pacific Coastal forests there are two major challenges that involve management of forests for biological diversity:

- Maintenance of biodiversity and ecosystem function in natural stands that continue to be harvested within the region; and
- Restoration of biological diversity and ecosystem function in forest stands and landscapes from which they have been lost as a result of past management.

Developing ecological forestry systems that will fulfill these needs requires attention to all three of the elements described earlier in this report (Lindenmayer and Franklin 2002):

- Incorporating the concept of biological legacies into harvesting prescriptions;
- Incorporating natural stand development, including small-scale disturbance processes, into silvicultural treatments of established stands; and
- Allowing for appropriate recovery periods between regeneration harvests.

Current approaches to restoration and maintenance of biodiversity and functionality utilize the first two of these elements, however, so we will concentrate on these in this report.

As noted, the current initiatives in ecological forestry are directed both to maintaining biodiversity in managed forests where it currently exists and restoring it to forests and landscapes where it has been lost. As will be noted, ownerships do vary substantially in the nature and intensity of their programs to maintain and restore biodiversity although all ownerships are involved in these practices to at least some degree. The initiatives include both terrestrial and aquatic ecosystems, since riparian forests and stream systems have also been dramatically simplified by a hundred years of timber harvest and related activity.

Reservation of forest lands from timber harvesting has also been an important part of programs for maintenance and restoration of biodiversity and ecosystem function. A notable example is the Late Successional Reserves established on federal forest lands within the range of the Northern Spotted Owl (Tuchmann et al. 1996). However, establishment of reserves has also provided a major impetus for restoration forestry, since significant portions of reserved areas are currently in a simplified condition.

Structural Retention at Harvest

Modified harvesting practices were initially emphasized in the development of ecological forestry because of the intense conflicts between the perceived needs for continued timber harvests in native forests, on the one hand, and maintaining biological diversity and ecosystem functions where they still exist, on the other. Significant timber harvesting of many natural stands as well as plantations is expected to continue into the indefinite future on all ownerships. However, it is very clear that the dramatic impacts of traditional clearcutting and even-aged management practices on both biodiversity and ecosystem functionality are no longer acceptable.

Consequently, harvest prescriptions are being developed and applied that incorporate the concept of biological legacies. Variable retention harvesting is the general term applied to the broad array of prescriptions that have been developed, as noted in an earlier section of this report. Retention of riparian buffers along streams and rivers and around other aquatic features is also an element of variable retention forestry.

Although the biological legacies of natural disturbance regimes provide the scientific basis for variable retention harvesting, it also evolved out of efforts to mitigate various negative impacts of clearcutting and even-aged management. Experimentation in regenerating Pacific Coastal forest using shelterwood and group selection techniques has been underway for many decades (see e.g., Franklin 1963). Shelterwood approaches were widely applied on environmentally severe forest sites on federal lands during the 1970s and 1980s providing practical experience in harvesting while retaining significant overstory. Retention of wildlife trees emerged as a common practice in the late 1970s and introduced the concept of permanent retention of structures from the harvested stand. Hence, when the concept of biological legacies emerged from ecological studies of the Mount St. Helens region in the early 1980s, it merged with several decades of practical experience with modified harvesting regimes that involved structural retention.

Variable retention harvesting is being applied widely on essentially all ownership groups in Pacific Coastal forests. Below we will review the application of variable retention harvesting on several ownerships and review evidence with regards to the effectiveness of these practices with regards to retaining and restoring biological diversity and functionality in harvested stands.

Federal Forest Management. The U. S. Forest Service was an early adopter of variable retention harvesting practices. This began with its experiences in attempting to retain wildlife trees and snags and in developing and applying shelterwood harvest prescriptions on several sites during the 1970s and 1980s. The emergence of the concept of biological legacies provided a scientific basis for developing a more comprehensive approach to alternative harvest practices and many Forest Service silviculturalists began to develop variable retention harvest prescriptions before they were recognized as such.

The Northwest Forest Plan adopted for all federal forest lands within the range of the Northern Spotted Owl now requires that all regeneration harvests incorporate significant structural retention effectively eliminating clearcutting. Any regeneration harvest conducted on federal forest lands in the region affected by the plan must include a minimum of 15% retention. The language of the Record of Decision states that "70% of the total area to be retained should be in aggregates of moderate to larger size (0.2 to 1 hectare or more with the remainder as dispersed structures (individual trees, and, possibly including smaller clumps less than 0.2 ha)" (U.S. Department of Agriculture and U.S. Department of Interior 1994b). Retained structures are to include some of the largest and oldest trees, large snags, and large down logs, objectives that can easily be met through aggregated retention.

Variable retention harvesting prescriptions by federal agency managers typically incorporate higher levels of retention than the 15% prescribed minimum (Figure 21). Many prescriptions retain essentially all old-growth trees that are present within the harvest unit.

Much scientific work on the effectiveness of variable retention harvesting is underway on federal lands. One large scale, replicated scientific experiment is currently being conducted by the U. S. Forest Service to compare the effects of different levels and patterns of retention on biodiversity and various ecosystem functions; this is called the Demonstration of Ecosystem Management Options (DEMO) project (Aubry et al. 1999). Central to the design is a 2 X 2 comparison of 15 and 40 percent retention and of aggregated and dispersed spatial patterns for the retention. Response

Figure 21. Retention harvesting as commonly applied on national forest lands in the Pacific Coast forests. A diversity of tree species and sizes (totaling about 25% of the original stand), including large old trees, snags, and down boles have been retained on this harvest unit on the Willamette National Forest, Oregon.

variables include flora, fauna (including songbirds and small mammals), mortality of retained trees, tree regeneration, and snow hydrology.

A silvicultural system that incorporates stand-replacement disturbance regimes and variable retention harvesting has been developed and is being implemented by scientists associated with the H. J. Andrews Experimental Forest (Cissel et al. 1999).

Variable retention harvesting is demonstrably much more effective at sustaining biological diversity than clearcutting regimes, considering both initial "lifeboating" of organisms and subsequent recolonization of harvested sites by displaced species. Its effectiveness has been demonstrated through 1) retrospective studies of sites where structural elements were accidentally retained following logging, 2) retrospective studies of naturally disturbed areas on which live trees had survived; 3) comparative studies of relatively recent harvest units that involved varying levels of retention; and 4) model simulations. The effects of variable retention do, of course, vary with the organism and process of interest.

Weyerhaeuser BC Coastal Forest Project. The most extensive and scientific application of variable retention harvesting is currently being carried out as the Weyerhaeuser BC Coastal Forest Project in coastal British Columbia. This application developed out of the merging of three independent (but socially related) processes.

One of these processes was the establishment of a Scientific Panel for Sustainable Forestry Practices in Clayoquot Sound (1995) by the government of British Columbia. This panel was asked to provide recommendations for management of crown lands in the Clayoquot Sound region of western Vancouver Island. The scientific panel recommended that the government, "replace conventional silvicultural [clearcut] systems . . . with a "variable retention silvicultural system." The purpose of this system is to preserve, in managed stands, far more of the characteristics of natural forests." The scientific panel recommended the retention of at least 15% of the forest, primarily as 0.1 to 1-hectare aggregates spatially distributed so that all parts of the harvest unit are within two tree heights of a stand edge, riparian buffer, or aggregate. The province adopted all recommendations of the scientific panel, including adoption of retention harvesting.

Figure 22. View of the Montane Alternative Silvicultural Systems" experiment which was designed to explore the practical and scientific consequences of various alternatives to clearcut harvesting in montane forests on Vancouver Island, British Columbia.

A comparative study of different harvest cutting prescriptions on Vancouver Island called "Montane Alternative Silvicultural Systems" (MASS) was a second contributing process (Phillips 1996) (Figure 22). This experimental comparison of clearcutting with several other harvest prescriptions was a collaborative supported by government agencies, timber companies (mainly MacMillan-Bloedel), and academic scientists. The experiment provided participants with practical experience and data on effects of prescriptions involving retention (at least temporarily) of live trees and, hence, at least some familiarity and comfort with retention.

Subsequently, MacMillan-Bloedel, which was the largest wood products corporation in Canada at the time, decided to phase out clearcutting, largely as the result of social, including market, pressures. The corporation adopted the variable retention harvesting approach as its primary replacement for clearcutting and in 1988 publicly laid out a 5-year program to phase over to the new approach (Mitchell and Beese 2002). This decision was not well received by many foresters, wood products companies, and the BC Forest Service, all of whom had been committed to the necessity for clearcutting in Pacific Coastal forests. It also required the adoption of a legal definition of variable retention harvesting by the BC government, since cutting permits could only be issued for officially recognized and defined silvicultural practices!

Weyerhaeuser Corporation committed itself to continue this transition from clearcutting to variable retention harvesting in managing lands acquired with its purchase of MacMillan-Bloedel in 1989, labeling this the BC Coastal Forest Project. As of the most recent review (Weyerhaeuser Corporation 2001), 62% of the harvesting on coastal forest lands was by variable retention harvesting, significantly ahead of the level of 40% retention harvesting planned for 2000/2001.

The original guidelines for retention were a minimum of 10% retention, the majority of which was expected to be in the form of aggregates. Experience has resulted in adoption of a wide variety of retention practices including dispersed, aggregated, and mixed retention prescriptions (Figure 23). Actual levels of retention based on a third-party monitoring of harvest units was close to 20%, over twice the minimum prescribed level of retention.

Figure 23. Example of aggregated retention on a helicopter-logged unit under the Weyerhaeuser BC Coastal Forest Project.

Acceptance of the variable retention harvesting by employees and the general public has been excellent. The corporation made safety the highest priority objective in implementing the new harvest system. All employees received extensive training in the underlying concepts and practical issues associated with variable retention so as to understand what was being done and why. A regular scientific review process, which included participation by environmentalists and other stakeholders and government agency personal, was initiated with the most recent in July 2001 (Weyerhaeuser Corporation 2001). This has resulted in credible scientific endorsements for the approach as well as significant acceptance of the validity of the approach from the environmental community; the BC Coastal Forest Project received the Corporate Award of the Ecological Society of America in 2001 for this work.

Adaptive management is a major element of the BC Coastal Forest Project. An extensive performance monitoring program is underway by an independent third-party forestry firm to ascertain that the corporation is meeting its performance goals with regards to implementation of

variable retention—i.e., it is doing what it said it was going to do! The corporation is conducting effectiveness monitoring programs to ascertain that the variable retention harvesting is lifeboating elements of biological diversity. Both terrestrial and aquatic ecosystems are receiving attention in the monitoring program.

Plum Creek Timber Company. Plum Creek Timber Company was the first timber corporation in the United States to adopt and apply the concepts of variable retention harvesting to Pacific Coastal forests. Motivations for developing an alternative to clearcutting included social issues as well as an emerging need to adopt forest management approaches that would reduce impacts on potentially threatened and endangered species.

Plum Creek Timber Company began exploring approaches to variable retention harvesting in 1989 and quickly developed the concept of aggregated retention in an effort to minimize harvesting costs and safety issues while maximizing effectiveness of retention from the standpoint of biodiversity and aesthetics (Figure 24).

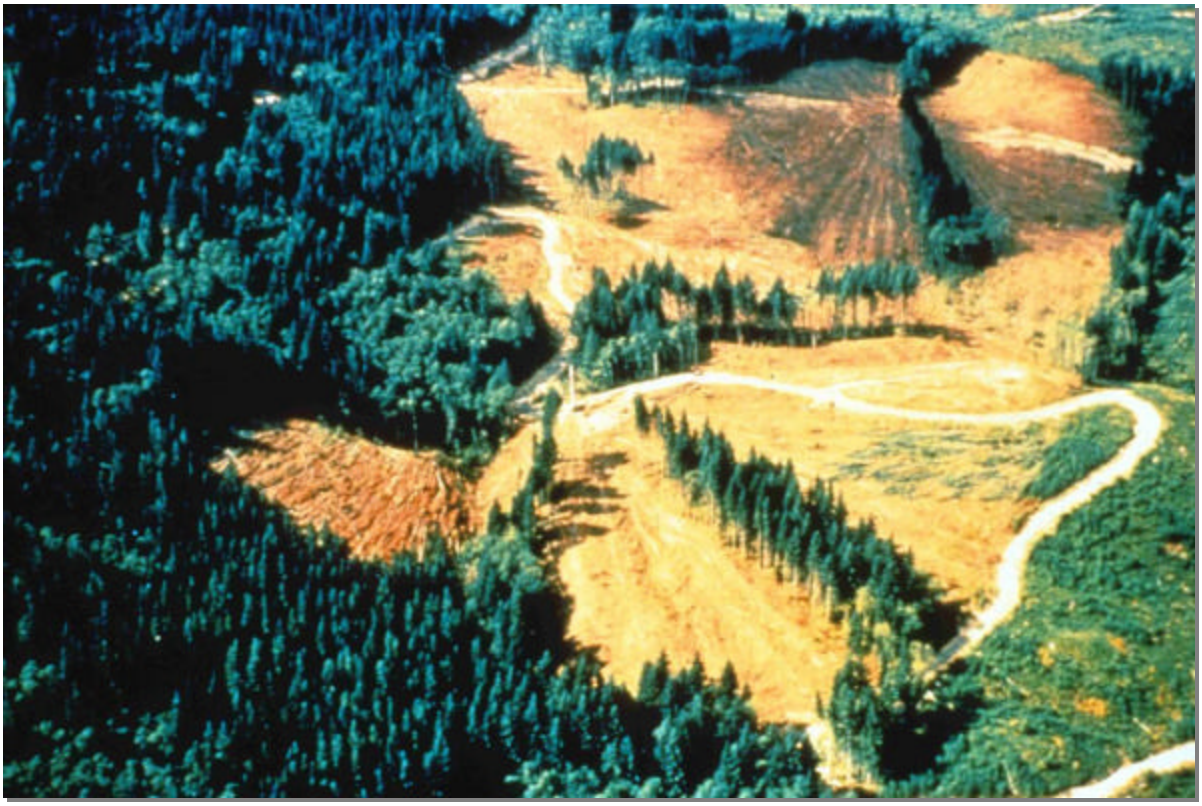

Figure 24. An early example of aggregated retention developed by Plum Creek Timber Company. This harvest unit (Cougar Ramp) contributed significantly to the evolution and adoption of the concept of aggregated retention.

Washington Department of Natural Resources. The Washington Department of Natural Resources has adopted variable retention harvesting practices in implementing its multi-species habitat conservation plan for its trust lands within the Pacific Coastal forest region.

Restoration of Structure and Biodiversity in Simplified Stands

Managing established forest stands for the development of structural and compositional diversity provides the basis for most of the forest restoration work currently planned and underway with the Pacific Coastal forests. The approach here is intermediate treatment of young stands ways modeled on processes in natural stand development (Franklin et al. 2002) so as to accelerate development of the structural and compositional complexity.

Forest restoration is a major issue within the region because of the desire to rapidly restore structural complexity and biodiversity to extensive areas of simplified young stands. Specific motivations and goals depend upon landowners. Examples of goals and landowners are:

- Restoring diversity to young stands in critical locations on federal lands, such as within Late Successional Reserves (LSRs);
- Restoring functional capabilities to simplified forests and landscapes on municipal watersheds, such as Seattle, Washington's Cedar River Watershed;
- Restoring and maintaining required levels of Dispersal and Nesting-Roosting-Foraging habitat for Northern Spotted Owls on trust lands administered by the Washington Department of Natural Resources; and
- Integrated management of forests for both ecological and economic goals.

Restoring Complex Forests on Federal Lands. Restoring structural complexity in simplified forests and riparian zones on federal forest lands is the largest single arena for restoration forestry in Pacific Coastal forests. The primary strategy adopted in the Northwest Forest Plan for sustaining old-growth forest ecosystems and related organisms was the creation of a system of large forest reserves (LSRs) (Forest Ecosystem Management Assessment Team 1993; Tuchmann et al. 1996). The LSRs are designed around the remaining concentrations of well-developed old-growth forests. However, due to the active history of dispersed timber harvest between 1950 and 1990, few large, un-fragmented concentrations of old-growth forest remain. Hence, the LSRs include significant areas of young forest, generally 10 to 50 years of age.

One goal of the NWFP is eventual restoration of contiguous late-successional forest cover in the LSRs, i.e., recovery of forest conditions to approximate their pre-harvest state. Presumably this will be accomplished through natural stand development processes but that could involve a considerable amount of time. Furthermore, some managers and scientists have even questioned whether the densely stocked plantations are even capable of evolving into classical old-growth forests, even over long time periods.

Consequently, a major program has been initiated to speed restoration of structural and compositional complexity to young managed stands within LSRs. A variety of silvicultural treatments can be applied in young stands to assist in restoration including creation of snags, logs, and other woody debris, stimulating development of decadence, accelerating development of large diameter trees, and re-introduction of missing plant and animal species.

Probably the most important single activity is *variable density thinning* in stands. Sometimes described as the "skips and gaps" approach to thinning, variable density thinning can be used to create a variety of desired effects. One important effect is to contribute to the development of spatial heterogeneity within the stand. The thinnings traditionally carried out to accelerate timber production generally involves removing suppressed smaller trees or "thinning from below". This approach accelerates development of dominant trees but also tends to create spatial homogeneity within the stand. Also, suppressed trees and non-commercial plant species

are typically eliminated. Variable density thinnings can certainly be designed to accelerate development of large diameter trees. However, varying thinning intensities spatially provides opportunities to maintain a greater diversity of biota and ecosystem processes. For example, "gaps" where dominant trees are removed can be used to maintain and enhance growth of desirable subdominant shade-tolerant conifers and hardwood species and to maintain islands of ground layer vegetation. Similarly, "skips" maintain habitat for species and processes dependent on heavy shade.

The analogy between variable density thinning and the gap-based mortality processes that are a part of natural stand development in Pacific Coastal forests should be obvious to the reader. The value of stimulating development of some spatial heterogeneity in uniformly dense plantations should also be apparent.

Restoration thinning is a relatively new approach so there are significant areas of disagreement and questions about its effectiveness in restoring late-successional structure and organisms. One area of controversy is the appropriate intensity of thinning in stands of various ages and conditions. Some managers favor a very heavy thinning in the belief that this will best replicate the wide spacing that was believed to have existed early in stand development of existing old-growth stands. Others feel that extensive heavy thinning may simply result in two-tiered stands with a low density tree overstory and a dense uniform understory of either shrub species or western hemlock; neither condition being desirable from the standpoint of structural diversification and biodiversity. Modeling and empirical data to quantify the effectiveness of restoration treatments in accelerating development of late-successional attributes are particularly needed.

Despite differences and unknowns, there is a clear consensus among scientists and managers regarding the benefits of restoration forestry in accelerating development of late-successional attributes. Extensive research programs are underway to develop relevant information as illustrated by empirical studies of biodiversity responses in young stands (e.g., Muir, et al. 2002; and work by Carey and his associates, cited below) and by modeling studies (e.g., Garman et al. in press).

Still, knowledge of restorative forest practices and their effects is currently quite limited. Hence, widespread adoption of one or a few simple prescriptions is risky; managers need to utilize a variety of silvicultural prescriptions on both a local and a regional scale until managerial experience and knowledge from monitoring and scientific studies accumulate. To exemplify some of the complexities, one might assume that restorative stand treatments would have comparable effects on all old-growth organisms. However, an analysis of approaches to young stand management in the coast redwood region concluded that silvicultural treatments that might benefit Northern Spotted Owl and its prey could be deleterious to Marbled Murrelet.

Restoring Complex Forest Stands on Trust Lands. Washington Department of Natural Resources (WADNR) has adopted, with US Fish and Wildlife Service approval, a habitat conservation plan (HCP) for management of trust lands in the western half of the state. As a part of that plan, WADNR is required to create and maintain specified levels of Dispersal and Nesting-Roosting-Foraging habitat for the Northern Spotted Owl. Dispersal and NRF habitat are defined in the HCP but, suffice it to say here, such forest stands are required to have significantly higher levels of structural complexity than is achieved in stands managed primarily for timber production on relatively short rotations.

WADNR needs to actively manage young stands to develop the stipulated levels of structural complexity. Initially on some sites, the goals for Dispersal and NRF habitat can be achieved by maintaining existing older stands; however, these stands cannot be harvested until replacement stands are available. In other locales, sufficient suitable Dispersal and NRF habitat currently is not present requiring that it be developed as rapidly as possible.

The approaches that are being used by WADNR to create Dispersal and NRF habitat for Northern Spotted Owl are those described earlier in this section, particularly variable density thinning and active efforts to create snags, woody debris and other decadence.

Restoring Late-Successional Forest Stands in the Cedar River Watershed. The Cedar River Watershed is owned and managed by the City of Seattle. Much of this watershed was logged during the last century so that extensive areas of forests 10 to 80 years of age are present; old-growth remains in the more remote and inaccessible portions of the watershed.

Recently, the City of Seattle has acquired ownership of all of the land within the watershed and adopted a habitat conservation plan that calls for restoration of late-successional forest conditions throughout the drainage. Consequently, one major activity will be treatment of young stands to accelerate development of structurally complex and biologically diverse stands.

Treatment of young stands is just beginning and follows the basic principles described above. Variable density thinning of very young stands began in 2002. The first thinning in older stands of commercial size will be conducted this year; some wood from thinned trees will be removed but much of it will remain behind to enrich the coarse woody debris on the forest floor.

Biodiversity Pathways. The discussion of management of stands to restore and maintain biological diversity has been in the context of habitat restoration rather than long-term management of stands for both economic and ecological purposes. Carey and his associates (Carey et al. 1996; Carey 1998; Carey et al. 1999) have developed an entire silvicultural system, which is designed to provide for both high levels of biological diversity and ecosystem function. This silvicultural system, which they call "Biodiversity Pathways", includes all three of the elements from natural forests mentioned earlier:

- Structural retention at time of regeneration harvest;
- Manipulation of established stands to stimulate development of structural complexity as well as wood production; and
- Longer rotations.

Biodiversity pathways are included because much of the emphasis is on intermediate stand-level treatments of established stands throughout their life and is designed to integrate both economic and ecological goals. In contrast, the restoration forestry we have previously described is largely designed to simply to develop late-successional structure, function and composition with no intent of incorporating economic goals.

Biodiversity Pathways was explicitly developed to provide WADNR with a management strategy that was an alternative to traditional timber emphasis forest practices for trust lands. Stand simulations produced promising results in terms of integrating ecological goals with positive monetary outcomes. In one analysis (Carey, Lippke and Sessions 1999) the biodiversity management strategy generated "fully functional" forest conditions using variable density thinning, alternating rotations of 70 and 130 years, and structural retention at harvest. This approach also produced 82% of the net present value generated under a traditional timber management regimen.

Summary and Conclusions—Status of Restoration Forestry on the Pacific Coast

Major changes in silvicultural practices have occurred in the Pacific Coastal forests designed to restore and maintain native biodiversity and ecosystem processes. They primarily involve

- Regeneration harvest practices that are modeled on natural disturbance regimes, particularly biological legacies; and
- Management of young stands to restore and maintain structural complexity and compositional diversity, by simulating natural stand development processes.

Variable retention harvesting has replaced clearcutting as the harvest method utilized on federal lands, many trust lands, and lands owned by two major timber corporations. Retention harvest prescriptions vary substantially in application depending upon management objectives and stand and landscape conditions. This silvicultural technique is know to be effective at retaining many elements of biological diversity through studies of natural disturbances, retrospective studies of past partial cuttings, and current research, including statistically designed experiments.

Management programs that restore structural complexity and biological diversity are currently widespread and include all ownerships. Activity is greatest on federal lands in connection with restoration of habitat within Late Successional Reserves and riparian zones. Proposals currently under consideration could result in tens of thousands of hectares being treated annually over the next several decades. Such silvicultural treatments should significantly accelerate development of late-successional attributes in these forests based upon our current understanding of forest development and its relation to biodiversity, experimental studies currently underway, and modeling studies.

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Supplemental Study: Southeastern Region

Ground cover recovery patterns and life history traits: implications for restoration bottlenecks and opportunities in pine savannas

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Report Summary

1. For a species-rich pine savanna, we identified species that were vulnerable to disturbance, which could be used as indicators of recovery by comparing the ground cover flora of a 64-yr old planted slash pine (*Pinus elliottii* Engelm.) stand to a nearby high-quality natural longleaf pine (*Pinus palustris* Mill.) forest. We also determined if life history traits are useful predictors of recolonization potential.
2. The floristic overlap in species among the benchmark and restoration sites and similar species richness at intermediate scales suggests that substantial vegetation recovery occurred over the 65 year period.
3. However, for areas < $10m^2$, the notably decreased species packing in the post-disturbance forest indicates that coexistence of a high number of species at small scales requires a much longer period to obtain.
4. The absence, or near absence, of some species from the disturbed site even after 65 years, suggests that a group of species may be particularly vulnerable to disturbance and may become re-established infrequently, if ever.
5. Our results identify several dispersal-restricted species across a range of guild types and taxonomic families that are important candidates for active reintroduction. While a particular guild of species did not emerge as an exceptionally valid indicator group in this study, our results identify a suite of species from several guilds that could furnish a metric for assessing the absence of prior soil disturbance or the degree of recovery that a restored system has attained.

Introduction

The life histories of established, as well as colonizing species influence the rate of succession following disturbance of plant communities, especially in understory and ground cover strata (Brewer 1980, Gross 1987, Kindscher 1994, McLachlan & Bazely 2001). Mechanisms of seed dispersal, flowering phenology, growth form, and persistent soil seed banking have been shown to influence post-disturbance changes in species richness in some forest and prairie communities (Tilman 1997, Eriksson & Jakobsson 1998, McLachlan & Bazely 2001). Thus, identification of life history traits restricting the persistence or species recruitment following soil disturbance is a primary step to developing appropriate restoration strategies, including propagule reintroduction for certain species (Pywell et al. 2003). Furthermore, the presence of species that are vulnerable to disturbance, or guilds of such species, can be used as indicators of recovery that reflect a trajectory of restored sites moving toward the composition of less disrupted, high quality reference sites (Kindscher 1994, Masters 1997, Lindenmayer 1999).

This approach may be especially appropriate for species-rich ecosystems such as pine savannas, where the native ground cover is the primary source of the diverse flora and provides a critical functional role, such as the fine fuel necessary to carry fire. In particular, the longleaf pine-wiregrass ecosystem of the southeastern US provides a distinctive challenge of ecological restoration in the recovery of floral communities with the relatively high level of species richness that typify this critically endangered ecosystem. The flora of fire-maintained longleaf pine communities is characterized by a sparse tree canopy of *Pinus palustris*, a dominance of perennial grasses and forbs, and an exceptionally large number of species (Bridges & Orzell 1989, Peet & Allard 1993). Species richness can be high, even at small scales (40-50 species m^{-2}) (Walker & Peet 1988, Kirkman et al. 2001). Thus, the long-term sustainability of this floristically diverse ecosystem with prescribed fire is dependent on the re-establishment of ground cover structure and composition.

Many plant species in the longleaf pine-wiregrass ecosystem are considered to be long-lived perennials, but evidence regarding persistent soil seed banking is lacking. Although little is known of the levels of seedling recruitment in this ecosystem, it is likely that the processes of species establishment operate over the temporal scale of decades to centuries, similar to that suggested for other grasslands systems (Franzen & Eriksson 2001, Morgan 2001). For the characteristically fragmented landscapes of the Southeast today, seed dispersal may especially influence patterns of species abundance and distribution in longleaf pine forests at both local and landscape scales (Kiviniemi & Eriksson 1999). Consequently, quantification of the number of species that assemble in an area with time since disturbance, or species packing (Kinzig et al. 1999), can direct attention toward identifying factors influencing the development and persistence of diversity in this plant community, while revealing plausible timelines for recovery.

Our objective is to determine if life history traits are useful predictors of recolonization potential by comparing the ground cover flora of a 64-yr old planted slash pine (*Pinus elliottii* Engelm.) stand to a nearby benchmark natural longleaf pine (*P. palustris* Mill.) forest. In this study, we address the following questions relative to the resilience of the restoration site: 1) How do species-area relationships vary between sites with different disturbance histories, i.e., restoration and benchmark sites? 2) Are dispersal-limited traits, or specific growth form, or flowering phenologies associated with species' vulnerabilities to disturbance? and 3) Within a growth form guild, which species are conservative indicators of high-quality longleaf pine-wiregrass systems?

Methods

Study site

The restoration and benchmark study sites are located on Ichauway, an 11,600 ha privately owned reserve of the J.W. Jones Ecological Research Center, in the Coastal Plain of southwestern Georgia (Baker County). The restoration site, an 88 ha slash pine plantation established in 1939, is in the initial stages of conversion to a diverse longleaf pine forest. The earliest available aerial photography (1938, black and white, USDA 371-21) indicates this site was in cultivation prior to tree planting. This evidence is substantiated by the absence of *Aristida beyrichiana* Trin. and Rupr. (wiregrass), a perennial grass that is recognized to decline with fire exclusion and excessive soil disturbance (Myers 1990). With the exception of periodic canopy thinning, the vegetation represents a 65 year successional stage since tree planting in an agricultural field. Based on aerial photographic interpretations, this stand of timber has been thinned twice since planting, once between 1953-1957 (1953, black and white, USDA 2M-108; 1957 black and white, USDA 5T-18), and again, between 1962-1968 (1962 black and white, IDD-122, ASCS 3-63 DC; 1968 black and white IKK-147, ASCS 1-69 DC). At the time of this study, the stand has a widely spaced canopy with an average basal area of 16 m^2/ha and tree density of 123 stems/ha. The pine plantation has been prescription burned irregularly at an approximate 5-8 year frequency (L. Neel, personal communication) and as a result, the stand has a mid-story composed of hardwood species such as *Quercus nigra* L., *Q. virginiana* Mill., *Sassafras albidum* (Nutt.) Nees., and *Diospyros virginiana* L. Ground cover includes numerous grass and forb species. Benchmark sites of frequently burned (1-3 years) longleaf pine-wiregrass vegetation were selected from a group of sites identified by a site classification of Ichauway based on landscape position, soil type, and vegetation (Goebel et al. 2001). The vegetation of the benchmark sites has been managed with frequent prescribed fire (return interval of 2-4 yr) for over seven decades to promote bobwhite quail habitat, and presumably, was burned frequently with human or lightning ignited fires for a long period prior to European settlement. The sites are characterized by the widely spaced single dominant overstory species, *Pinus palustris* Mill. A mid-story is generally absent, with the exception of patches of young longleaf pines. Dense ground cover at these sites is dominated by the perennial grass, *Aristida beyrichiana* Trin. & Rupr., with numerous species of other perennial grasses and forbs also present as interstitial species (Goebel et al. 2001).

Study design

This study was designed as a component of a long-term restoration project with the goal of converting the slash pine plantation to a multi-aged longleaf pine forest with a diverse ground cover, sustainable with prescribed fire. Prior to restoration canopy thinning in 1999 and planting of longleaf pine seedlings, we randomly located 60 plots (20 m x 20 m). Similar plots for vegetation sampling were established at 12 benchmark locations.

Vegetation was sampled in each 20 m x 20 m plot using a nested sampling design (adapted from Peet et al. 1998) to obtain species area curves and vegetation abundance measures. Each plot consisted of four 10 m x 10 m modules. Within each module, vegetation was sampled in nested units of area 0.1 m^2, 1 m^2, 10 m^2 and 100 m^2. This nested approach was repeated twice within each module, with the sample initiation point located in two different corners (8 corners sampled per plot). Species present in each module were recorded. Vegetation of the restoration

plots was sampled in summer 1998 following a dormant season burn that year. Vegetation of 3 benchmark plots was sampled in summer 1993 and the remainder was sampled in summer 1998.

Species nomenclature was based on Wunderlin (1998) with the exception of *Chamaecrista deeringiana* Small & Pennell, which is recognized at the specific level by Isley (1990). A few species were combined for analyses due to difficulties in consistently identifying vegetative individuals (Appendix I). To characterize species life history traits, we assigned a guild designation and dispersal distance category to each species. The suite of guild classes we used was modified from a classification developed for tallgrass prairie (Kindscher 1994). We considered this classification a reasonable approximation of the longleaf pine ecosystem guilds based on similarities of the structure and composition between the communities (Kirkman et al. 2001). These guilds included C_3 photosynthetic pathway grasses, C_4 photosynthetic pathway grasses, spring/summer perennial forbs, fall perennial forbs, legumes, woody species, ferns, and annuals. Guild designation was determined from floristic manuals and lists of C_3 and C_4 species (Downton 1975, Raghavendra & Das 1978, Hakansson 1995). Dispersal distances have been demonstrated to vary according to dispersal agents; seeds with structures that facilitate wind or vertebrate dispersion have the greatest dispersal distances, whereas, explosively-dispersed, gravity-dispersed, or ant-dispersed seed have the shortest dispersal distances (Stamp and Lucas 1990, Willson 1993). First, we determined the dispersal agent based on the following assumptions: plants with fleshy fruit are vertebrate consumed, seeds with protrusions for adherence are carried externally by vertebrates, seeds with adaptations (such as plumose pappus bristles) permitting seeds to be airborne are wind dispersed, seeds with elaiosomes are ant dispersed, ballistically-dehiscing fruits are explosive, and all others are considered to be gravity-dispersed. Because seeds of several species with ballistically-dehiscing fruits are also ant dispersed, we combined this category prior to data analyses. The dispersal agents were then classed as either restricted in distance (gravity and ant [including explosive]), or unrestricted (wind, vertebrate carried, and vertebrate consumed) following McLachlan & Bazely (2001).

Analysis

Species richness was determined as the number of species occurring in each of the nested levels within each module and summed cumulatively for the total vegetation sampling plot. Values for the nested units of area < 100 m^2 were obtained as a mean of values from the two corners of each module. Values for area units = 100 m^2 were obtained by cumulative addition of species in each module. This process was computed iteratively for each possible starting module and then averaged to obtain the mean species richness for each area within a plot. Differences in mean species richness of benchmark plots with that of pre-treatment restoration plots were examined using a one-way analysis of variance for each unit of area.

We used multi-dimensional scaling (MDS) to present differences between benchmark and restoration sites with respect to overall species composition. For these analyses, we used the Jacaard Index as a measure of plot distance for presence/absence of species and the Cityblock distance measure for plots based on frequency of each species (SAS PROC MDS LEVEL=INTERVAL, SAS version 9.0). For both variables, we used a 3-dimensional MDS minimum spanning tree to position plots such that ranking of Euclidean distance between points is maximally correlated with the ranking of the distance measure of species composition. This enables us to present the three- dimensional information within the two-dimensional plot. We computed the correlation between presence-absence of species, or frequency, with 2 dimensions

(axes) from the MDS solution. We represented these correlations as vectors in a graph to show dominant species associated with each dimension.

To examine the relationship of vulnerability to disturbance and dispersal mechanism, we first calculated species frequency of occurrence for both site conditions as the proportion of 1 m^2 nested subplots in which a species occurred for the benchmark plots (n=96) and restoration plots (n=480). Those species that had a higher occurrence in the benchmark site than that of the restoration site were considered vulnerable to disturbance. Those equal to or having greater occurrence in the restoration site were considered resilient to disturbance. To determine if vulnerability or resilience to disturbance was related to dispersal mechanism, we used a likelihood ratio chi square test for the 2 x 2 contingency table (dispersal mechanisms versus vulnerability-resilience classes) using SAS (PROC FREQ, SAS version 9.0). To control for the fact that the species are correlated (sampled together on the same plots), we used a Monte Carlo randomization procedure to calculate the p-value associated with the test statistic. To simulate the null hypothesis of no vulnerability-resilience effect, plots were randomly permuted among benchmark and restoration sites, and then vulnerability-resilience was recomputed for each species using the new site assignments. This randomization process was performed 9999 times for each specific dispersal category (5 dispersal agents) plus the dispersal-restricted category (ant and gravity, combined). The test statistic was computed for the original data plus the 9999 randomized data sets. The original test statistic was then ranked among the 10,000 total values (9999 + original) to obtain the p-value of the test statistic (Good 1994). If the site on which a plot was sampled has nothing to do with the dispersal characteristic, then the test statistic would be similar to those for which the site labels are simply randomized. If dispersal differs, then the test statistic should be an extreme value when ranked with the randomized data. Statistical significance was determined at $p= 0.05$. We examined the relationship between life form guild categories and vulnerability-resilience to disturbance with the same Monte Carlo test procedure.

To depict relative vulnerability to disturbance among species, we calculated a vulnerability score for each species similar to that developed by McLachlan & Bazely (2001). We defined vulnerability score as the proportional frequency of occurrence in benchmark sites divided by the proportional frequency of occurrence in restoration sites; the higher the ranking of this score for a species, the more vulnerable to disturbance.

Results

Differences in mean species richness between restored and benchmark ground cover vegetation were scale-dependent (Fig. 1). For larger sample areas (= 10 m^2), no differences in the number of species occurred between restoration sites and benchmark sites ($p>0.05$). However, the mean number of species on restoration sites was strongly reduced for sample areas <10 m^2 relative to that of benchmark sites ($p< 0.0001$). A total of 218 species were sampled, of which 185 occurred in restoration sites and 134 in benchmark sites.

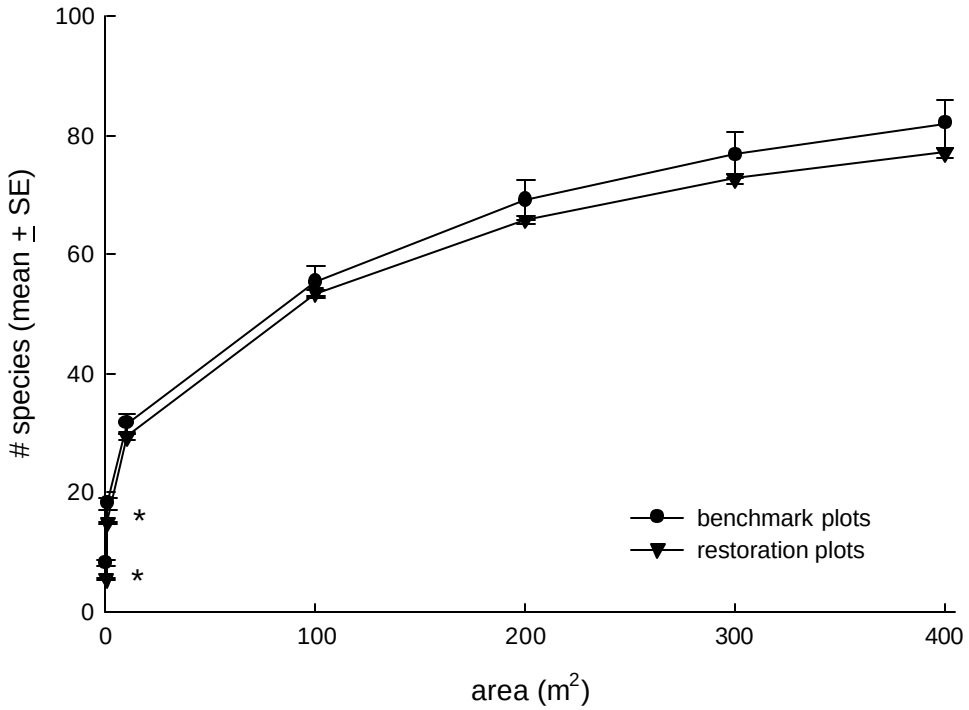
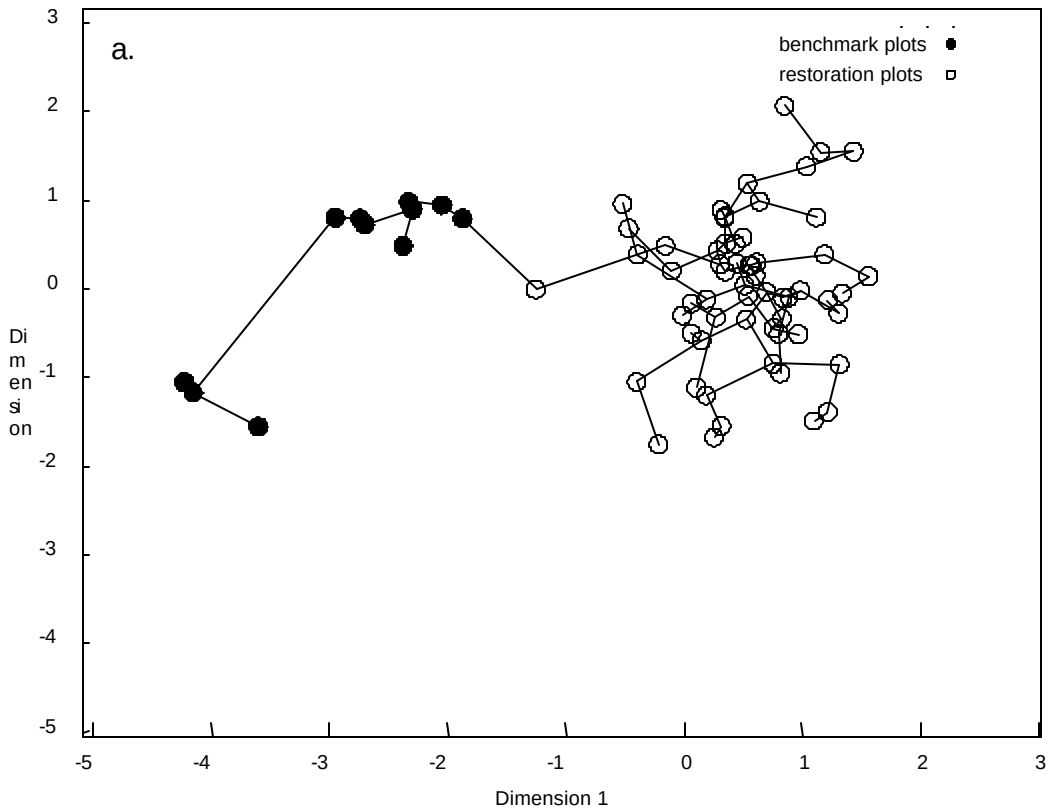


Fig. 1. Species richness patterns and sampling area. Data points with * indicate differences in species richness ($p<0.0001$), otherwise no difference in mean values compared ($p>0.05$).

Species composition was also strongly affected by disturbance history, both for presence/absence of species and species abundance patterns (frequency). MDS analysis represented the plots well in three-dimensional space (MDS Badness of Fit=0.05). Plots from restoration and benchmark sites are well separated from each other in MDS ordination space, indicating greater dissimilarity in composition between the site types than among plots within either restoration or benchmark sites (Fig. 2).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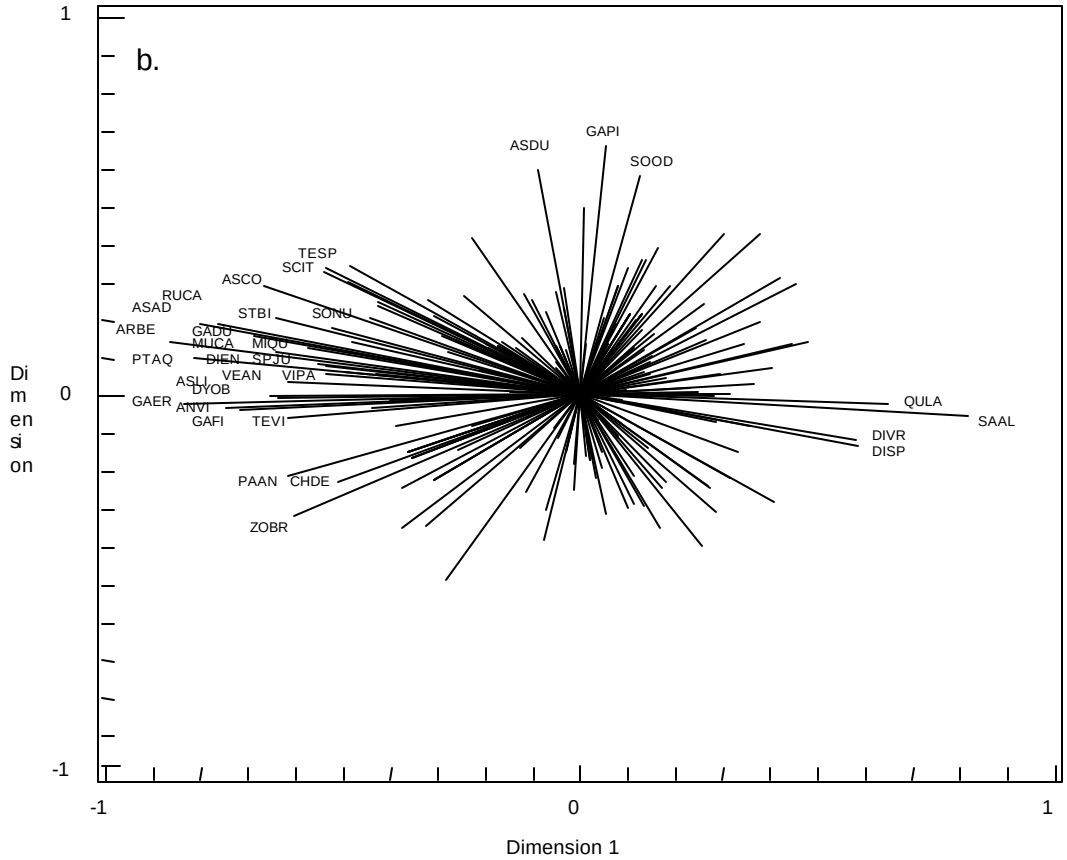
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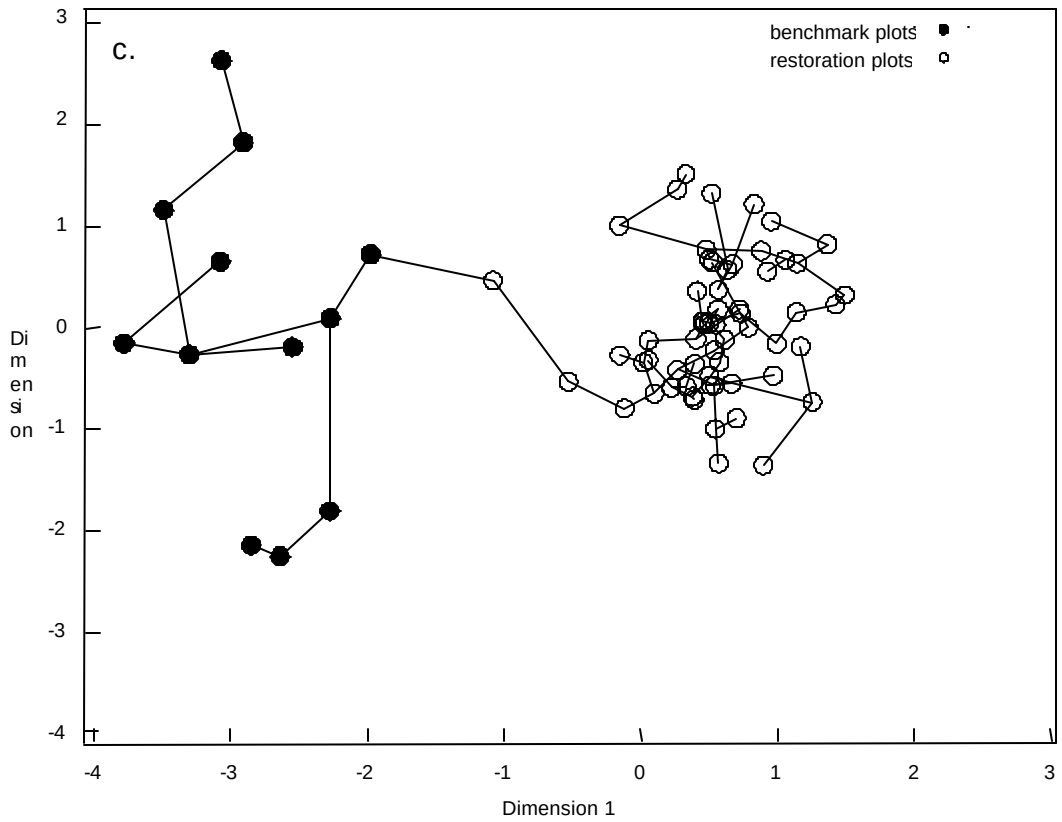
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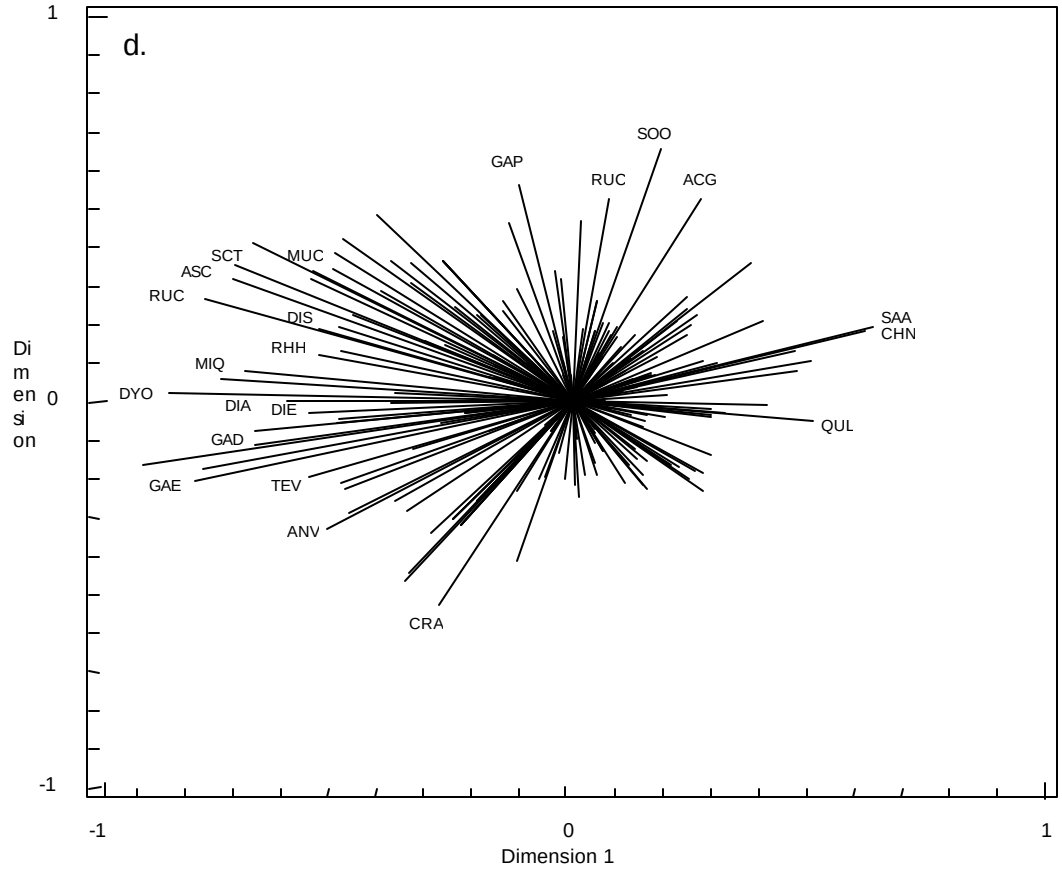
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Figure 2. Minimum spanning tree using MDS analysis for bench mark and restoration sites. (a). Euclidean distances based on species presence absence. (b). Vectors indicating correlation between presence-absence of each species with axes from MDS solution for. Species labeled are highly correlated with axes 1 or 2 (r>0.5). (c). Euclidean distances based on frequency of occurrence of species. (d). Vectors indicating correlation between frequency of a species with axes from MDS solution. Species labeled are highly correlated with axes 1 or 2 (r>0.5). Species codes: ACGR – *Acalypha gracilens*, ANVI - *Anthaenantia villosa*, ARBE – *Aristida beyrichiana*, ASAD – *Aster adnatus*, ASCO – *Aster concolor*, ASDU – *Aster dumosus*, ASLI – *Aster linariifolius*, CHDE – *Cassia deeringiana*, CHNI – *Chamaecrista nictitans*, CRAR – *Croton argyranthemus*, DIAC – *Dichanthelium aciculare*, DIEN – *Dichanthelium ensifolium* var. *unciphyllum*, DISP – *Dichanthelium sphaerocarpon*, DIVR – *Diospyros virginiana*, DYOB – *Dyschoriste oblongifolia*, GADU – *Gaylussacia dumosa*, GAER – *Galactia erecta*, GAFI – *Gaura filipes*, GAPI – *Galium pilosum*, MIQU – *Mimosa quadrivalvis*, MUCA – *Muhlenbergia capillaris*, PTAQ – *Pteridium aquilinum*, QULA – *Quercus laurifolia*, RHHA – *Rhynchospora harveyi*, RUCA – *Ruellia caroliniensis*, RUCU – *Rubus cuneifolius*, SAAL – *Sassafras albidum*, SCIT – *Scutellaria integrifolia*, SCTE – *Schizachyrium tenerum*, SONU – *Sorghastrum nutans*, SOOD – *Solidago odora*, SPJU – *Sporobolus junceus*, STBI – *Stylosanthes biflora*, TESP – *Tephrosia spicata*, TEVI – *Tephrosia virginiana*, VEAN – *Vernonia angustifolia*, VIPA – *Viola palmata*, ZOBR – *Zornia bracteata*

Of the total species sampled, 88 were classified as vulnerable to disturbance and 130 were classed as resilient based on proportional frequencies in benchmark versus restoration sites (Fig. 3). Nearly half of the total species (46 %) were characterized by gravity dispersal. Of the group of gravity-dispersed species, approximately equal numbers of species occurred more frequently in either benchmark or restoration sites (Fig. 4). Less than 20 % of the species were represented by each of the other dispersal agents (wind=17 %, animal consumed =17 %, animal carried =11 %, ant=8 %). Of the species that were unique to benchmark sites, 86% were in the restricted distance dispersal group (Fig. 4, Table 1). In contrast, 60% of the species more common to, or restricted to restoration sites, were in the non-restricted distance dispersal group (wind, vertebrate-carried or vertebrate consumed) (Fig. 4).

Both the vulnerability and the resilience class of species were significantly associated with some specific dispersal agents. A positive association was found with species vulnerable to disturbance and restricted distance dispersal agents (ant and gravity dispersed combined, ? ^{2}=18.05, p<0.01) and individually for both dispersal mechanisms (ant dispersed, ? ^{2}=5.53, p<0.05; gravity dispersed, ? ^{2}=8.7, p<0.05). In contrast, resilient species were significantly associated with animal consumed seed dispersal and animal carried seed dispersal (? ^{2}= 9.25, p<0.05; ? ^{2}=10.9, p<0.01). The proportion of wind dispersed species was not related to the vulnerability-resilience class of the species (? ^{2} =0.01, p>0.05).

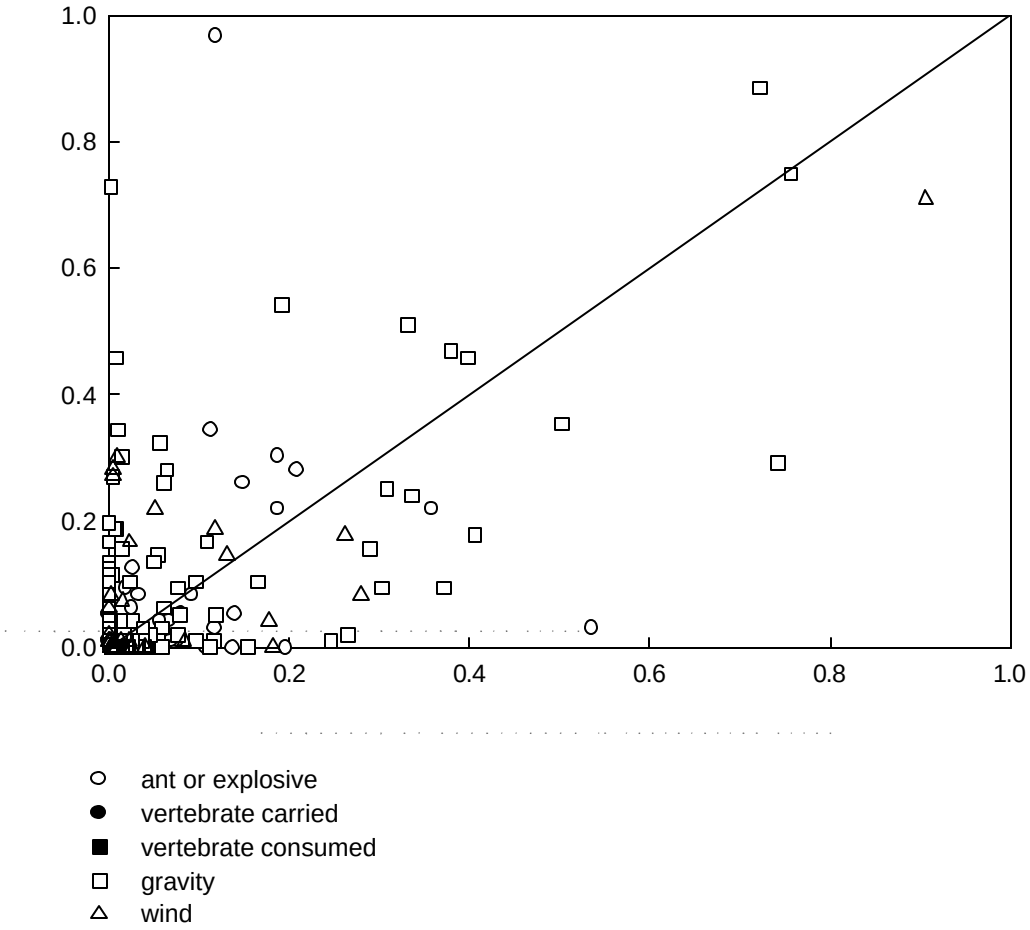

Figure 3. Frequency of occurrence of species in benchmark and disturbed sites. The diagonal line marks the null hypothesis that a species proportional frequency=1. Species above the line are more frequently associated with benchmark sites (= vulnerable to disturbance); species below the line are more frequently associated with restoration sites (= resilient to disturbance).

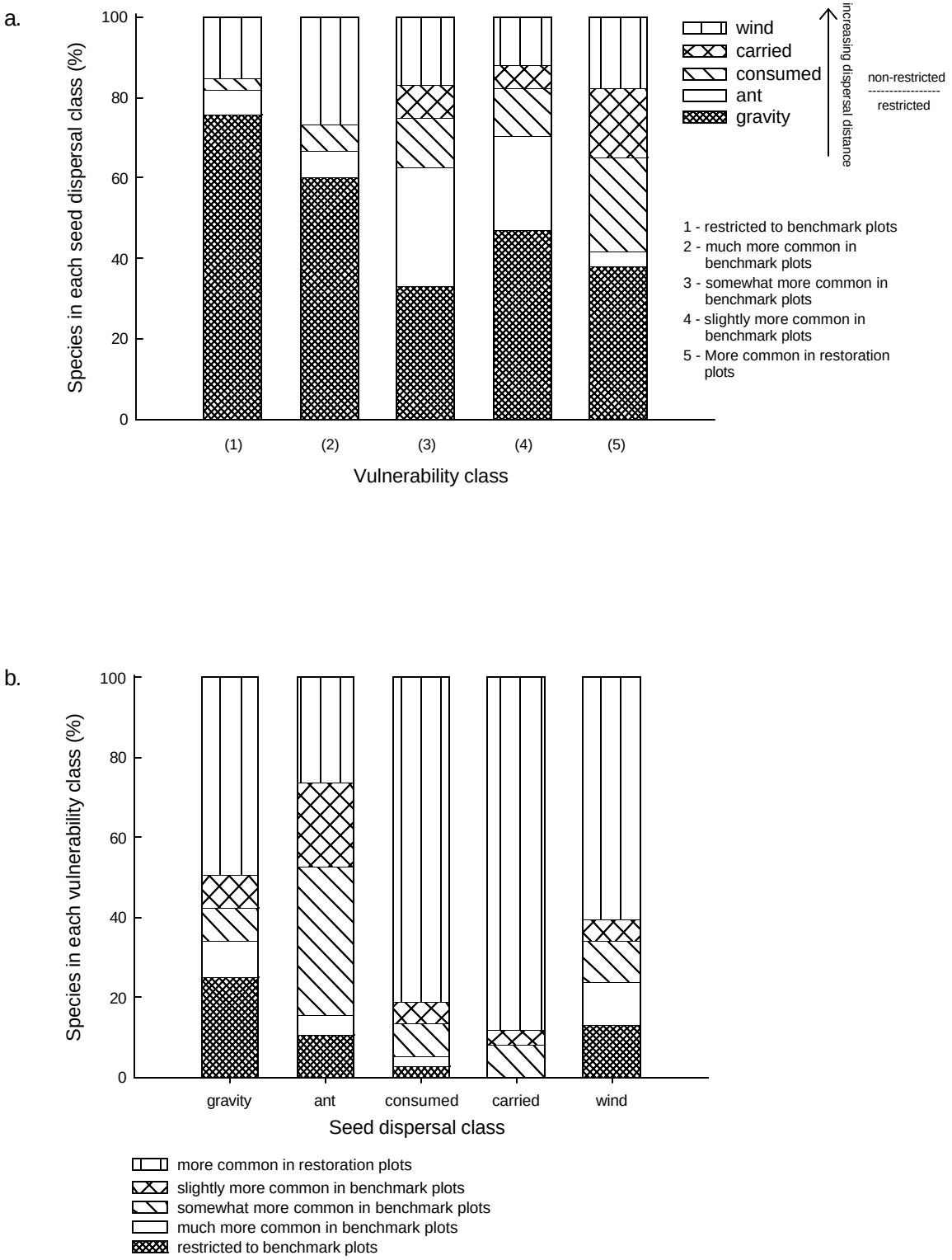

Figure 4. Vulnerability-resilience class and distance restricted and non-distance restricted seed dispersal mechanisms. Vulnerability classes are defined in Table 1 by vulnerability ratios. (a). Percentage of total

species in each dispersal type by classes of vulnerability. (b). Percentage of total species in each vulnerability class by dispersal type.

The resilient class of species was significantly associated with only one life form guild, woody species (? ^{2}=11.43, p<0.05). The proportions of other life form guilds were not related to the vulnerability-resilience class of the species (? ^{2} <5, p>0.05). The assemblage of most highly vulnerable species (unique to benchmark sites) included all life form types except annuals, and was equally represented by species with summer and fall phenologies (Table 1).

Discussion

Our findings regarding the presence, absence, and abundances of various plant species answer several questions about post-disturbance processes and resilience in this forest type. Importantly, the floristic overlap in species among the benchmark and restoration sites and similar species richness at intermediate scales suggest that substantial recovery in the vegetation occurred over the 65 year period. However, for areas < 10m^2, the notably decreased species packing in the post-disturbance forest, indicates that coexistence of a high number of species at small scales requires a much longer period to obtain. The absence, or near absence, of some species from the disturbed site even after 65 years, suggests that a group of species may be particularly vulnerable to disturbance and may become re-established infrequently, if ever. Our finding of a positive association between vulnerability and ant and gravity dispersal is consistent with other patterns of recovery and dispersal limitations (McLachlan & Bazely 2001). Our results identify several dispersal-restricted species across a range of guild types and taxonomic families that are important candidates for active reintroduction in longleaf pine ecosystem restoration sites.

We produced a list of species most vulnerable to disturbance that can provide a tool for assessing high quality ground cover conditions that are associated with minimally disturbed ecosystems. While a particular guild of species did not emerge as an exceptionally valid indicator group in this study, our results suggest a suite of species from several guilds that could furnish a metric for assessing the absence of prior soil disturbance or the degree of recovery to which a restored system has attained. Such a technique, known as floristic quality assessment (FQA), has been applied in prairie habitats (Swink & Wilhelm 1994, Masters 1997) and could be a useful model for site assessments in longleaf pine as more data emerges to corroborate the conservatism of individual species across multiple sites. Our findings were markedly consistent with other studies of benchmark/non-benchmark observations in longleaf pine stands. Hedman, Grace & King (2000) identified eight indicator species of benchmark longleaf pine sites in southwestern Georgia using similar ordination procedures. Of these species, six were among our list of vulnerable species including *Dyschoriste oblongifolia* (Michx.) Kuntze, *Aristida beyrichiana*, *Pteridium aquilinum* (L.) Kuhn, *Aster adnatus* Nutt., *Ruellia caroliniensis* (Walt ex. Gmel.) Steud., and *Tephrosia virginiana* (L.) Pers. Because we did not distinguish *Schizachyrium scoparium* (Michx.) Nash separately from *Andropogon virginicus* L. in our study, we are unable to compare their result with our data for this species. However, in our study, *Solidago odora* Ait. was actually found more frequently in the restoration sites than in the benchmark sites. Smith (2000) also found greater abundance of these six species in natural versus planted longleaf stands in South Carolina. Our results also concurred with that of Smith (2000) for several other species with greater affinities for natural longleaf pine stands, such as *Dicanthelium ensifolium* var. *unciphyllum* (Trin.) B. F. Hansen & Wunderlin (=*D. tenue* in Small

[2000]), *Viola palmata* L. (=*V. septemloba*), *Strophyostyles umbellata* (Muhl. ex Willd.) Britt. , *Gaylussacia dumosa* (Andrz.) T. & G., *Mimosa quadivalvis* (Torrey & Gray) Barneby (=*Schrankia microphylla*), and *Dicanthelium aciculare* (Desv. Ex Poir.) Gould & C. A. Clark.

Several ant-dispersed species were found to be extremely vulnerable to disturbance, particularly *Viola palmata*, *Dyschoriste obtusifolia*, *Croton argyranthemus* Michx., and *Ruellia carolinensis* (Walt. Ex Gmel.) Steud. The role of native ant dispersal in this system, as well as the increasing impact of the imported fire ant (*Solenopsis invicta*) (Carroll & Hoffman 1997) on the recruitment process needs further investigation.

The species-area relationships we observed, coupled with the fact that gravity and ant dispersed species were considerably less represented in the post-disturbance sites, are consistent with current knowledge of processes that govern species richness and composition in this fire-maintained ecosystem. The coexistence of many species in the longleaf pine-wiregrass system is partially due to the frequent removal of woody vegetation with fire, the perennial life histories of the ground cover flora, and the non-rhizomatous characteristic of the matrix species, wiregrass (Kirkman et al. 2001). In relatively undisturbed ground cover sites subjected to frequent fire, soil moisture appears to be an important factor regulating the number of species present across the xeric-mesic landscape. In contrast to that of many temperate grasslands (Abrams & Hulbert 1987, Gibson & Hulbert 1987, Franzen & Eriksson 2001), evidence of competitive exclusion as a factor regulating species richness in the ground cover of longleaf pine-wiregrass forests is lacking (Kirkman et al. 2001). Thus, water limitation may be implied as particularly stressful for seedling establishment. Once established, however, individuals of many perennials may persist for several to many years. Provided this is the case, long adult life spans decrease the probability of population decline over a series of low-recruitment periods (Warner & Chesson 1985).

Recruitment in this system is probably explained by a basic stochasticity in recruitment success, as suggested for other grassland ecosystems (van der Maarel & Sykes 1993, Franzen & Eriksson 2001), where an occasional favorable recruitment event can sustain population numbers over long periods (Warner & Chesson 1985). Accordingly, in the longleaf pine-wiregrass ecosystem, site moisture conditions suitable for establishment (as opposed to space limitations) and the available seed pools are feasible factors limiting recruitment (Zobel 1992, 1997, Franzen & Eriksson 2001). Seed pool composition, in turn, is likely controlled by dispersal distances, seed production rates, fragmentation of the surrounding landscape, and seed longevity in the soil (Gross 1987, Eriksson & Ehrlen 1992). The importance of recruitment in the restoration process will also depend on the soil disturbance history. For sites without agricultural soil disturbance, but degradation primarily due to fire suppression, the persistence of species as rootstocks or buried seed in unfavorably shaded conditions may play a more critical role in the recovery process following introduction of frequent fire regimes.

While this study addresses the importance of understanding life history traits in determining the diversity and abundance of species in plant communities, we recognize that such information cannot provide a simple prescription for restoring a damaged or destroyed community. In fact, it underscores the need for co-directed approaches to bridge the gaps in understanding natural and managed communities (Gross 1987, Sharitz et al. 1992). We have provided some explanation as to why these species behave as they do in community reassemblies – information that is potentially important in devising appropriate management or restoration plans for the longleaf pine-wiregrass community. However, other key factors in the recovery process, such as critical thresholds of soil disturbance intensity and persistence of seed banks,

rates of recovery relative to soil types, and interactions with hardwood encroachment due to fire suppression, remain to be examined.

Acknowledgments

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Table 1. Frequency of occurrence, relative vulnerability to disturbance and life history traits of species. Species presented had frequency > 0.02 in benchmark sites and a vulnerability ratio = 2.5.

Species by vulnerability ranking	Family	Common name	Occurrence of species (mean freq of nested plots)		Vulnerability ratio (Vratio)	Dispersal type	Guild
			Benchmark sites (Fb)	Restoration sites (Frs)	(Fb / Frs)		
Species restricted to reference sites							
Tephrosia virginiana	Fabaceae	Goat's rue	0.20	0	8	Gravity	Legume
Anthaenantia villosa	Poaceae	Silky scale	0.17	0	8	Gravity	C_4 grass
Gaura filipes	Onagraceae	Slenderstalk bee blossom	0.14	0	8	Gravity	Summer forb
Dichanthelium ensifolium var. unciphyllum	Poaceae	Witchgrass	0.13	0	8	Gravity	C_3 grass
Panicum anceps	Poaceae	Beaked panicum	0.11	0	8	Gravity	C_4 grass
Rhynchospora harveyi	Cyperaceae	Harvey's beaksedge	0.10	0	8	Gravity	C_3 grass
Dichanthelium strigosum	Poaceae	Roughhair witchgrass	0.08	0	8	Gravity	C_3 grass
Rudbeckia hirta	Asteraceae	Black-eyed susan	0.08	0	8	Gravity	Fall forb
Zornia bracteata	Fabaceae	Viperina	0.08	0	8	Gravity	Legume
Panicum virgatum	Poaceae	Switch grass	0.06	0	8	Gravity	C_4 grass
Pinus palustris	Pinaceae	Longleaf pine	0.06	0	8	Wind	Woody
Viola palmata	Violaceae	Blue violet	0.05	0	8	Ant/explosive	Summer forb
Helianthus radula	Asteraceae	Rayless sunflower	0.04	0	8	Gravity	Fall forb
Dichanthelium commutatum	Poaceae	Variable witchgrass	0.03	0	8	Gravity	C_3 grass
Strophostyles umbellata	Fabaceae	Sand beans	0.03	0	8	Gravity	Legume
Species much more common to reference sites							
Aristida beyrichiana	Poaceae	Three-awn wiregrass	0.73	<0.01	350.0	Gravity	C_4 grass
Aster adnatus	Asteraceae	Scale leaf aster	0.28	<0.01	67.5	Wind	Fall forb
Aster concolor	Asteraceae	Eastern silver aster	0.27	<0.01	65.0	Wind	Fall forb
Gaylussacia dumosa	Ericaceae	Dwarf huckleberry	0.27	<0.01	65.0	Consumed	Woody
Schizachyrium tenerum	Poaceae	Slender bluestem	0.46	<0.01	55.0	Gravity	C_4 grass
Aster linariifolius	Asteraceae	Stiff-leafed aster	0.08	<0.01	40.0	Wind	Fall forb
Pteridium aquilinum	Pteridaceae	Bracken fern	0.30	<0.01	36.3	Wind	Fern
Galactia erecta	Fabaceae	Erect milkpea	0.34	0.01	33.0	Gravity	Legume
Scutellaria integrifolia	Lamiaceae	Skullcap	0.19	<0.01	30.0	Gravity	Summer forb
Ruellia caroliniensis	Acanthaceae	Wild petunia	0.11	<0.01	27.5	Ant/explosive	Summer forb
Sporobolus junceus	Poaceae	Dropseed	0.11	<0.01	27.5	Gravity	C_4 grass
Sorghastrum nutans	Poaceae	Yellow indiangrass	0.19	<0.01	22.5	Gravity	C_4 grass
Mimosa quadrivalvis	Fabaceae	Sensitive briar	0.30	0.01	20.7	Gravity	Legume
Sorghastrum secundum	Poaceae	Lop-sided indiangrass	0.04	<0.01	20.0	Gravity	C_4 grass
Muhlenbergia capillaris	Poaceae	Muhly grass	0.15	0.01	10.7	Gravity	C_4 grass

Table 1 continued.

Species by vulnerability ranking	Family	Common name	Occurrence of species (mean freq of nested plots)		Vulnerability ratio (Vratio)	Dispersal type	Guild
			Benchmark sites (Fb)	Restoration sites (Frs)	(Fb / Frs)		
Species more common to reference sites							
Dyschoriste oblongifolia	Acanthaceae	Twin flower	0.97	0.12	8.1	Ant/explosive	Summer forb
Elephantopus elatus	Asteraceae	Elephant's foot	0.17	0.02	7.3	Wind	Fall forb
Stylosanthes biflora	Fabaceae	Pencil flower	0.32	0.06	5.7	Gravity	Legume
Croton argyranthemus	Euphorbiaceae	Silver croton	0.09	0.02	5.0	Ant/explosive	Summer forb
Chrysopsis mariana	Asteraceae	Golden aster	0.07	0.01	5.0	Wind	Fall forb
Lespedeza repens	Fabaceae	Creeping lespedeza	0.13	0.03	4.6	Carried	Legume
Tephrosia spicata	Fabaceae	Hoary pea	0.10	0.02	4.5	Gravity	Legume
Vernonia angustifolia	Asteraceae	Ironweed	0.22	0.05	4.4	Wind	Fall forb
Vaccinium myrsinites	Ericaceae	Shiny blueberry	0.28	0.06	4.4	Consumed	Woody
Lechea sessiliflora	Cistaceae	Pineland pinweed	0.26	0.06	4.3	Gravity	Fall forb
Aristolochia serpentaria	Aristolochiaceae	Snakeroot	0.04	0.01	3.3	Gravity	Summer forb
Euphorbia pubentissima	Euphorbiaceae	False flowering spurge	0.34	0.11	3.1	Gravity	Summer forb
Dichanthelium aciculare	Poaceae	Witchweed	0.54	0.19	2.8	Ant/explosive	C_3 grass
Hedyotis procumbens	Rubiaceae	Innocence	0.15	0.05	2.7	Gravity	Summer forb
Galactia mollis	Fabaceae	Soft milkpea	0.14	0.05	2.7	Gravity	Legume
Polygala grandiflora	Polygalaceae	Showy milkwort	0.08	0.03	2.5	Ant/explosive	Summer forb

Appendix 1. List of species combined at time of data collection due to identification constraints of vegetative plant material.

Taxon used in analyses	Taxa included
Ambrosia artemisiifolia	*A. psilostachya* DC., *A. artemisiifolia* L.
Andropogon virginicus	all species of *Andropogon*, *Schizachyrium scoparium* (Michx.) Nash
Anthaenantia villosa	*A. villosa* (Michx.) Beauv., *A. rufa* (Ell.) Shult.
Chrysopsis mariana	*C. gossypina* (Michx.) Ell., *C. mariana* (Michx.) Ell.
Pityopsis graminifolia	*P. graminifolia* (Michx.) Nutt., *P. adenolepis* (Fern.) Semple
Stylisma humistrata	*S. humistrata* (Walt.) Chapman, *S. patens* (Desr.) Myint
Vaccinium myrsinites	*V. myrsinites* Lam., *V. darrowi* Camp

Supplemental Study: Great Lakes Region

Ground layer plant community responses to contrasting silvicultural treatments

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Report Summary

This report summarizes two studies examining stand management impacts to ground layer plant communities in northern hardwood ecosystems. In Part I we summarize stand-scale responses of ground layer plants in a long-term study contrasting a range of silvicultural approaches. Treatments included diameter limit cutting, shelterwood cutting, and three levels (light, medium, heavy) of individual tree selection, as well as an uncut control. Plant diversity and community composition were examined after 40 years of management. We detected no strong treatment effects on ground layer plant communities. Overall, richness averaged 4.4 species/m^2, diversity averaged H=0.7, and evenness averaged E_H=0.4 in all treatments. Community composition was similar among the treatments, as well between treatments and the control. Our results suggest that ground layer plant communities in northern hardwood ecosystems are resilient within the 40-year time frame since disturbance in the even-aged treatments, or the 10-year time interval since disturbance in the uneven-aged treatments.

In Part II, we examine responses of ground layer plant diversity and composition to canopy gap size. In this study, a range of gap sizes (0, 6, 10, 20, 31, 46 m diameter) was cut in mature second-growth, northern hardwoods in 1994. Ground layer plant cover was sampled in 1999. We found a strong connection between gap size and ground layer plant community response. Overall, richness averaged 18.7 species per m^2 and diversity was H=1.9. However, both species richness and diversity displayed a quadratic response to the gap size gradient; intermediate gap sizes had highest richness and diversity, while both the control and 46 m gaps had the lowest richness and diversity. Evenness was not influenced by gap size, averaging E_H=0.7 across the size range. Composition differed among gap sizes. Larger gaps (20, 31, 46 m) separated from smaller gaps and control in ordination space. Important species driving compositional differences included sugar maple (*Acer saccharum*), found primarily in the control and small gaps, and raspberry (*Rubus strigosus*), which was more abundant in the larger gaps. Our results support use of silvicultural approaches that incorporate a range of gap sizes, if a goal of management is to sustain the full complement of northern hardwood ground layer plants.

PART ONE:

Comparing Ground Layer Plant Communities After 40 years of Management in Northern Hardwoods Ecosystems

Introduction

By the middle part of the last century, there was increased concern over a lack of regeneration in second-growth, even-aged northern hardwood forests in the upper Great Lakes region. Most stands supported abundant sugar maple (*Acer saccharum* Marsh.) seedlings, but regeneration of other species, also characteristic of northern hardwood ecosystems, was often lacking. In response, the North Central Research Station installed a "cutting methods" experiment in 1952 in second growth northern hardwoods. The study was designed to contrast a range of silvicultural treatments for their efficacy at meeting timber production and regeneration objectives. In 1991, an additional objective was added that focused on ground layer plant community response to the treatment gradient. It is the results of this later objective that we summarize here. Specifically, our interest is in evaluating degree of similarity in ground layer plant diversity and community composition among stands managed using different silviculture approaches, including even-age and multi-age systems.

Methods

Study Site

The study site is located in a second-growth, northern hardwood forest on the Argonne Experimental Forest in northern Wisconsin, USA. The forest is dominated by sugar maple (averaging 63% of overstory basal area), with lesser amounts (4-9% basal area each) of white ash (*Fraxinus americana* L.), yellow birch (*Betula alleghaniensis* Britton), basswood (*Tilia Americana* L.), hemlock (*Tsuga canadensis* L.), and red maple (*Acer rubrum* L.). The soils of the study area are classified as Iron River – Wabeno series, with more boulders than typical. The habitat type, following Coffman (1984), is described as Acer – Viola – Osmorrhiza (Coffman 1984). At the time of study establishment, the forest was approximately 60 years old.

Design

The study was established in 1952 as a randomized block design. Treated stands were 1 ha and replicated three times. Even-age treatments included a diameter limit and shelterwood cuts. The diameter limit treatment removed all trees greater than 20 cm diameter at 30 cm stem height (~17 cm DBH). The residual basal area averaged 5.3 m^2/ha in 1952. The shelterwood treatment was cut to a basal area of 14 m^2/ha in 1952, with overwood removal in 1964.

Uneven-age treatments included three levels of individual tree selection. Selection levels included light (20.6 m^2/ha residual basal area), medium (17.2 m^2/ha residual basal area) and heavy (13.8 m^2/ha residual basal area). These treatments were applied 4 times prior to 1991, in 1952, 1962, 1972, and 1982.

In 1991, ground layer vegetation (herbaceous species, woody and shrub species below 0.5 m tall) was sampled in each treatment stand. Sampling occurred at five points within each stand. At each point, species cover was recorded in eight 1-m^2 plots. Plots were arrayed in a 2 x

4 grid centered on the point and oriented in a random direction. Additionally, a 10 x 15 m plot (also centered on the point and oriented parallel to the grid of small plots) was used record presence of species not found in the eight 1-m^2 plots. Cover classes included: rare (1 or 2 individuals), 0.1-1%, 1-5%, 6-15%, 16-25%, 26-50%, 51-75%, and 75-100%. This sampling scheme was repeated twice in 1991; once in mid-spring to capture early developing ephemerals and again in mid-summer.

Analysis

A complete species list was compiled from the eight plots at each point and compared to the species list from the 10 x 15 m plot. Species that were only found in the 10 x 15 plot were added to the list generated from the 1-m^2 plots. Species were divided into three data sets including 1) summer species; 2) spring species; and 3) functional groups. For the functional group analysis, species were classified and grouped into: 1) exotics, 2) native annual/biennial, 3) native non-leguminous forbs, herbaceous vines, and ferns, 4) native sedges, grasses, and rushes, 5) native legumes, 6) native shrubs, 7) native trees, 8) native woody vines, and 9) unknowns.

For each data set, cover estimates from the eight 1-m^2 plots were averaged at each of the five points. Species found only in the 10 x 15 m plot were rated as rare in cover for that point. The five points in a stand were averaged to generate a stand mean cover value. Diversity was calculated at each of the five points in a stand using the Shannon Diversity Index:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where H is diversity and p_i is cover of species i. Cover classes were converted to midpoints for these calculations. The points were averaged to generate a stand mean. Mean stand-level evenness was calculated similarly, from the point estimates of diversity using:

$$E_H = H / H_{max} = H / \ln S$$

where E_H is evenness, H is diversity of a plot, H_{max} is maximum potential diversity of the plot, and $ln\ S$ is natural log of species richness. Mean evenness by treatment was estimated as with diversity. Richness, diversity, and evenness were tested for treatment differences using a randomized block analysis of variance.

Nonmetric multidimensional scaling (NMS) was used to graphically compare difference in ground layer plant communities among treatments. NMS is effective with ecological data because it does not assume linearity of species responses to gradients, it uses rank order information in a dissimilarity matrix that eliminates the ‘zero truncation” problem in most ordination methods, and can use any distance measure. We ran NMS separately for each of the three data sets using matrices of: 1) 18 experimental units (6 treatments replicated 3 times) by cover of 82 summer species; 2) 18 experimental units by 9 spring ephemeral species; and 3) 18 experimental units by 9 plant functional groups.

For each analysis, species that occurred in only one experimental unit were deleted. For the summer species analysis, the data matrix was relativized by 1 to reduce the influence of highly abundant species and improve normality. For the spring species and functional group analyses, data were square root transformed to improve normality. Sorenson distance measure was used for all three data sets. Analyses were confined to 2 axes. For each data set, the analysis included 50 runs of real data and 20 runs of randomized data for use in a Monte Carlo

permutation procedure (McCune and Mefford 1999). Treatment differences were tested with multi-response permutation (MRPP), a non-parametric hypothesis test, in PC-ORD. In this test, the A statistic describes effect size: when A=0, groups are no more or less different than expected by chance; when A=1, sample units within each group are identical (Peck, 2003).

Results

The summer ground layer plant community was not strongly related to treatment differences. Species richness averaged 4.4 (+/- 0.5) species per m^2 overall. There was no significant difference in richness among treatments (p = 0.25), perhaps because variation was quite high in some treatments (Figure 1).

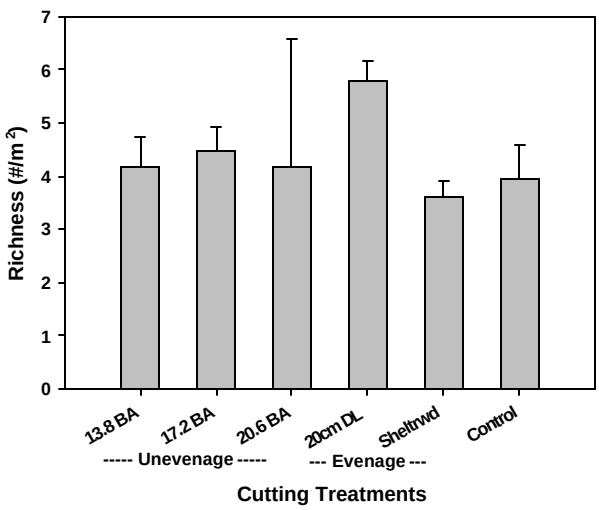

Figure 1. Summer species richness per m^2. Values are means +/- standard error (N=3).

Similarly, diversity and evenness were similar among treatments, averaging H=0.7 (+/- 0.07) (Figure 2) and E_H=0.4 (+/- 0.03), respectively (Figure 3). Treatment means were not significantly different for either measure (p = 0.71 for diversity and p = 0.75 for evenness).

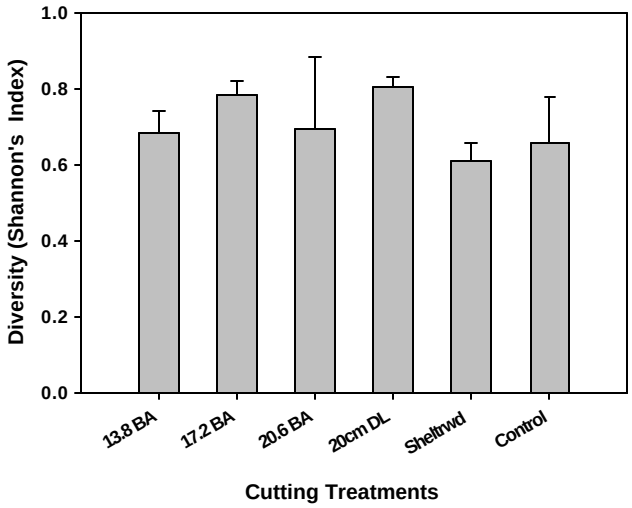

Figure 2. Summer species diversity. Values are means +/- standard error (N=3).

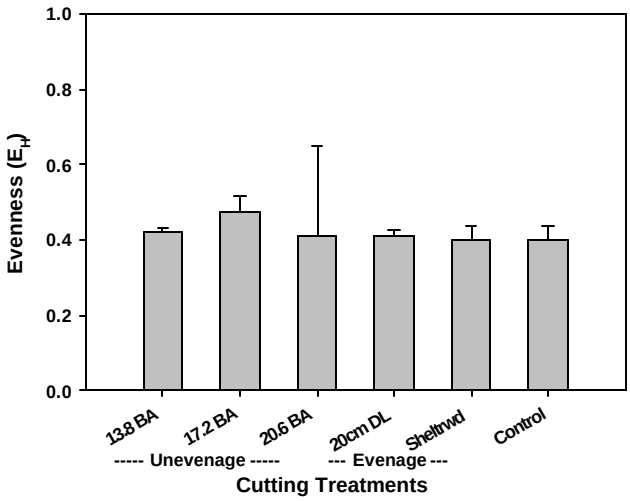

Figure 3. Summer species evenness. Values are means +/- standard error (N=3).

Diversity measures based on functional groups (using summer species only) were not related to treatment (data not shown). Overall, richness averaged 1.8 (+/- 0.1) groups per m^2, diversity averaged 0.2 (+/- 0.04) and evenness averaged 0.3 (+/- 0.05). There were no significant differences among treatments for any parameter (p = 0.71 for diversity and p = 0.60 for evenness). Similarly, diversity measures based on spring ephemerals appeared to be unrelated to treatment (data not shown). Across all treatments, richness averaged 3.6 (+/- 0.5) species per m^2, diversity averaged 0.6 (+/- 0.1), while evenness averaged 0.4 (+/- 0.08). There were not significant treatment effects for any measure (p = 0.96 for richness, p = 0.81 for diversity, and p = 0.43 for evenness).

The first two axes of NMS ordination accounted for 63% of total variation among stands in summer ground layer composition. However, little of this variation appeared to be related to overstory treatment (Figure 4). The multi-response permutation test for differences among treatments in ordination space was not significant (p = .79). Similarly, NMS ordination of plant

functional groups and spring plant communities was not conclusive in NMS, suggesting weak data structure and little effect of treatment (graphs not shown). Therefore, in both cases, multi-response permutation test was not possible. An A statistic (measure of within group similarity) was not generated for any of the three ordinations.

Discussion

Increasingly, more than growth and yield and regeneration responses of commercial tree species judges success of silvicultural systems. Effects of silvicultural treatment on a wide variety of non-commodity values, as well as non-tree commodities, are considered when selecting and evaluating stand management approaches. In particular, sustainability of biological diversity, including species diversity, is considered an important metric by which to judge the efficacy of silvicultural approaches. It is with this need in mind that we evaluated the range of treatments included in the northern hardwood "cutting methods" experiment.

Although the original objectives of the study focused on responses in tree growth and quality, as well as regeneration dynamics, the design presented an opportunity to examine ground layer plant community dynamics in response to treatment. Specifically, we were interested in evaluating the potential for long-lasting or persistent changes in ground layer plant community diversity and composition across the range of silvicultural treatments.

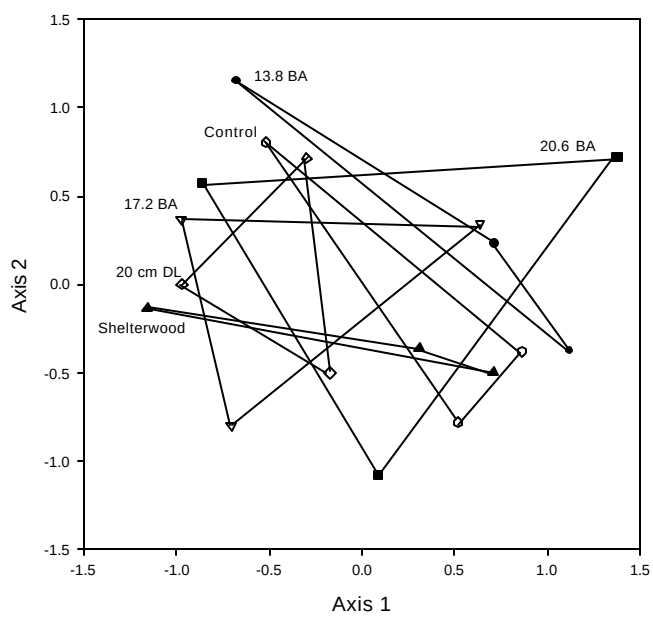

Figure 4. NMS ordination of summer plant composition.

Our results point to little differences in ground layer diversity or composition among silvicultural approaches, or relative to old untreated forest, given the unique circumstances of the study design. Specifically, time since last harvest for the two even-age treatments has been considerable, 40 years between harvest and ground layer sampling for the diameter limit cutting

and 25 years since overwood removal in the shelterwood treatment. Given these time spans, one might conjecture that the ground layer plant communities of the study ecosystem have recovered to levels of richness, diversity, and evenness, as well as composition, that are indistinguishable from the 105 year old, untreated forest. Alternatively, ground layer plant communities may be resilient to change in the face of such disturbances. We cannot distinguish between the two alternatives, but hypothesize that the latter is not likely to be the case, based on evidence from similar studies. Regardless, the fact that there is little imprint of past even-age management treatment on ground layer plant communities in the study system is informative and suggests that time since disturbance is an important mitigating factor to consider in management planning.

Time between last harvest and ground layer sampling in the selection treatments was nine years, considerably shorter than the even-age treatments. Moreover, the selection treatments have been applied four times through the course of the study, compared to once in the even-age treatments. Ground layer diversity and composition appear to be unrelated to level of selection and do not differ from responses in the even-age treatments. Again, one can hypothesize that nine years since selection harvest is sufficient time for recovery of ground layer plant communities to levels and patterns similar to the control. Alternatively, ground layer plant communities may be resilient to change, given the level and frequency of disturbance associated with selection harvesting. We cannot distinguish between these alternatives, however the latter explanation may be plausible for these treatments.

Regardless of the mechanism behind our results, they stand in contrast to recent work on understory species diversity in northern hardwood forests. Working in similar forests, Scheller and Mladenoff (2002) found that richness and diversity of understory plants (individuals < 2 m tall) increased from old-growth forest, to managed even-aged forests (clearcut 65-82 years before sampling), to unevenaged forest managed with selection harvest (single "selection" harvest 10-12 years before sampling). The difference was greatest between selection stands and both old-growth and even-aged stands. Moreover, community composition was measurably different with selection management, relative to old-growth and even-age management, but to a lesser extent between the latter two conditions.

There are several possible reasons for these differences, compared to our study. First, our study stands were relative small (1 ha) and were embedded in a matrix of intact, mature forest (60 years old in 1952). This arrangement may facilitate reestablishment of plant species, having limited dispersal distance capabilities, which may have been lost or depleted initially after treatment. Second, our old forest control was not old-growth. Rather, control stands were unmanaged second growth that was 60 years old at study initiation and 100 years old at the time of ground layer sampling. Scheller and Mladenoff (2002) sampled true old-growth, primary forest stands. The latter may be markedly different in ground layer community composition and structure than our old forest controls and from managed stands, as found by Scheller and Mladenoff (2002). Finally, high light levels in the so called selection stands examined by Scheller and Mladenoff (2002) suggest that the single harvest was heavy, removing more overstory than would generally be done in a true selection system. The fact that mean light levels were high (7.2%), relative to old-growth and even-aged stands (3.5%), 10-12 years after treatment further suggests the cutting was heavy. These authors do not provide the specifics of the selection treatment, but our interpretation is that their uneven-aged treatment was measurably greater in disturbance intensity than the selection treatments examined in our study. As such, the 10-12 year period since disturbance may be insufficient for recover to levels of diversity and composition similar to old-growth forest.

Based on their results, Scheller and Mladenoff (2002) suggest that uneven-age management in northern hardwoods, using selection systems, may be problematic over the long-term if periodic disturbance leads to a bifurcation of compositional states, characterized by weedy and early successional species. Our results for true selection systems, with harvesting implemented four times during the course of the study, suggests that this is not the case; ground layer plant communities in the selection treatments were largely indistinguishable for those occurring with even-age management or in the old-forest control. In fact, a lack of intolerant and mid-tolerant, earlier successional species is an apparent drawback of the selection treatments, specifically the light and medium treatments, which has prompted work on the importance of large gaps for sustaining populations of less tolerant species in managed northern hardwood forests (see Part II).

Key Points

1. We found little evidence for differences in ground layer plant diversity or community composition among five contrasting silvicultural treatments, including diameter limit cutting (40 years since treatment), shelterwood (25 years since overwood removal), light, medium, and heavy selection (harvests at 39, 29, 19, and 9 years prior to sampling).

2. Ground layer plant communities in treated stands did not differ appreciably from those in control stands (unmanaged forest, 100 years old at time of sampling).

3. Lack of treatment differences may results from recovery since disturbance or resilience to the disturbances.

4. Small size and position of treatment stands within mature forest may influence these results. Large stands that are isolated from mature or old forest may recover more slowly or not at all to an undisturbed condition.

5. Contrary to suggestions by others, repetitive selection treatments did not result in a compositional bifurcation into a state characterized by dominance of weedy and early successional species.

PART TWO:

Ground Layer Plant Community Response to Gap Size in Northern Hardwoods Ecosystems

Introduction

Increasingly, management guidelines for second-growth, northern hardwood ecosystems include approaches employing canopy gaps, this in order to better emulate the dynamics and structure generated by natural wind disturbance. One objective of such approaches is the creation of multi-cohort age structure. Canopy gaps are expected to facilitate new cohort establishment and if created on a periodic basis, lead to multi-aged structure. Canopy gaps also can influence tree composition of a forest. Large gaps may favor species of lower shade tolerance and earlier successional status, relative to small gaps. Incorporating a range of gap size in a stand may better ensure sustainability of a wide range of plant species. While also leading to multi-cohort structure, individual tree selection systems have the potential to move northern hardwood stands towards reduced tree diversity and increased dominance by single species. For example, light selection favors tolerant species, notably sugar maple (Acer saccharum Marsh.), while heavy selection may favor less tolerant species at the expense of tolerants. In fact, such compositional alterations associated with true selection systems have been a motivating factor in the development of canopy gap based approaches in northern hardwood ecosystems. Another motivating factor is the belief that canopy gap based management will better sustain many aspects of northern hardwood ecosystem structure and function, such as plant species diversity, because of the apparent similarity of this disturbance regime to natural wind disturbance. However, little is known about the ecological responses of plant communities to canopy gaps in northern hardwood ecosystems. Consequently, the stand-scale implications of gap-based management on plant community diversity and composition are not well known. To address this need, we examined the effects of canopy gap size on ground layer plant community diversity and composition in northern hardwood ecosystems. Our goal is to provide information on gap size-plant community relationships that can be used to guide development of stand-scale management approaches for these ecosystems.

Methods

Study Site

Our study site is located in second growth northern hardwood stands on the Nicolet National Forest in northeastern Wisconsin. Study stands are classified into two similar habitat types (following Kotar and Locey 1988), including *Acer-Tsuga/Dryopteris* and *Acer/Viola-Osmorhiza* types). Soils are primarily in the Stambaugh Series, consisting of 75 cm of medium acid silt loam loess, overlying stratified sand and gravel. The general landscape is hummocky, kame/kettle-like topography with many closely spaced depressions that resulted from glacial action.

At the time of study establishment in 1994, treatment stands were even-aged and approximately 60 years old. Sugar maple dominated the overstory. Mean overstory basal area

was 30.3 m^2/ha. Diameter at breast height (1.37 m) varied from 14 to 30 cm and density ranged from 541 to 1740 trees per ha. An initial survey of ground layer species in the study area found 17 tree species, 12 shrub species, 70 herbs and forbs, 15 fern and club moss species, and 18 grass, sedge, and rush species.

Design

The study area was divided into four blocks ranging in size from 15 to 25 ha. Within each block, five canopy gap sizes were replicated three times. Gap sizes included diameters of 6, 10, 20, 31, and 46 m. Additionally, we delineated controls (gap size zero), which were 0.4 ha areas where no trees were cut. Gap locations were randomly selected in each block, but overlap was avoided. Gap size was delineated on the ground by measuring appropriate distances between the crown edges of border trees in four directions (N-S, E-W, NE-SW, NW-SE). As prescribed, our gap sizes reflect the area actual gap, rather then expanded gap. Gaps were cut by falling all trees greater than 2.5 cm in diameter. Merchantable portions of the trees were removed from the gaps, leaving the logging slash. The matrix between gaps (with the exception of control areas) was marked for thinning following Erdmann (1986) by removing high risk, cull, and trees in overstocked size classes. Harvesting took place in 1994-1995.

Ground layer vegetation (individual less than 0.5 m tall) was sampled prior to harvest and again 2000, five years after harvest. In this report, we present only post harvest data. We established a series of 1 m^2 plot within each gap and control area. The number of plots varied with gap size (Table 1). Plots were established in a systematic fashion including one at gap center (and control area center) and one or more on north, south, east, and west running transects beginning at gap center. Transect plots were spaced 3.7 m from gap center and each other until full forest canopy was reached (approximately 3.7 m interior from gap edge). All gap size, except the 6 m gaps, included four plots under full forest canopy and five or more in the gap proper. In the 6 m gaps, only the center plot was actually in the opening; the four additional transect plots were in closed forest.

Table 1. Number of vegetation plots sampled for each gap size (diameter in m, area in m^2).

Gap Diameter	Gap Area	Number of Plots
6	28	5
10	79	9
20	314	13
31	755	13
46	1662	17
Control	---	17

In each vegetation plot (1 x 1 m^2), we recorded species coverage using the following classes: rare = 1 or 2 individuals, + = 2-20 individuals, 1 = > 20 individuals, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, and 5 = 75-100%. Trees and shrubs <0.6 m tall, herbs, forbs, and grasses were included in the survey.

Analysis

Species richness was calculated for each 1-m^2 plots within a gap treatment. The 1-m^2 richness estimates were then averaged within a gap and the three gap replications were averaged for a treatment mean for each block. The block level mean was used in comparisons among treatments. We calculated diversity for each 1-m^2 plot using the Shannon Index:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where H is diversity and p_i is cover of species i. Mean diversity by treatment was calculated as with richness. Cover classes were converted to midpoints for these calculations. Evenness was calculated using diversity as:

$$E_H = H / H_{max} = H / \ln S$$

where E_H is evenness, H is diversity of a plot, H_{max} is maximum potential diversity of the plot, and $ln\ S$ is natural log of species richness. Mean evenness by treatment was estimated similarly to richness and diversity. Treatment means for richness, diversity, and evenness were compared among gap sizes using a randomized block analysis of variance.

We used nonmetric multidimensional scaling (NMS) to graphically display differences in plant community composition among gap sizes. For this analysis, we used a matrix consisting of 24 experimental units (six gap sizes replicated four times) and cover estimates for 98 species. Species found in 5% or less of the experimental units were eliminated from analysis to reduce noise. Because of excessive skewness in the dataset, we standardized the matrix with a power transformation of $x^{0.125}$. Sorenson distance measure was used in the analysis. The ordination was limited to two axes and was run 50 times with real data and 20 times using a randomized data set for use in a Monte Carlo permutation procedure (McCune and Mefford 1999). Treatment differences were tested with multi-response permutation (MRPP), a non-parametric hypothesis test, in PC-ORD. In this test, the A statistic describes effect size: when A=0, groups are no more or less different than expected by chance; when A=1, sample units within each group are identical (Peck, 2003).

Results

Overall, species richness averaged 18.7 (+/- 1.2) species per m^2. However, richness varied with gap size significant way (p=0.007, Figure1). Intermediate gap sizes had greater richness than both the control and large gaps sizes (quadratic contrast, p=0.03). Richness was highest in the 20 m gaps, averaging about 21 (+/-1) species/m^2.

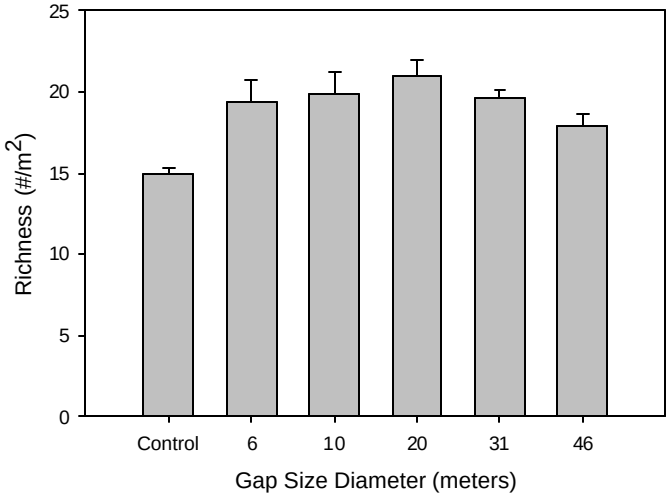

Figure 1. Species richness by gap size. Values are means +/- standard error (N=4).

Overall, diversity averaged 1.9 (+/- 0.07), but had a quadratic response to gap size (Figure 2). Diversity peaked in middle gap sizes (10, 20, 31 m) and was lowest in the control and 46 m gaps. The overall gap size response was significant (p = 0.02), as was the quadratic contrast (p=0.04). Overall, evenness averaged 0.7 (+/- 0.01) Among treatments there was a similar quadratic response to gap size (Figure 3). However the treatment effect was not significant (p = 0.35).

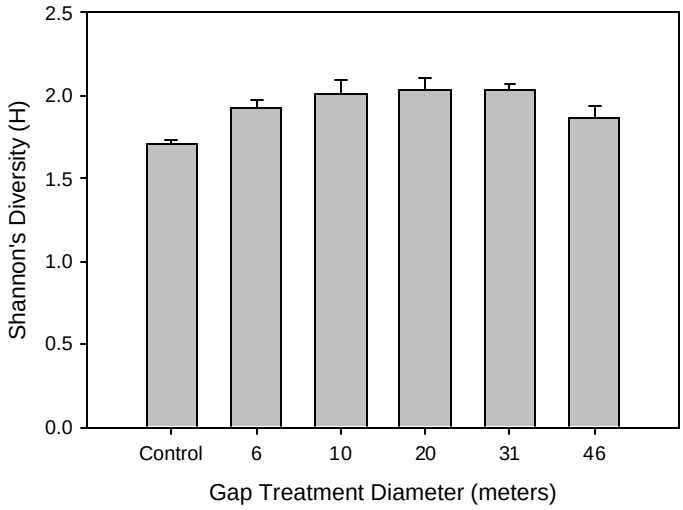

Figure 2. Diversity by gap size. Values of means +/- standard error (N=4).

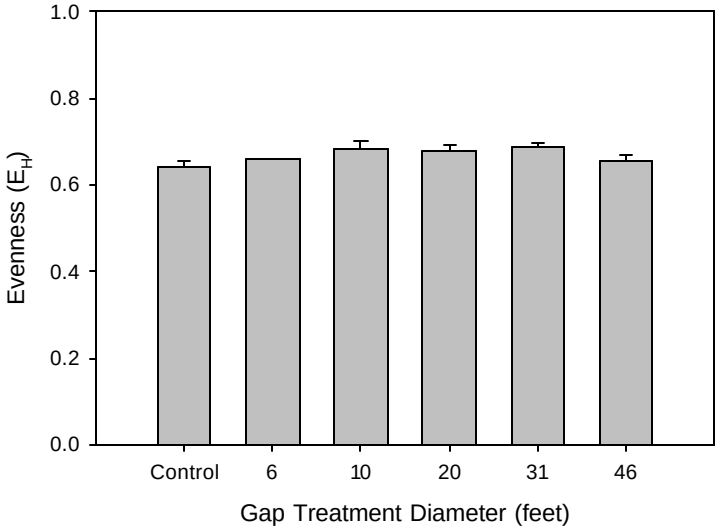

Figure 3. Evenness by gap size. Values are means +/- standard error (N=4).

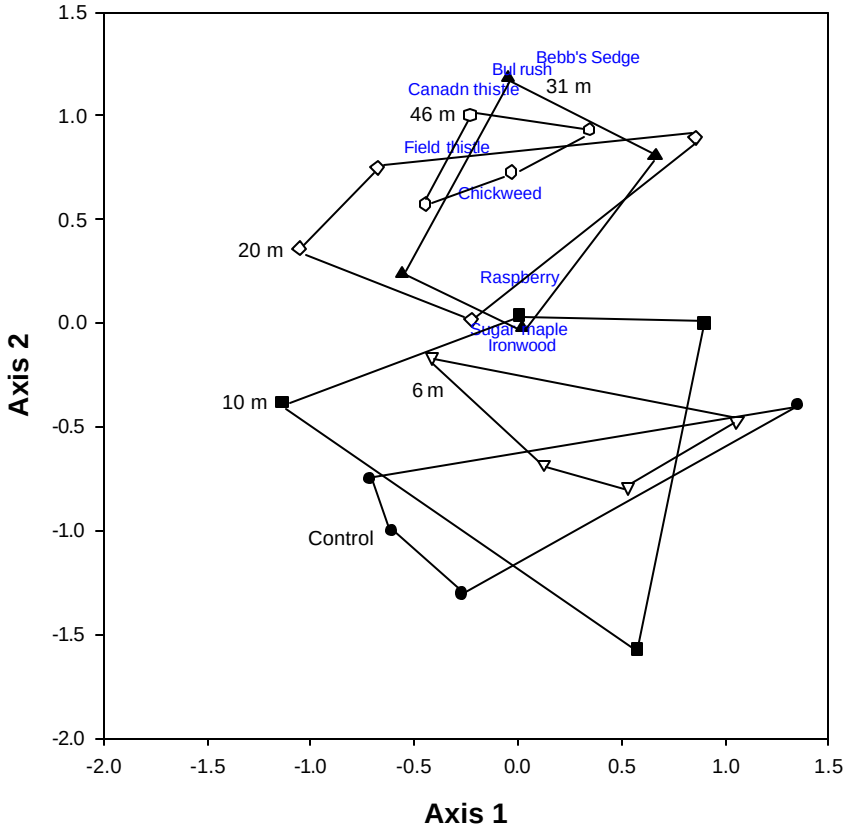

Figure 4. NMS ordination of ground layer composition.

The first two axes of the NMS ordination explained 68% of total variation in ground layer community composition. Some of this variation was clearly related to gap size (Figure 4). Treatment differences were significant (*p*=0.0002), but with low confidence that stands within a group were identical (A=0.056). The larger gap sizes (20, 31, 46 m) were largely distinct from the smaller gap sizes (10, 20 m) and the control (Figure 4). Within these two groups, gaps sizes were not distinct, hence the low A value. The separation of large and small gaps occurred largely along axis 2 of the ordination. Several species had high to moderate correlations with Axis 2 and were significant indicators species for either 6 m or 46 m gaps, including sugar maple (r= –0.580, p=0.046 in 6 m gaps), ironwood (*Ostrya virginiana*, r=-0.356, *p*=0.036 in 6 m gaps), raspberry (*Rubus strigosus*, r=0.71, p=0.002 in 46 m gaps), checkweed (*Stellaria media*, r=0.689, *p*=0.012 in 46 m gaps), Bebb's sedge (*Carex bebbii*, r=0.694, *p*=0.035 in 46 m gaps; Canadian thistle (*Dirsium arvense*, r=0.703, *p*=0.045 in 46 m gaps), field thistle (*Cirsium discolor*, r=0.432, *p*=0.006 in 46 m gaps), and bulrush (*Scirpue atriovirons*, r=0.666, *p*=0.002 in 46 m gaps). Several other species had high correlations with axes 2, but were not significant indicators of a specific gap size. Rather, these species tended to be associated with larger gaps (positive correlations). These species included downy woodmint (*Blephillia ciliata*, r=0.640), yellow birch (*Betula allegheniensis*, r=0.596), *Carex leptonervia* (r=0.764), braken fern (*Pteridium aquilinum*, r=0.633), rosey twisted stalk (*Streptopus roseus*, r=0.707), large flowered belwort (*Uvularia grandiflora*, r=0.689), alsike clover (Trifolium hybridum, r=0.666), and climbing false, buckwheat (Polygonum scandens, r=0.754).

Discussion

Our results demonstrate significant effects of gap size on ground layer species diversity and composition in the northern hardwood ecosystem examined. Specifically, ground layer species richness and diversity displayed a quadratic response to gap size, with lowest values of both measures in uncut forest and in the 46 m diameter gaps. Richness peaked in 20 m gaps, while diversity was highest and similar in 10, 20, and 31 m gaps. These results suggest exclusion of some species by more tolerant competitors in uncut forest and small gaps (<10 m diameter) and by more disturbance-oriented species in the largest gaps. Mid-range gap sizes (10-31 m diameter) appear to offer opportunities to sustain a wider range of species.

Gap size also had a significant effect on ground layer community composition. Specifically, composition in large gaps (20, 31, 46 m diameter) differed measurably from composition in small gaps (6, 10 m) and the uncut forest. The effect of gap size on tree composition is well established in the literature (e.g., Runkle 1982), however there is only limited data on these effects for ground layer communities in northern hardwood ecosystems (Collins and Pickett 1988).

Differences in ground layer plant communities between large and small gaps results from two sources of variation; a greater abundance of particular species in the small gaps or control, relative to large gaps, or the reverse, a greater abundance of particular species in the large gaps, relative to the small gaps or control. Both influences were at play in our study, but the latter had a much greater influence. Sugar maple and ironwood seedlings were somewhat more abundant in smaller gaps (5, 10 m), and leatherwood was much more abundant in uncut forest, compared to the 20-46 m gaps. More importantly, a large number of species were substantially more abundant in larger gap sizes, especially the 46 m gaps, including species that are known to be disturbance opportunists, such as raspberry and several thistles, or intolerant of understory

conditions, such as yellow birch. Our casual observations suggest that the high abundance of raspberry in the largest gaps likely creates a strong competitive barrier to other species colonizing these gaps.

Restoring structural complexity and diversity in degraded northern hardwood stands

Mature, single-cohort northern hardwood stands, as well as multi-cohort stands managed using regionally traditional selection systems, both tend to be dominated by sugar maple (Strong et al. 1997). In contrast, the tree layer in old-growth northern hardwood stands often support 4 or 5 species in abundance and 10 or more species in total (Curtis 1959). Increasingly, canopy-gap based silviculture is promoted as an effective way to "rapidly" move compositionally degraded even-age stands towards a mixed-species, multi-cohort structure. Moreover, such approaches are being used as a natural disturbance-based alternative to traditional single-tree selection systems, again with a goal of restoring and/or sustaining mixed-species, multi-cohort structure.

When taking this approach, it is important not simple to cut gaps, but do so in a way that reflects an appropriate temporal and spatial frequency of gap sizes across the range of sizes that occur naturally. Evidence in mesic hardwood forests suggests that new gaps occupy less than 2% of stand area annually (Runkle 1982; Lorimer and Frelich 1994), providing a benchmark against which to measure gap cutting frequency in managed stands. Average gap sizes in similar forests span a range from 10s to 100s of m^2, e.g., 12 to 121 m^2 (Tyrrell and Crow 1994) and 40 to 364 m^2 (Lorimer and Frelich 1994). In old-growth stands, small gaps are much more frequent than large gaps. Rarely, large gaps occur that are on the order of many hundred to several thousand m^2 in size. Evidence suggests that such large disturbances may occur about every 300 years (Lorimer and Frelich 1994). The range of gap sizes we used in this study includes the average gap size gradient (28 to 314 m^2), as well as larger gaps sizes (755 and 1662 m^2) that occur only rarely. The literature data on gap size distribution provide benchmarks to formulate appropriate gap sizes in managed stands. Moreover, our work provides information useful for predicting gap-level and stand-level compositional responses to gap size and size distribution.

Key Points

1. Ground layer plant species richness, diversity, and evenness differed along a range of canopy gap sizes, ranging from uncut forest to large gaps (46 m diameter; 1662 m^2). The differences were quadratically related to gap size. Richness, diversity, and evenness peaked at moderate gap size (10, 20, 31 m diameter), but were lower in uncut forest, small gaps (6 m diameter), and the largest gaps (46 m diameter).
2. Diversity responses suggest that greater competitive exclusion occurs at the ends of the gap size gradient, relative to the middle.
3. Ground layer plant community composition also varied with gap size. Specifically, uncut forest and small gaps (6, 10 m diameter) differed significantly in composition from larger gaps (20, 31, 46 m diameter).
4. Larger gaps had greater abundance of disturbance-oriented herb and shrub species, and less tolerant tree species. Uncut forest and small gaps had somewhat greater abundance of more tolerant woody species.
5. Compositional responses to gap size should be considered when defining desired future conditions and developing silvicultural approaches based on canopy gap dynamics in northern hardwood ecosystems.

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