Predicting Regeneration in Appalachian Hardwood Stands Using the REGEN Expert System

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ABSTRACT

A study was initiated to adapt the REGEN regeneration prediction model to the Appalachians of Virginia and West Virginia. REGEN generates predictions via expert created REGEN knowledge bases (RKBs) that contain competitive rankings and stochastic parameters for selected species and size classes of advance reproduction. We developed RKBs for four site productivity classes (xeric, subxeric, submesic, mesic), and tested two (subxeric and submesic) using field collected inventory data in this study. To test the model we collected data from 48 paired sites which contained a mature stand and an adjacent regenerating stand (clearcut) of similar site productivity harvested within the past 20 years. Across all 48 sites, model predictions were within 5% of measured values on average, and explained 32% ($R^2 = 0.32$) of the variation in species composition in regenerating stands.

The species compositions of 41 of the paired stands on the Appalachian Plateau in West Virginia were further analyzed to compare species composition. Species composition was compared between the mature and regenerating stands in the subxeric and submesic site classes. A comparison of the upper canopy (dominant and codominant) species composition in regenerating stands to that of all stems ≥ 1.5 in dbh in the mature stands was conducted as well. Our results suggest that the future species composition of stands regenerating following clearcut harvests will likely differ from previous rotations with mesophytic, shade intolerant species being more numerous. Oaks will likely assume a smaller role as the clearcuts mature, particularly on the submesic sites.

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1. INTRODUCTION

Introduction

The Southern Appalachian Hardwood Region described by Smith (1994) is the world's largest contiguous hardwood forest. This region covers three distinct physiographic provinces (Fenneman 1938) and is covered by several forest types (Braun 1950, Eyre 1980, Smith 1994) creating a diversity that is unparalleled in the United States. Although the utilization of this resource has been essential to the development of the region since the arrival of Europeans, prior to the mid-20th century the extraction of the resource was seldom more than timber mining. As a result, there are few records that describe the establishment of the current forests. Most of the forests in the region have been dominated historically by oak (*Quercus spp.*), or oak has been a major component therein (Lorimer 1993). While problems with oak regeneration have been noted since the late 1800s, it wasn't until the 1930s that discussion of these problems began to appear with frequency in American forestry literature (Clark 1993). Given the array of landowners, including significant portions of public, private, and industrial holdings, it is understandable that the management of this vast resource provides opportunities as diverse and challenging as the region itself.

Justification

As of 2008, there are approximately 65.5 million acres of timberland in the Appalachian Hardwood Region (Oswalt and Turner 2009). Oak is a keystone species given its economic importance, impact on wildlife habitat, social appeal, and historical dominance. Oak appears to have a certain charisma among landowners, making it a desirable species regardless of economic influences at the time of forest planning. As has been outlined by numerous authors, regenerating oak is often difficult particularly on more productive sites (Loftis and McGee 1993). Poor oak regeneration is also geographically widespread, suggesting potential for substantial and widespread changes in forest composition following harvest across the eastern United States. This scenario places increased emphasis on the ability of forest managers to prescribe sound practices and understand the impact of their actions. With limited resources, managers must efficiently identify stands that will respond positively to silvicultural treatments.

In response to this need, several regeneration prediction models have been developed for central hardwoods, including models for single species (Loftis 1990a), species groups (Sander et al. 1984, Gould et al. 2007, Steiner et al. 2008), and others for multiple species (Dey 1991, Marquis and Ernst 1991). An effort to develop a regeneration prediction model for Appalachian hardwood stands has resulted in the REGEN model by David Loftis of the USFS Bent Creek Experimental Forest (Loftis 1989). REGEN is an expert system that allows an expert user to assign competitive rankings to species-size combinations of advance reproduction based on regeneration strategy and local growth potential in model knowledge bases. Previous work has created knowledge bases for hardwood forests of the Blue Ridge physiographic province. Currently, efforts are being made to adapt the system throughout the Southern Appalachians. An effort to adapt REGEN to the Appalachians of Virginia and West Virginia is the primary topic of this thesis and the sole focus of Chapter 4.

Objectives

The goals of this project were to gain insight into regeneration trends of hardwood forests in the Appalachians of Virginia and West Virginia, and to use that information to adapt the REGEN model for the region. For these goals to be met 4 objectives were established.

1) Inventory advance reproduction of hardwood stands across the Appalachians of Virginia and West Virginia.
2) Inventory regeneration following clearcutting on hardwood stands across the Virginia and West Virginia Appalachians.
3) Adapt the REGEN model to the Appalachians of Virginia and West Virginia by creating REGEN knowledge bases.
4) Compare the model predictions to the information obtained from the inventories.

Additional Work

The data collected for evaluating the adaptability of the REGEN model also provided insight into the composition of mature Appalachian hardwood stands and adjacent stands regenerating following clearcutting. An attempt to summarize the species composition found in these stands and identify possible shifts in species composition following clearcutting was completed. The work described in Chapter 3 is the culmination of this effort.

2. LITERATURE REVIEW

Natural Oak Regeneration Ecology and Silviculture

OAK REGENERATION ECOLOGY

Natural regeneration of an oak forest is a complex process starting with flowering, fruiting, and seed dispersal from mature trees, followed by germination, seedling establishment, and growth (Johnson et al. 2002). The culmination of events that must transpire in order to ensure the successful establishment of a seed crop in any given year occurs only sporadically, creating ephemeral waves of regeneration cohorts (Johnson 1993b).

Oak Reproduction

Although oaks usually produce small crops of acorns annually, seed crops capable of producing a stand replacing population generally are initiated by a bumper crop of acorns which typically occurs only about one out of every four years (Olson 1974). Beck and Olson (1968) found that sound acorn production ranged from 6,600 to 94,600 per acre over the course of 3 yrs in a North Carolina upland hardwood forest. In central Pennsylvania, Steiner (1995) found a range of 540 to 198,510 northern red oak (*Quercus rubra*) acorns per acre over a 4 yr period across five stands.

Seed survival and germination is a problem in oak stands. Over the course of 12 yrs, Beck (1977) found that, on average, a third of fully developed acorns produced became infested with insects, varying from 29% in above average production years to 67% in poor years. Steiner (1995), found only 53.5% of total acorn production to be viable for northern red oak in central Pennsylvania. Steiner (1995) recorded only 7.9% of predation was due to insects.

Nearly 200 species of forest wildlife consume acorns (Beck 1993). Steiner (1995) found that losses due to wildlife could be as high as 38.6% of production, of which deer (*Odocoileus virginianus*) accounted for nearly half. Once acorns have fallen, they are quickly consumed by animals or deteriorate very rapidly. Auchmoody et al. (1994), found that burial of acorns 1 in below the surface resulted in a loss of about 50% of acorns to small mammals and insects compared to about 91% predation of surface sown acorns. Although these losses to wildlife are highly detrimental, their service as dispersal agents does not go unnoticed. Small mammals and birds play a vital role in regenerating oaks. Jays (C*yanocitta spp.*) and squirrels (*Sciurus spp.*)

bury acorns while caching, potentially dispersing acorns to sites more favorable to growth than if dispersed by gravity alone (Crow 1988). While dispersal of acorns by rodents and birds is an important means of distributing seeds, due to the amount consumed, it is only during years of heavy production that substantial numbers of acorns survive predation by wildlife (Johnson et al. 2002, Beck 1993). Autumn germination by white oaks (*Leucobalanus*) allows for the "escape" of some acorns from extended periods of predation (Johnson et al. 2002). In contrast, red oak (*Erythrobalanus*) acorns require a stratification period before germination in the spring, thus allowing for longer exposure to predation (Crow 1988).

Mature acorns must come to rest in a micro-environment suitable for fall germination in the case of the white oaks, or overwintering followed by spring germination for the red oaks. Both of these require particular temperature and moisture regimes, as well as protection from insects, rodents, and other wildlife. Beck (1993) warned that those acorns which avoid predation are still not guaranteed to germinate. Even sound, undamaged acorns only have 75-95% germinative rate (USDA 1974). Contact with mineral soil under a thin litter layer (around 1 in deep) enhances germination of all upland oaks (Burns and Honkala 1990). To germinate, moisture content of acorns must not drop below 30-50% for white oaks and 20-30% for red oaks (Korstian 1927). Incorporation in the litter layer prevents excessive drying of acorns (Beck 1993). Johnson et al. (2002) contend that the burial of acorns by natural means is likely the reason for the origin and regeneration of many, if not most oak forests.

Germination in all upland oaks is hypogeal (Burns and Honkala 1990). Establishment is best on loose soil which encourages root penetration (Burns and Honkala 1990). Initial establishment is favored on cool moist sites such as those on northeast facing slopes under shade (Johnson 1993b). Crow (1988) concluded that very early in development red oak germinants are similar in tolerance of shade to northern hardwoods because of reduced temperature and water stress. This tolerance of shade persists until the cotyledon reserves are depleted, thereafter survival and growth depends on the ability of the seedling to produce photosynthate and translocate carbohydrates (Crow 1988). Following germination, light intensity appears to be the most limiting factor affecting early growth (Burns and Honkala 1990). The most common oaks in the Appalachians range from intermediate to very intolerant of shade, most being intermediate (Burns and Honkala 1990). Carvell and Tryon (1961) found that greater amounts of sunlight reaching the forest floor led to more oak seedlings found. This presents a challenge for survival of oak germinants that emerged under the once favorable conditions found under dense canopies. Shoot development is slow, but primary roots develop rapidly (Burns and Honkala 1990). The rapid development of a taproot, which primarily serves as a food storage organ, at the expense of shoot growth is characteristic of all oaks (Johnson et al. 2002).

In order to continually grow, seedlings must maintain a positive carbon balance, that is, the amount of carbohydrate produced through photosynthesis must exceed that required for maintenance of existing structures (Pallardy 2007). When environmental conditions are such that these requirements cannot be met, the plant must become more efficient. This often leads the aboveground portion of the plant to die back either to a more sustainable size, or to the root collar where a large number of dormant buds await to develop under more suitable conditions (Larsen and Johnson 1998). Dormant vegetative buds are continually formed on new branches, thereby enabling sprouts to originate anywhere along the stem between the root collar and terminal bud (Johnson et al. 2002). Seedlings that have died back and resprouted are known as seedling-sprouts and are very common among Appalachian hardwoods (Kelty 1988). As a result of this trait, seedlings that appear to be young based on stature may, in fact, be considerably older than anticipated (Merz and Boyce 1956). The continued sprouting and subsequent dieback also increases the root to shoot ratio over time, enabling oak seedling-sprouts to develop large root systems which can respond with rapid growth when favorable environmental conditions do occur (Kelty 1988, Larsen and Johnson 1998, Sander and Clark 1971).

Larger hardwoods can also sprout when the stem is destroyed or looses vigor. Sprouts that originate from the stump of these larger trees are termed stump-sprouts. The development of stump-sprouts is biologically similar to seedling-sprouts; however, seedling-sprouts are somewhat arbitrarily defined as having a diameter less than 2 in dbh (Kelty 1988). In part, this distinction is due to the fact that the callused small stumps of seedling-sprouts are resistant to infection by pathogens (Kelty 1988). Seedling-sprouts are often the predominant form of oak reproduction (Johnson et al. 2002). Seedlings and seedling-sprouts that develop under the parent stand are referred to as advance reproduction. It has long been recognized that advance reproduction is crucial to the regeneration of oak (Carvell and Tryon 1961, Beck 1970, Sander 1972, McQuilkin 1975).

Oak Growth Strategy

Oaks exhibit a regeneration strategy that initially allocates more fixed carbon to root growth. This larger root system enables oaks to outcompete other species for belowground resources (Larsen and Johnson 1998), and is of great benefit on marginal to poor sites where water stress can be a limiting factor. Consequently, it is on these sites that oak regeneration is most successful (Lorimer 1993, Gould et al. 2005, Weitzman and Trimble 1957, Carvell and Tryon 1961, Cook et al. 1998). The more drought-tolerant of the upland oaks, which includes chestnut (*Quercus prinus* L.), scarlet (*Quercus coccinea* Muenchh.), and black (*Quercus velutina* Lam.) oaks in the Appalachians, often dominate stands on these sites. These sites typically occur on more southerly and westerly aspects on ridges, shoulder and backslopes (Meiners et al. 1984). The understory vegetation is usually a well developed shrub layer dominated by mountain laurel (*Kalmia latifolia*), huckleberry (*Vaccinium spp.*), and blueberries (*Vaccinium spp.*) with scattered pines (*Pinus spp.*) and a sparse oak overstory (Ross et al. 1986). Johnson (1993a) coined these sites "auto-accumulators" in that the environmental conditions are such that lead oak to be a climax species when present.

While vital to the regeneration of oaks on marginal to poor sites, the early growth strategy is often cited as a major hindrance to oak regeneration on highly productive sites where other species allocate more resources to height growth (Beck 1970, Trimble 1973b, McGee and Hooper 1975, Beck and Hooper 1986, Loftis 1990a, Loftis 1990b). Hodges and Gardiner (1993) introduced the "regeneration window" concept for oaks. This concept summarizes that the advantages provided to oaks by large root systems make the window of opportunity larger on more xeric sites, but competition becomes more intense with increased available resources, making successful oak regeneration more difficult.

Oaks are generally classified as intermediate in shade tolerance and the development of large root systems from repeated dieback and sprouting leaves potential for rapid height growth once released. This characteristic suggests an ecological reliance on disturbance for perpetuation on non auto-accumulating sites. "Mesophytic mixed hardwood forests generally occur where oak site index is greater than 65 ft (base age 50)" (Johnson et al. 2002). On these higher quality sites, oak should actually be considered a subclimax species (Crow 1988, Peet and Loucks 1977); likely succeeded by a mixed mesophytic forest in the Appalachians (Braun 1950). However, in many of these areas oak currently dominates the overstory. The fact that their dominance is widespread on many highly productive sites, and according to pollen records have been so for the past 6000 yrs (Delcourt and Delcourt 1985), implies that some disturbance regime must have occurred naturally or was anthropogenically practiced throughout the Appalachians (Lorimer 1993). Poor understanding of formative factors and subsequent influences that have contributed to the sustainment of oak forests have left researchers the task of rediscovering or simulating those influences in a predictable fashion. Whatever the cause for the historical dominance of oak in this ecosystem may have been, the situation appears to have changed rather abruptly following the turn of the 20th century. Several authors contend that the most plausible reasons for the decline in oak are fire suppression and restricted forest land clearing (Abrams 1992, Lorimer 1993).

Oak Regeneration Problems

Lorimer (1993) states that the "bottleneck" of oak regeneration is not in the seedling germination stage, as advance reproduction is often numerous. Cook et al. (1998) found when surveying oak regeneration literature that, of reported cases, there was none that averaged less than about 1000 seedlings per acre, with a region wide average of over 3600. Most oak regeneration is in the form of small seedlings and germinants which do not compete well with their associated species on high quality sites (Johnson et al. 2002). Newly established oak seedlings grow too slowly to compete with other species and cannot be considered a viable source of regeneration (Loftis 1990a). This phenomenon was plotted for a cohort of red oak seedlings (Loftis 1983a). Loftis (1983a) plotted the survival of this cohort of red oak seedlings growing in undisturbed conditions. The reported downward trend is typical for highly productive sites throughout the southern Appalachians.

Loftis (1990a) cautions that the presence of red oak advance reproduction does not ensure regeneration success. Beck (1970) found that height growth for advance red oak seedlings that were small before release only averaged about 1 ft in height growth per year. The tallest observed red oak seedling after 5 yrs was only 5.1 ft tall, compared to yellow-poplar (*Liriodendron tulipifera* L.), which may grow upwards of 15 ft in 5 yrs, and sprouts faster still (Beck 1970).

Sander (1972) reports that size of advance reproduction before harvest is critical. In order for oak regeneration to be successful post harvest there must be large advance regeneration present, at least 4.5 ft tall, and in sufficient numbers to occupy the stand (Sander, 1972). For this reason, seedling sprouts are often the most reliable variety of advance regeneration. Sander (1972) warns that the buildup of such advance reproduction could take 20 yrs or longer. Beck and Hooper (1986) suggest that perhaps even sapling size advance reproduction may be required in some scenarios. Loftis (1990a) showed that as site quality increases, the probability of a red oak attaining dominance is much lower for a given sized seedling.

REGENERATION SILVICULTURE

Natural regeneration is preferred in the Appalachians given the rough terrain, economic barriers, and poor success associated with artificial regeneration. Johnson et al. (2002) refer to this as the 'ecological model' in that it relies on existing vegetation as the source of regeneration. In many stands regeneration is an afterthought to the economic benefits of a harvest; therefore, the predominant methods of timber harvesting are commercial clearcutting, diameter limit harvesting, and other forms of high-grading (Johnson et al. 2002). Nyland (2002) declares that effective regeneration programs must have five key goals: 1) Make the results predictable, 2) Secure utilitarian species, 3) Realize an appropriate degree of site utilization by sought after species, 4) Set the stage for future management, and 5) Minimize chances of failure. Traditionally, in managed forests, one of several silvicultural systems is employed to regenerate a mature stand. Regeneration systems that are commonly used are typically divided into three categories: even-aged, two-aged, and uneven-aged. The regeneration period in these systems vary from relatively short periods of time to being essentially constant. For example, in even-aged systems the regeneration period may last for the last two and first two decades of a rotation, compared to continuous or frequent periods of regeneration for uneven-aged systems (Johnson et al. 2002).

Even-aged

"Even-aged systems remove the entire community of trees in one or more cuttings within a short time interval, creating a new cohort of trees all having comparable ages," (Nyland 2002). Smith et al. (1996) further define that the range of ages in an even-aged population must not exceed 20% of the rotation age. There are essentially three different harvest methods that when implemented properly, and completed, lead to the establishment of an even-aged community. Those three methods in order of initial harvest intensity are as follows: the clearcut method, the seed-tree method, and the shelterwood method.

Clearcut

Clearcutting removes all the mature trees in a single cut to make way for the new even-aged community (Nyland 2002). Clearcutting is a frequent regeneration method employed in Appalachian hardwood forests. Implementation is straightforward and the financial returns are maximized because of the high volumes extracted from a relatively small area (Johnson 1993a) Silvicultural clearcuts differ from commercial clearcuts in that silvicultural clearcuts remove all trees greater than approximately 2 in dbh to make room for the next generation. Silvicultural clearcuts avoid the dysgenic consequences of the commercial clearcut, which removes only the merchantable timber (Smith et al. 1996). Commercial clearcuts frequently create poorly-stocked, high-graded stands with little genetic potential to produce quality offspring for the subsequent stand (Nyland 1992). While clearcutting is a popular choice for industrial landowners, it has fell out of favor on public lands due to litigation and public distaste.

When implemented to regenerate oak dominated stands, results from clearcutting are variable. Without preharvest manipulation on oak dominated sites, the resultant postharvest regeneration depends on site quality. On the poorer sites (oak SI <65), oak regeneration is normally adequate to perpetuate dominance, or remain a significant portion of the new stand. On fair sites (oak SI 66-75), oak regeneration will be present but in fewer numbers than the parent stand. On the most productive sites (oak SI >75), oak regeneration is substantially fewer in number and significantly less competitive than other species and is not expected to be present in the subsequent stand with any considerable abundance. Key studies in North Carolina, Virginia, West Virginia, and Pennsylvania have all observed this trend (Beck and Hooper 1986, Ross et al. 1986, Trimble 1973b, Gould et al. 2005).

Beck and Hooper (1986), found that 20 yrs following the harvest of a North Carolina stand initially comprised of 53% oak and 33% yellow-poplar, the regeneration was dominated by yellow-poplar, black locust (*Robinia pseudoacacia* L.), red maple (*Acer rubrum* L.), and sweet birch (*Betula lenta* L.). Site quality was high for yellow-poplar reaching greater than 100 in areas. The oak component was minor and continued to decrease from previous observations by

McGee and Hooper (1975). Beck and Hooper (1986) concluded that aggressive shade-intolerants, particularly yellow-poplar, will dominate regeneration following clearcutting on good sites in the southern Appalachians. Beck and Hooper (1986) suggest that measures to foster competitive advance reproduction along with competition control are necessary to regenerate a large oak component.

In southwest Virginia, Ross et al. (1986) studied regeneration following the clearcutting of ten mid-slope stands in the Ridge and Valley physiographic province. Site quality ranged from poor (oak SI < 55) to medium (oak SI 55-75). Chestnut oak was the dominant species in most of these preharvest stands. Three years post harvest, density of well established oak advance reproduction was greatest on stands on the medium site, while decreasing on both better and poorer sites. The authors found that the success of advance oak reproduction was most highly correlated with preharvest advance reproduction density when they were included in the pre-harvest inventory.

Trimble (1973b) summarized that species composition was strongly influenced by site quality, and that in West Virginia clearcuts, on good to excellent sites, a good representation of black cherry (*Prunus serotina* Ehrh.) and yellow-poplar seedlings will be present if there is viable seed present, and on fair sites a variable number of oak stems will be present. After 7 yrs he found that all of the larger free-to-grow stems had at least one of the following characteristics: 1) great sprouting vigor (basswood (*Tilia Americana* L.), red maple, oak,), 2) shade tolerance permitting a start under the parent stand (sugar maple (*Acer saccharum* Marsh.)), 3) fast early growth (black cherry, hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), sweet birch), 4) tendency to root-sucker (black locust, sassafras (*Sassafras albidum* (Nutt.) Nees)).

In Pennsylvania, Gould et al. (2005) followed the post-harvest development of 90 previously oak-dominated stands across all three physiographic provinces and over the course of three decades. The authors found that oak-dominated stands basically follow one of four distinct developmental pathways following clearcutting: 1) The OAK pathway: maintains oak dominance throughout stand development, with stands averaging about 84% oak stocking in the third decade after harvest. 2) The MIXED pathway: leads to stands that lack a clearly dominant species in the third decade, but have significantly higher stocking levels of black birch and less common species than any other class. 3) The RED MAPLE pathway: contains stands with the highest stocking of red maple (about 70%). 4) UNSTOCKED: stands resulting from regeneration failures, with total stocking averaging only about 15%.

Gould et al. (2005) found that the MIXED pathway was the most common (34%) and the OAK pathway was the least (12%). RED MAPLE and UNSTOCKED were about equally as frequent (26% and 28% respectively). The authors also found that the OAK class occurred with equal frequency on the Ridge and Valley and Blue Ridge, but was absent from the Appalachian Plateau. The authors postulated that the overriding factor leading stands down the OAK pathway was the advance reproduction composition of the preharvest stands. The advance reproduction composition of the MIXED, RED MAPLE, and UNSTOCKED stands all differed from the OAK stands. As early as 2 yrs post-harvest, stands in the non-OAK classes showed no evidence of returning toward an oak dominated community. The authors were not able to draw any solid conclusions about what preharvest factors led to the establishment of adequate advance reproduction to steer development down the OAK pathway, but observed that stands in the OAK pathway were generally on drier sites and must have been auto accumulators. Factors such as browsing intensity, past overstory disturbances, or a seed crop shortly before harvest may have contributed to stands on more mesic sites.

Studies throughout the southern and central Appalachians as well as across the entire central hardwood region have found difficulty or failure in regenerating oak-dominated stands back to oak via the clearcut method, observing species shifts to faster growing more shade-intolerant species on the higher quality sites. Hilt (1985a), observed the same trend across Ohio, Kentucky, and Indiana. Several other studies have noted this pattern as well (Elliot et al. 1997, Brashears et al. 2004, Johnson 1993a, Loftis 1989).

Seed-Tree

The seed-tree method removes most of the mature trees in one cut, but retains widely-spaced, seed-bearing residuals to serve as a seed source for the new even-aged community (Nyland 2002).

Wendel and Trimble (1968) began a study in West Virginia evaluating stands regenerated via the seed-tree method. The preharvest stands were well-stocked and had not been disturbed by cuttings or fire for the previous 35 yrs. Three site qualities were observed: oak site index 60, 70, and 80. Predominant species were: hickories (*Carya spp.*), sugar maple, northern red oak, white ash (*Fraxinus americana* L.), and black cherry on the excellent site (SI 80). Yellow-poplar, northern red oak, hickories, chestnut oak, and white oak (*Quercus alba* L.) on the good site (SI 70), and chestnut oak, northern red oak, blackgum (*Nyssa sylvatica* Marsh.), and white oak on the fair sites (SI 60). The number of seed-trees left varied by site quality. Three years later the authors found no difference in the total number of stems of reproduction among varying site classes. They found a higher percentage of sprouts on the good and fair sites as compared to the excellent site. Sugar maple was found to be the most numerous species on the excellent and good sites. Sassafras was the most numerous on the fair site. Sweet birch and yellow-poplar were also common species 7 yrs post harvest.

Trimble (1972) re-examined the study and found that site quality had a strong influence on species composition. Yellow-poplar, black cherry, and sugar maple were more abundant on the excellent site; sassafras, red maple, and oaks were more numerous on the fair site. The good sites were found to be transition zones for species composition and had higher numbers of species. Northern red oak was the most numerous sawtimber sized tree on the excellent sites preharvest, but constituted only a very small proportion of the reproduction. The author did not feel that the seed-trees had an appreciable effect on species composition or abundance.

At 12 yrs post harvest, Smith et al. (1976) proclaim that the seed-tree method is not required for adequate regeneration. After 12 yrs, 85% of all sample plots were stocked with commercial species. Sugar maple and sweet birch accounted for 70% of the total commercial species on the excellent site, sugar maple made up 45% of the good site, and red maple, sweet birch, and northern red oak made up 52% of commercial stems on the fair sites. The results of this seed tree harvest essentially follow the same trend as the previously discussed clearcuts, with the exception of sugar maple making up a more significant component of the reproduction.

Johnson (1993a) concluded that the seed-tree method generally should not be recommended for oak regeneration because the seed-trees provide too little reproduction too late in the regeneration period; but, it can be used to sustain acorn production for wildlife objectives if good seed producing trees are left.

Shelterwood

The shelterwood method establishes an even-aged community under the protection of residuals from the parent stand that will eventually be removed in a series of successive cuts (Nyland, 2002). A textbook shelterwood harvest can include a sequence of harvests including: a preparatory cut to favor crown expansion and increase seed production, an establishment cut that prepares the seed bed, and a removal cut to serve as the final release of the reproduction (Johnson et al. 2002). The shelterwood method has shown great potential for regenerating oak forests given the increased ability to manipulate light conditions and maintain seed sources prior to complete overstory removal. There are several variants of the traditional shelterwood system and researchers and forest managers alike have often advocated some form of it for oak regeneration. However, it is well documented that this technique alone is unreliable, and often unsuccessful in achieving desirable oak regeneration. Researchers have modified shelterwood harvests in combination with competition control to reduce the midstory and understory of mature forests, which often are the primary detractors of adequate oak advance reproduction survival and development. These variations will be discussed in the following sections in greater detail. The primary focus of this section is the results of the application of a basic shelterwood using only harvest intensity to manipulate the regeneration of oak-dominated stands. In theory, the shelterwood appears to be the ideal solution to the struggles associated with oak regeneration, there is sufficient light available to favor the establishment of oak reproduction, but not so much as to allow fast growing intolerants to dominate the reproduction as frequently occurs in clearcut and seed tree harvests. In practice, traditional shelterwoods have yielded mixed results.

Johnson et al. (1989) observed the successful regeneration of two oak-dominated forests in Wisconsin. Site index for northern red oak across the range of the study varied from 60 to 70. The first stand was regenerated using three successive cuts: reducing the basal area from 123 to 103 ft^2 per acre with the first cut, further reducing it to 75 ft^2 per acre 10 yrs later, and finally reducing it to 60 ft^2 per acre 6 yrs after that. All of the removals were from below. Five years later, the overwood was completely removed. Eleven year results found that northern red oak made up a third of the total stems and a quarter of the total basal area in the stand, and 34% were at or above mean stand diameter. The second stand was regenerated using two cuts: the first reducing basal area from 96 ft^2 per acre down to 63 ft^2, the second cut 8 yrs later completely removed the overwood. Eleven growing seasons after the final harvest there were 804 northern red oak trees per acre, most being more than 5 ft tall. The largest oak per sample plot averaged 16.6 ft tall compared to the average competitors 20 ft tall.

Researchers in West Virginia found that the results of shelterwood harvesting failed to establish oak reproduction after 10 yrs on stands dominated by northern red oak, chestnut oak, and white oak that also included red maple, sugar maple, sweet birch, and yellow-poplar, (Schuler and Miller 1995). Overstory treatments reduced residual stocking to 75% and 60% of upland oak stocking on two different sites, and an uncut control stand was monitored. Selection of residual trees favored oaks for seed production and a uniform spacing. After ten growing seasons, the establishment of northern red oak seedlings greater than 1 ft tall was low. Before treatment, there was an average of 1,154 red oak seedlings less than 1 ft tall per acre. After 5 yrs, many were recruited into larger size classes; however, at years seven and ten, total numbers of oak seedlings taller than 1 ft declined with increased competition from other species responding to the initial treatment (Schuler and Miller 1995). The authors noticed that greater reductions in basal area triggered a response in recruitment of smaller oak seedlings into larger size classes, though the effect was ephemeral. The faster growing species became established and surpassed oak seedling development in total height and competitive position. The authors warned that attempts to establish oak through partial overstory reductions could create conditions that favor the establishment of species from shade-tolerant to shade-intolerant. Schuler and Miller (1995) concluded that successful oak regeneration on high quality sites in West Virginia is not achieved by simply manipulating stand stocking levels alone (Schuler and Miller 1995).

Two-aged

In order to establish a two-aged community there is essentially one harvest method implemented: the deferment, or leave-tree method. To establish two-aged communities, most of the mature trees are removed to make room for regeneration, but the remaining widely-spaced mature trees are retained for an indefinite period of time (Nyland 2002). The deferment cut was introduced to ameliorate aesthetic concerns associated with clearcutting (Smith et al. 1989). After a deferment cutting the stand resembles a seed-tree cut; however, the residuals are not harvested when regeneration is established (Smith et al. 1989). Stringer (2002) states that the potential continued sexual reproduction in the deferred stand may be important for sporadic seed producers such as oak. This continued seed production will aid in the establishment of advance reproduction to facilitate long-term maintenance of oak.

In West Virginia, Smith et al. (1989) installed a deferment cut on areas with site index for northern red oak of 70 and 55. All trees 1 in dbh and larger were cut except for about 12-15 deferment trees per acre, representing about 20 ft^2 of basal area per acre. Those deferred were selected for potential timber value among dominants and codominants with no signs of decay. Though results were incomplete, reported reproduction after 5 yrs was similar to a clearcut. Both intolerant and tolerant species were abundant with yellow-poplar and sugar maple being the most numerous. Miller et al. (2006) followed up on the study and found that 20 yrs after the harvest, yellow-poplar, black cherry, red maple, and sweet birch made up most of the dominant and codominant reproduction. Sugar maple and northern red oak were present, but in relatively smaller proportions. The authors assert that the growth of reproduction near the reserved trees has been slowed and that the likelihood of intolerants reaching the canopy diminishes with closer proximity to reserve trees.

Thomas-Van Gundy and Schuler (2008) reported on 20 and 25 yr results of the four deferment cuts first described by Smith et al. (1989). Regeneration is pole sized and yellow-poplar dominates in all but one stand. Black birch is also prevalent. Although beech (*Fagus grandifolia* Ehrh.) and sugar maple dominated the advance reproduction preharvest, the postharvest dominance of yellow-poplar reflected the open conditions and influence of nearby deferred yellow-poplar as a seed source. These sites were not dominated by northern red oak preharvest, and the absence of oak regeneration is no surprise, given the low amount of oak advance reproduction and its gradual relegation to overtopped status. The authors suggest that most regeneration methods would have lead to a decline of oak, but offer that retention of oak in the overstory can serve as “insurance” for the future by continuing to be a source of regeneration.

Uneven-aged

Uneven-aged communities are created, and subsequently maintained by some sort of selection system. The two types most commonly used are the single-tree selection and group selection methods.

Single-Tree

Single-tree selection removes individually selected mature trees more or less uniformly across a stand (Nyland 2002). The single-tree method is potentially feasible for those stands that intrinsically accumulate oak, although the sustainability is yet to be verified (Johnson et al. 2002). Given the economics involved with such applications, the practice is questionable, and in general is not considered a viable regeneration method for oak (Johnson et al. 2002). Della-Bianca and Beck (1985) found that single-tree selection in the Southern Appalachians failed to recruit desirable reproduction into larger size classes, and in the absence of desirable shade-tolerant species single-tree selection is unsustainable.

Group-Selection

Group-selection removes all mature trees in small groups across the stand (Nyland 2002). Typical opening sizes range from 0.2 to 0.5 ac (Johnson et al. 2002). The group-selection method is essentially the combination of even-aged harvesting techniques under area or volume regulation at the stand level. This creates a collection of different even-aged groups that, when collectively considered a stand, form a reverse-j shaped diameter distribution typical of an uneven-aged stand. Small groups are successively harvested within a stand until the entire stand has been regenerated.

Smith (1981) studied the effects of different size openings on hardwood stem development in West Virginia. Ten year results indicated that to gain the silvicultural effects of larger clearcuts, groups should be at least 0.5 ac in size. He predicted that on fair sites (oak SI 60), openings 50 ft in diameter will be dominated by red maple, oaks, and beech, but in the larger openings (150 ft and 250 ft), red maple, oaks, and sweet birch should dominate. On good sites (oak SI 75), sugar maple will dominate smaller openings (50 ft and 100 ft), and yellow-poplar, black cherry, and sweet birch will dominate on the larger openings (150 ft, 200 ft, 250 ft).

Dale et al. (1995), in a study across West Virginia, Illinois, Ohio, and Kentucky, found that the number of stems per acre increased with opening size. Shade-tolerants constituted a greater proportion of the smaller openings (<0.5 ac) while intolerants increased in larger openings. They also found that site quality had an effect on species composition, and observed more oaks and red maples on fair sites while sugar maple dominated the good growing sites.

After 50 yrs of three types of partial harvesting across three site qualities (northern red oak SI 79, 69, and 59) in West Virginia, one of which was group selection (0.5 ac openings), Schuler (2004) found that although northern red oak and chestnut oak were the two most abundant species preharvest, sugar and red maple were the two most abundant species postharvest. Other than the maple, beech and black birch increased in importance as well. Oaks were less abundant overtime, while sugar maple, yellow birch (*Betula alleghaniensis* Britton), black birch, and beech became more abundant through time. Unmanaged and single-tree selection showed the greatest trend towards shade-tolerants and the author postulated that the group selection openings may provide canopy gaps large enough to avoid said trend.

Miller et al. (1995) observed with group openings of 0.4 ac in size that species composition is dominated by black birch, sugar maple, black cherry, yellow-poplar, and American basswood.

Weigel and Parker (1997) observed in Indiana that although the parent stands were oak-hickory dominated forests, after group selection those stands will include a diversity of species dominated by yellow-poplar. Oak-hickory was the least abundant species in the regeneration.

Silviculture Overview

According to Johnson (1993a), even-aged management became the “modus operandi” in the 1960’s for much of the upland hardwood community. It was accepted because it met ecological requirements of intolerant commercial species (including oak), it was economically efficient, and much easier to implement than uneven-aged management schemes (Johnson 1993a). Clearcutting was the most widely recommended regeneration method (Roach and Gingrich 1968), although its success was limited to more xeric sites (Ross et al. 1986). Environmental activism created negative perceptions of clearcutting and practices were modified to ease this concern, but further decline in use, especially on national forests, has shifted focus toward alternative harvesting strategies (McGee 1987). The shelterwood method became popular, and shows potential (Loftis 1990b, Brose and Van Lear 1998), albeit with potentially socially unacceptable variations.

The shelterwood method shows potential for oak regeneration; but without special considerations, species that are much more competitive than oak often increase in height and exhibit dominance over the remaining reproduction. With too little light available shade-tolerant species create a mid and understory that suppress the intermediate oak regeneration. Even when released, as in group-selection, if the openings are not large enough, the shade-tolerant advance reproduction that had accumulated under the preharvest shaded conditions grows rapidly.

When oak forests are regenerated by clearcutting, seed-tree, or large group-selection openings the intolerant competition expresses dominance early. Species such as yellow-poplar have the ability to persist in the canopy for relatively long times, and are unlikely to relinquish their dominance. While seed-tree harvesting invariably favors intolerants, some partial harvesting systems such as deferment, shelterwoods, and group selection have the potential to provide ideal conditions for either shade-tolerant or shade-intolerant competition depending on implementation. It is obvious that, in most cases, classical regeneration systems have failed to regenerate desired quantities of oak. This paradox, and obvious flaw, in classical silvicultural systems for oak regeneration on highly productive mesic sites has become a growing concern of researchers and land managers (Holt and Fischer 1979, Smith et al. 1988, Loftis and McGee 1993). Schuler and Miller (1995) advise prudence when harvesting high quality sites if oak regeneration is an objective, and suggest partial retention of oaks until adequate oak regeneration is achieved to ensure a future oak component following harvest.

TREATMENTS TO ENHANCE OAK REGENERATION

The development of silvicultural techniques to facilitate the regeneration of oaks on productive sites has been a primary objective of upland hardwood research for decades. As a result of those decades of research, several methods intended to facilitate oak regeneration have been tested. Most of these methods involve fire, partial harvesting, or herbicides.

As Sander (1972) established, the key to successful oak regeneration is numerous, large advance reproduction. In addition to advance reproduction, managers can expect some contribution to the next stand from stump-sprouts in most cases in the Appalachians. Though stump-sprouts are highly competitive, their contribution to future stands is sometimes problematic. First, not all stems will produce sprouts, and the probability that a stem will sprout decreases with increasing diameter and age (Johnson 1977). Second, it is commonplace for multiple low quality stems to emerge from a single stump (Ross et al. 1986). It has been observed that silvicultural treatments can impact stump-sprouting probability as well. Partial harvesting practices such as deferment and shelterwood harvests reduce stump-sprouting of upland oak in the Appalachians compared to clearcutting (Atwood et al. 2008). This trend was also observed in the Missouri Ozarks, with upland oak sprouting frequency generally decreasing as residual basal area increased (Dey et al. 2008).

Preharvest Techniques

Since large advance regeneration is difficult to obtain, and given the superior growth rates of stump-sprouts it is suggested that a reasonable goal for treatments designed to enhance oak regeneration is to provide sufficient numbers of large advance reproduction to augment the expected contribution from stump-sprouts (Sander et al. 1976).

Prescribed Fire

The Native American burning practices of periodic, low intensity fires are generally considered to be a key formative process in the establishment and maintenance of pre-European Appalachian oak forests (Van Lear and Watt 1993, Lorimer 1993). Following the settlement of these areas by Europeans the occurrence of fire has undergone several radical shifts. As landscape scale logging became more feasible with the introduction of railways across the rugged topography of the Appalachians, fire became more frequent and much more intense (Brose et al. 2001). With the establishment of the national forests in the early 20th century and introduction of the Smoky Bear campaign mid century, fire was all but removed from the Appalachian landscape (Brose et al. 2001). This suppression for the last 60 yrs is thought to be a primary reason for the decline in regeneration of fire-adapted species (Lorimer 1993). As this trend has become more widely recognized, there has been increased interest in restoring the practice of periodic, low intensity prescribed burning to facilitate the perpetuation of oak dominated forests.

Prescribed Fire Alone

Fire has the potential to facilitate oak regeneration by improving seedbed conditions, discouraging acorn predation, and improving light conditions in the understory by controlling fire-intolerant competitors (Van Lear and Watt 1993). The hypogeal germination of oaks combined with early belowground allocation of resources helps to favor the survival of oak during a fire as opposed to red maple and yellow-poplar which have epigeal germination (Brose and Van Lear 1998). Research results have been mixed, however, regarding the improvement of oak regeneration with prescribed burning. Several researchers have found that prescribed burning alone does little to enhance the regeneration of oak forests (Arthur et al. 1998, Blankenship and Arthur 2006, Hutchinson et al. 2005). The literature suggests that single prescribed fires do not facilitate oak regeneration, but may, in fact, promote competition. Repeated fires have had more short-term success in developing advance oak reproduction, however this strategy remains unrefined.

Wendel and Smith (1986) found that 5 yrs after a late April prescribed fire in West Virginia, 66% of overstory trees were damaged and 5% were killed. The authors predict that if the stand were harvested soon after the burn that red maple and black locust would be major components of the next stand. The authors cite poor timing as the principal reason that oak reproduction was not improved. Because there were few stems of advance oak reproduction present prior to the burn, the authors speculate that to improve the establishment and growth of oak advance reproduction the overstory must first be opened and the understory reduced prior to a good seed crop, using several light fires to control competition until the oak reproduction reaches a competitive size.

Arthur et al. (1998) observed that a single March prescribed fire promoted red maple regeneration, as well as the sprouting of mid and understory blackgum and sourwood on a xeric Kentucky ridge. A March wildfire 2 yrs later also increased the number of red maple and blackgum sprouts per tree, but reduced overall sprouts per acre. Blankenship and Arthur (2006) found that repeated late winter fires on three ridges in Kentucky substantially reduced midstory density and effectively top-killed red maple; however, 4 yrs after burning ceased density rebounded for red maple, but not oak. The authors suggest that stand manipulation using a longer term combination of thinning, herbicide, and fire may be necessary to successfully regenerate oak and that burning later in the spring may have a greater impact on the fire sensitive species.

Barnes and Van Lear (1998) observed three upland hardwood stands in the South Carolina Piedmont using three burning treatments. A series of three winter burns ranging from December to January was carried out on one stand, a single spring burn in mid-April on another, and the remaining stand was left unburned. The authors found that a single spring burn reduced mid/understory density by 54%, the same amount as three winter burns. Oak density in the mid/understory was reduced by 76% and 84% by the spring and winter burns respectfully. Yellow-poplar, the most serious competitor present, was reduced 71% by winter burns. Burning increased the root to shoot ratio of oaks while improving seedbed conditions and xerifying the site.

Hutchinson et al. (2005) found in southern Ohio that March and April fires substantially reduced sapling density. However, as in other studies, the authors reported only a short-lived decrease in red maple abundance. The authors also observed that sugar maple was not as sensitive to top-kill by fire as red maple. Repeated prescribed burning, both twice and four times, failed to consistently alter the competitive status of oak seedlings relative to shade-tolerant competition, and the authors speculated that burns later in April would likely have a greater impact on maple sprouting.

Shelterwood and Burn

Because of the inconsistent results achieved from prescribed burning alone, researchers have investigated the use of shelterwood harvests followed by a prescribed fire to facilitate oak regeneration (Loftis 1990b, Brose and Van Lear 1998). On a stand in Georgia, Loftis (1990b) reduced basal area by 0, 10, 20, 30, and 40% from below along with a cut-stump herbicide application and followed 1 yr later with an April prescribed fire to study the impact of basal area reduction and fire on oak advance reproduction. Loftis (1990b) observed that although basal area reduction increased basal diameter growth of oak advance reproduction, burning did not. Burning also failed to control the development of other regeneration and decreased red oak seedling survival. Loftis (1990b) conceded that a single prescribed fire shows little promise for regenerating red oak.

Brose and Van Lear (1998) conducted two winter burns (February), a spring burn (April), and summer burn (August) on three hardwood stands in the Virginia piedmont that had received a shelterwood harvest 2-4 yrs earlier. The authors found that regardless of season, all fire treatments reduced density of red maple and yellow-poplar; however, spring and summer burns reduced density more than winter burns. Mortality varied by fire intensity and season of burn with high intensity spring burns creating the largest deficits in non-oak to oak mortality. The spring burn caused 92% and 74% mortality for yellow-poplar and red maple, respectively, compared to only 26% mortality for oak. Summer burning caused the greatest decrease in oak and hickory density, but there was no difference between spring and winter burning. Oak stem form was improved by burning. Two years after the fire treatments, yellow-poplar, followed by red maple, was the most common, tallest, and fastest growing species in the control. Oak density increased in the stands burned in the spring and winter compared to pre-burn conditions. In the burning treatments, density of oak regeneration was equal, or greater, than red maple and yellow-poplar. Growth rates were similar. The authors suggest allowing several years to elapse following a shelterwood harvest before a prescribed fire is conducted. This will allow oak reproduction to develop sufficient root systems so that sprouting will be vigorous following top-kill, as well as allowing seed of yellow-poplar stored in the forest floor to germinate, thereby becoming vulnerable to surface fires. The authors also suggest medium to high intensity spring burning during leaf expansion due to the significant reduction in yellow-poplar and red maple density with minimal oak loss, as well as more favorable burning opportunities compared to summer.

Brose et al. (1999) revisited the stands initially described by Brose and Van Lear (1998) a year later and found that in the unburned control, yellow-poplar outnumbered oak eight to one, while in the burned treatments both species were equivalent. Within the fire treatments, oak reproduction was most abundant in the high intensity spring burn (66% stocking) and low to medium intensity summer burn (60% stocking); yellow-poplar density was highest in the control (77% stocking) and was reduced with greater fire intensity. Yellow-poplar occurred in clusters, whereas oak was uniformly distributed. Oak was in a more competitive position in the burned areas compared to the control. Growing space for oaks increased as fire intensity increased. The authors found an average of about 172 and 147 free to grow oak stems per acre for spring and summer burns respectively, with free to grow oaks being the most numerous in the high-intensity spring burn with about 337 stems per acre. While these numbers are lower than the recommended guidelines of 433 stems per acre by Sander et al. (1976), they are nonetheless an improvement upon otherwise existing conditions. The authors predict that areas receiving high intensity spring and summer burns will likely develop into oak-dominated stands comprised of 75-80% oak (Brose et al. 1999).

Herbicides

Although there are no herbicides that can be broadcast to release oak from hardwood competition, herbicides can be used as part of a silvicultural system designed to regenerate oak. Undesirable species can be targeted with individual tree applications, which can remove them from the regeneration pool. Herbicides alone however, cannot ensure the development of oak reproduction, there must be favorable germination and growing conditions in place to ensure that a population of oak seedlings can develop (Loftis 1983b). Most research concerning the use of herbicides to facilitate oak regeneration is an attempt to find a combination of harvesting and herbicide application that will foster the establishment of a cohort of oak advance reproduction while simultaneously controlling competition to ensure oak will maintain a dominant position in the developing stand.

Preherbicided Clearcut

Johnson and Jacobs (1981) studied the regeneration of an oak dominated Wisconsin stand (red oak SI 70) with a shrub layer comprised primarily of hazel (*Hamamelis spp.*), dogwood (*Cornus spp.*), blackberry (*Rubus spp.*), and fern. The understory was treated with an application of 2,4,5-T twice to ensure mortality of all understory vegetation prior to a clearcut harvest that followed a moderately good acorn crop. Five years later, the authors found an average of 2,872 red oak seedling and seedling-sprouts per acre, most of which were less than 5 ft tall. Dominant competitors averaged 7.3 ft tall. The authors reasoned that because most of the reproduction originated from the preharvest seed crop, the herbicide treatment created more favorable conditions for seedling establishment and development compared to a shelterwood harvest studied simultaneously. The authors contend that although the regeneration in the clearcut is relatively small, it is abundant (1,500 2-4 ft tall seedlings per acre), and well distributed with 41% of plots observed containing free to grow oak, and that given sufficient competition control, the possibility of regenerating oak without any advance reproduction could potentially be achieved if harvests coincided with good acorn crops.

Shelterwood and Herbicide

Because the shelterwood harvest method allows for the most flexibility during the regeneration period, researchers have studied several variants of this method in conjunction with other silvicultural tools. Schlesinger et al. (1993) studied the effect of ten different shelterwood treatments on Missouri Ozark stands. Three different levels of overstory stocking (40, 50, or

60%) were combined factorially with three understory herbicide treatments (heavy, medium, or none), as well as the addition of a prescribed burning treatment to the 50% overstory stocking treatment. The authors found that the prescribed burning treatment was as effective as the heavy understory treatment. For the average site (SI 60), the number of large oak saplings per acre was significantly greater in the 40% overstory stocking treatment. Although understory treatment had no statistical effect, the number of large oak saplings was greatest for the heavy understory treatment under a 40% overstory with 588 stems per acre. The authors postulate that in order to develop adequate oak advance reproduction it may be necessary to reduce non-oak competitors by prescribed fire or herbicide while retarding the development of future competition with a denser overstory. This process will require more than 10 yrs and additional understory treatments to complete. The authors conclude that the shelterwood system has the potential to be adapted to the regeneration requirements of oaks, although there is not likely to be a universal prescription.

After reviewing the failure of several shelterwood variants in the Southern Appalachians, Loftis (1983b) proposed that in order to favor oak, a shelterwood method must maintain a high residual basal area that impedes yellow-poplar development, while eliminating the sub-canopy to prevent subsequent sprouting of competition. If this is achieved the survival of oak should respond similar to what is illustrated by Loftis (1983a). This concept led Loftis (1990b) to develop a shelterwood method to regenerate red oak in the Southern Appalachians. The study was located in North Carolina on high quality sites ranging from oak site index of 80 to 96. Prior to stand manipulation, northern red oak acorns were direct seeded to simulate the development of a catch of natural seedlings following a bumper acorn crop. Four treatments were implemented in a factorial combination of two canopy treatments, which consisted of removing 20% of the basal area of main canopy trees, and a sub-canopy treatment which eliminated all sub-canopy stems 0.6 in dbh or greater with a herbicide. Nine years following application, the treatments significantly increased basal diameter and survival of red oak seedlings, with both overstory and understory treatments increasing basal diameter, but only the overstory treatment affected survival. The results of this study culminated in a prescription of basal area reduction from below using herbicides to 60, 65, and 70% of initial basal area for oak site indices 70, 80, and 90 respectively, to create stand conditions capable of enhancing the development of established northern red oak advance reproduction. Loftis (1990b) suggested that this treatment should be carried out at least 10 yrs prior to overstory removal to allow for the development of oak into a competitive position before release. If successful, the height response should follow a trend similar to that illustrated by Loftis (1983a). Loftis (1990b) cautioned, however, that this prescription facilitates the development of established seedlings, rather than promoting establishment, and offered that underplanting may be an option to obtain such reproduction quickly, although new seedlings are usually abundant following a bumper acorn crop.

Schuler and Miller (1995) conducted a similar treatment in West Virginia. Two overstory density treatments and control were combined factorially with an understory herbicide treatment and control to attempt to establish oak seedlings. These treatments were unsuccessful in establishing natural or planted oak seedlings.

Postharvest Treatments

Ideally, following a regeneration harvest there will be sufficient numbers of developing oak seedlings capable of populating a fully-stocked mature oak dominated forest with high-quality individuals. In reality, this is the exception rather than the rule. Mast production may be sparse, or when present in sufficient numbers, seedlings may be subjected to severe competition, even under a shelterwood (Zaczek and Lhotka 2004). In this case of inadequate oak regeneration, there still remain options for the landowner to rehabilitate the regeneration pool. For natural regeneration the primary tool available is crop-tree management to encourage the survival and growth of small seedlings into competitive saplings.

Early crop-tree release is the most often discussed treatment in young stands. Lamson (1989) defines it as, “The selection and release of individual trees by eliminating stems that compete with or are likely to compete with the crop tree.” Smith and Lamson (1986) suggest that crop-trees should be of high-value, high-quality, competitive, and vigorous. Perkey and Wilkins (2001) provide detailed guidelines for selection and management of many upland hardwood trees. Smith and Lamson (1983) summarize many previous studies of crop-tree release and the reported success or failure of each. Heitzman and Nyland (1991) also provide a summary of crop-tree release in northern hardwoods.

Smith and Lamson (1983) indicate that crop trees are released to maintain codominance, manipulate species composition, accelerate growth, and to reduce rotation length. The majority of the literature commonly reports two different methods used to achieve release. The first is a crown-touching technique where all stems are removed that are in direct competition with the crop-tree crown. The second is a fixed-radius release in which all woody competition is removed within a given distance from either the crop-tree stem or crown. Release is usually carried out via mechanical means using chainsaws, brushsaws or hand tools. It is also applied chemically using injection or basal applications. Stem injection involves the application of 1-2 ml of pure or diluted herbicide into a wound in the cambial layer (Zedaker 1986). Basal applications are applied directly to lower portions of the stems of unwanted vegetation such that the chemical spreads around the stem with minimal loss (Zedaker 1986).

Trimble (1974) studied seven-year-old red maple stump-sprouts and northern red oak advance reproduction in West Virginia. Dominant and codominant red maple stump-sprouts and dominant, codominant, and intermediate northern red oaks were also released within a 5 ft radius. After 5 yrs, there was improved diameter growth for red maple and intermediate northern red oak and improvement in crown class regression and survival, but no height growth improvement for either species and retarded natural pruning. Trimble (1974) concluded that if a crop-tree release is to be made, it should be postponed until the stand is 15 ft tall, or in the presence of grapevine, 25 ft tall.

Lamson and Smith (1978) released nine-year-old dominant, codominant, and intermediate yellow-poplar, northern red oak, black cherry, and sugar maple from competition within a 5 ft radius in West Virginia. After 5 yrs, only intermediate northern red oak and codominant black cherry showed significant height growth response, but dominant yellow-poplar height growth was significantly less for released stems. Released codominant and intermediate yellow-poplar and codominant northern red oak had significantly greater diameter growth. Codominant northern red oak and intermediate yellow-poplar had significantly shorter lengths of clear bole, and crown-class regression was prevalent among all classes and species. The authors concluded that young stands of sugar maple, northern red oak, yellow-poplar, and black cherry should not be released until the dominant and codominant crop-trees are about 25 ft tall, instead of the 16 ft stems that were released in this study.

Wendel and Lamson (1987) chemically released-8-12-year-old black cherry, northern red oak, and sugar maple comparing glyphosate injection within a 5 ft radius of the crop-tree stem and glyphosate injection of competition using the crown-touching technique in West Virginia.

Codominant and intermediate black cherry, codominant, intermediate, and suppressed northern red oak, and intermediate sugar maple were treated. After 5 yrs, there was no significant difference for height growth, but significantly greater diameter growth for all released trees except suppressed northern red oak, greater survival except for codominant black cherry and intermediate sugar maple, and greater crown-class retention compared to control stems. The authors recommended releasing intermediate black cherry and sugar maple, but not northern red oak. The authors also cautioned that chemical release may not be appropriate for stump-sprout origin crop-trees.

Generally older stands (> 10 yrs) have more consistent responses to crop tree release (Smith and Lamson 1983). Research suggests that crop-tree release treatments not be conducted until crown closure is achieved and dominance has been expressed (Trimble 1971, Trimble 1973a). Further, it has been advised to postpone release treatments until dominant and codominant trees are about 25 ft tall, especially if there is a significant presence of grapevine (Lamson and Smith 1978, Trimble 1973a). Trimble (1971) recommends selecting and mechanically releasing crop trees in the dormant season to speed along the process due to easier access, however cautioned that care should be given not to underestimate the effects of nearby competition of surrounding trees when the canopy is bare. Wendel and Lamson (1987) recommend that chemical release via injection be carried out when stems are dormant or approaching dormancy because sap flow can force chemical out of the incision. Kochenderfer et al. (2004) indicate that injection in the Appalachians should be restricted to the growing season between June and November to avoid sap flow.

Across all of the reported cases on crop-tree release, a few overriding trends seem to emerge. The first trend reported by most researchers is the lack of response in height growth to crop-tree release (Trimble 1973a, Trimble 1974, Smith 1977, Lamson and Smith 1978, Lamson and Smith 1989, Smith and Lamson 1983, Wendel and Lamson 1987, Miller 2000). The second trend found is the positive response of diameter growth to release (Trimble 1974, Della-Bianca 1975, Lamson and Smith, 1978, Lamson and Smith 1989, Smith and Lamson 1983, Wendel and Lamson 1987, Johnson et al. 1998, Miller 2000, Kochenderfer et al. 2001). Lamson and Smith (1978, 1989), Trimble (1973a, 1974), and Miller (2000) all report that released stems did not develop a clear bole as rapidly as unreleased stems. Wendel and Lamson (1987), Trimble

(1973a, 1974), and Della-Bianca (1975) all reported a survival advantage for released crop-trees, although Della-Bianca (1975) cautioned that crop-tree release did not ensure survival. While release from competition artificially positions crop-trees in the dominant category; it is often found that this effect is short lived. Most studies have shown that across both released and control treatments crown-class retrogression is commonplace (Smith and Lamson 1983, Lamson and Smith 1978, and Trimble 1973a). However, Wendel and Lamson (1987), Trimble (1974), Miller (2000), and Smith (1977) all reported greater retention of crown-class among released stems compared to unreleased crop-trees. Often too few trees are removed to have a remarkable impact on species composition. A more attainable goal is to ensure the survival and dominance of select desirables in the new stand.

REGENERATION PREDICTION

Prior to the implementation of any silvicultural action aimed at fostering oak regeneration an estimate of regeneration potential should be obtained. Rogers and Johnson (1998) review various approaches to regeneration modeling previously taken. For practicing foresters, perhaps the most useful regeneration models are those that are predictive in purpose. These models provide information that can assist with management decisions. There are several predictive regeneration models that have been published for eastern hardwood forests. A key distinction can be made between those that are intended to evaluate adequacy and those that provide a more quantitative output.

Although models have been used in forestry for over 250 yrs, models for mixed species stands began to appear in the first half of the 20th century (Porté and Bartelink 2002). Early models were primarily forest yield tables. Following the acceptance of initial floristics (Egler 1954) and secondary succession as the primary method of forest development in managed forests, and the development of upland oak stocking guides (Gingrich 1967) along with the recognition of the impact of advance reproduction size on the success of oak regeneration (Sander 1972), probabilistic models and resulting management guidelines were developed to evaluate regeneration potential in oak dominated forests (Sander et al. 1976, Sander et al. 1984). These models were intended to serve as management tools to be used by practicing silviculturists and forest managers. Sander et al. (1976) published an evaluation guide for advance reproduction. Adequate regeneration was considered to provide 30% stocking of dominant or codominant oak when mean stand diameter is 3 in, which requires 221 dominant or codominant stems. To meet this requirement, an estimated 433 stems of advance reproduction 4.5 ft or taller are necessary based on projected success rates. The number of stump-sprouts required to offset a given deficiency in advance reproduction based on the probability of a stump to produce a dominant or codominant sprout at target is provided as well. Sander et al. (1984) provided updates for their previous guide including more detailed probability rates for successful stems resulting from stump-sprouting considering site index, dbh, and age of the parent tree. Updates were also made to the success probabilities for advance reproduction stems of various heights, groundline diameters, and site qualities (aspect and slope positions).

The concepts behind the regeneration evaluations and guidelines by Sanders et al. (1976, 1984) can, and have been applied to a variety of regions; however, long term empirical data would are required to amend success rates given regional differences in competition composition and intensity. Other researchers have developed evaluation guides for different regions and often include prescriptions based on output (Steiner et al. 2008, Johnson 1980).

Other models are more quantitative in nature, and provide some numerical output of expected successful regeneration. Loftis (1990a) and McQuilkin (1975) developed models for single species following clearcutting by tracking advance reproduction from pre harvest and remeasuring at some point post harvest. McQuilkin (1975) developed probabilities of various types of white oak advance reproduction (new seedlings, seedling-sprouts, stump-sprouts) to attain a height of 15 ft, 10 yrs post harvest in the Missouri Ozarks. After conducting an advance reproduction survey the model provides the number of white oak stems that are expected to be 15 ft at ten yrs post harvest. Loftis (1990a) developed a similar type model for northern red oak following clearcutting in the Southern Appalachians. By tracking advance reproduction from preharvest to 8 yrs post harvest across a variety of site qualities, Loftis (1990a) derived projected probabilities for an advance reproduction stem of a given basal diameter to become dominant or codominant 20 yrs post harvest for site index 70, 80, and 90. Using these probabilities in conjunction with an advance reproduction survey provides the number of expected dominant and codominant northern red oak stems at age 20. Researchers have developed similar models for only stump-sprouts (Dey et al. 1996, Gould et al. 2007). Numerous growth models have been developed in which quantitative results of regeneration models could be projected to rotation including: FVS (Dixon 2003), OAKSIM (Hilt 1985b), TWIGS (Miner et al. 1988), NE-TWIGS (Hilt and Teck 1989), STEMS (Belcher et al. 1982), and FIBER (Solomon et al. 1987).

There are computer based models that combine several single species models similar to those described above into one program. Dey (1991) developed a computer based model that predicts height and diameter distribution at multiple stand ages as well as stocking values and diameter class by species at age 21 for several important species in the Ozark Highlands. Solomon and Leak (2002) developed FOREGEN, a computer based regeneration prediction model for northeastern hardwoods adapted from the FORET framework (Shugart and West 1977). FOREGEN simulates percent species composition 3 yrs following harvest for openings of various sizes using user specified options considering a variety of factors affecting regeneration (Solomon and Leak 2002). FORCAT was developed by Waldrop et al. (1986) to model stand development on the Cumberland Plateau. Marquis and Ernst (1992) describe a stand analysis, prescription, and management simulator for the Alleghenies (SILVAH). The primary focus of SILVAH is to provide prescription and management guidelines to forest managers based on stand inventories and selected objectives. These prescriptions and guidelines are based on regional research trials and experiences.

A key issue concerning regeneration models is the target. Among published regeneration models, the point at which regeneration is predicted can be quite variable. In part, the development of regeneration models is limited by the amount of available data and the requirement of multiple long-term datasets to properly calibrate the models. Communities are in a constant state of flux during the regeneration period post harvest. This combined with considerable regional differences in composition of eastern hardwood forests, data requirements, and limited resources has not allowed for a disciplinary established standard age in which conditions become stable enough to reliably reflect a future state. Further complicating standardization is the intended use of output from regeneration models. However, the third decade of stand development is often used as a benchmark of the end of the regeneration period (Steiner et al. 2008, Sander et al. 1984, Dey 1991).

3. Characteristics and Composition of Developing Appalachian Hardwood Forests Following Clearcutting

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ABSTRACT

We examined species composition using data from 41 paired stands on subxeric or submesic sites on the Appalachian Plateau in West Virginia. Paired stands contained a mature stand free from known recent disturbance adjacent to a regenerating clearcut of similar site quality that was harvested within the past 20 yrs. All observed tree species were placed into one of eight species groups: 1) black cherry, 2) conifers, 3) maples, 4) midstory, 5) oaks, 6) other overstory, 7) pioneer, or 8) yellow-poplar. We compared the mean proportion of species composition for each species group between the mature and regenerating stands. In addition, only the upper canopy (dominant and codominant) species composition of the regenerating stands was compared to the composition of all stems ≥ 1.5 in dbh in the mature stands for each species group. Black cherry, pioneer, and yellow-poplar groups were significantly more common in regenerating stands compared to mature stands in both site classes. Maples were significantly less common in regenerating submesic stands, but nominally remained the most common group in regenerating stands across both site classes. Although oaks were less common in regenerating stands across both site classes than in mature stands, these changes were not significant. Clearcutting in Appalachian hardwood stands appears to have resulted in stands regenerating numerous commercial species. Our results suggest that the future identity of stands regenerating following clearcut harvests will likely differ somewhat from previous rotations. Oaks will likely assume a smaller role as the clearcuts mature, particularly on the submesic sites.

INTRODUCTION

Appalachian hardwood forests are some of the most diverse in the United States. Complex geologic, climatic, and anthropogenic influences have allowed a variety of species to thrive in close proximity. More than 50 important species are present in mixed hardwood stands across the Appalachians (Smith 1994); with over 20 commercial species commonly found (Miller and Kochenderfer, 1998). These mixed stands contain species representing vastly different silvical characteristics (Burns and Honkala 1990). The forests in the region are maturing and shifting into larger diameter classes (Oswalt and Turner 2009). The ecological variety of commercial species provides potential for many silvicultural systems to be used to harvest these maturing forests depending on management objectives. Greater than two-thirds of the forestland in the Appalachians is under the ownership of nonindustrial private holders (Smith 1994). In West Virginia, about 79% of the timberland is held by nonindustrial private landowners, about 9% by forest industry, and about 12% in public ownership (USDA 2000). Given this array of landowners, it is understandable that the management of this vast resource provides opportunities as diverse and challenging as the region itself.

Partial harvesting, particularly selection cutting, was the method of choice in the first half of the 20th Century (Smith et al. 1996). Around midcentury, even-aged management, primarily clearcutting, was increasingly recommended for upland central hardwoods (Roach and Gingrich 1968, Sander and Clark 1971). This was largely in response to unfavorable results from partial harvesting and to remedy degradation from past neglect (McGee 1987). Clearcutting was widely accepted because it was ecologically and economically efficient, and simple to implement (Johnson 1993). Clearcutting typically regenerates fully stocked stands of commercial species (Roach and Gingrich 1968). The resulting composition is often initially dominated by early successional species such as yellow-poplar (*Liriodendron tulipifera* L.), black locust (*Robinia psuedoacacia* L.), sweet birch (*Betula lenta* L.), and black cherry (*Prunus serotina* Ehrh.) when seed sources are available (Trimble 1973, McGee and Hooper 1975, Hilt 1985).

In the early 1960s, even-aged management became national forest policy and was subsequently prescribed throughout National Forests in the Appalachians (Yarnell 1998). The intense public debate about clearcutting on the Monongahela National Forest that followed ultimately led to the National Forest Management Act of 1976 and the ensuing controversy has shifted management focus back towards alternative partial harvesting systems (Roth and Harmon 1995). Apart from social concerns, the longstanding grievance of clearcutting as a silvicultural technique has primarily been unfavorable oak (*Quercus spp.*) regeneration resulting from harvests without adequate advance reproduction (Sander et al. 1976, USDA 1971, Holt and Fischer 1979). Despite this, clearcutting is still a widely practiced regeneration technique, and the implications of post harvest species composition can be far reaching. Therefore, this study was conducted to examine the differences in species composition between stands regenerating following clearcutting and older mature stands across a portion of the Appalachian Plateau in West Virginia.

METHODS

This study was conducted using a paired stand sampling approach. Using this approach, at each study site a mature hardwood stand free from known recent disturbance was located adjacent to a regenerating stand of similar site characteristics (aspect, slope, topographic position) that was harvested via clearcut within the past 20 yrs. The regenerating stands ranged from 5 to 18 yrs post harvest with an average of 11 yrs. This approach assumes that the two stands were once contiguous and of similar composition and productivity. It is further assumed that if any mature stand were harvested it would regenerate in a similar fashion to its paired regenerating stand. Stand histories were based on the best available knowledge and records of the landowners. A total of 41 paired stands were located within the Allegheny Plateau and the Allegheny Mountains sections of the Appalachian Plateau Physiographic Province within West Virginia (Fenneman 1938). Paired stands were located across 5 counties including 4 in Fayette, 16 in Greenbrier, 13 in Nicholas, 6 in Tucker, and 2 in Webster (Figure 3.1). These paired stands were under the ownership of a variety of public and private entities. Because of the complex assemblages of species that occur across this area we created eight species groups for data analysis: 1) black cherry, 2) conifers, 3) maples, 4) midstory, 5) oaks, 6) other overstory, 7) pioneer, and 8) yellow-poplar. Species groups are composed of either a single species that is numerous throughout the area, or a collection of species that are expected to occupy similar stand structural positions (Table 3.1).

Paired stands were sampled between May and September, 2008 using a systematic grid with a plot spacing of 165 ft and a row spacing of 264 ft. The distance from the stand boundary to the first plot was randomly determined. A total of up to 20, 0.004 ac plots were installed at a density of one plot per acre in each mature stand. At each plot, basal area of all stems ≥ 1.5 in dbh was measured using a 10 BAF prism, advance reproduction within the plot was tallied by species and height class (Large: ≥ 4 ft, Medium: ≥ 2 ft, Small: < 2 ft, Germinant: newly germinated seedlings), and dbh of all stems ≥ 1.5 in dbh within the plot was measured. Regenerating stands were sampled at a density of one plot per acre, using 0.001 ac plots unless stands had developed such that plots were frequently unpopulated. In this case, sample plots were reestablished as 0.004 ac plots throughout the stand. In the regenerating stands, regeneration was tallied by species, stem origin (seed or sprout), and crown class (dominant, codominant, intermediate, suppressed).

To ensure similar site productivity between the paired mature and regenerating stands, measurements of slope, aspect, and landscape position were used to estimate site index using the Forest Site Quality Index (Meiners et al. 1984). Paired stands were also placed into site classes based on indicator species using the method proposed by McNab et al. (2002). In this ecological classification system, certain species serve as indicators of moisture and nutrient availability and provide insight into relative site quality. We applied the species moisture weights from this methodology to a list of species present at each mature stand to classify sites into one of four moisture regimes: xeric, subxeric, submesic, and mesic. All sites in our study fell within subxeric or submesic regimes with 32 paired stands in the submesic regime and 9 paired stands in the subxeric regime.

Tests for normality indicated that the data did not fit a normal distribution. Therefore, the Wilcoxon Signed Rank test, a nonparametric analog to a paired *t*-test, was used to test for differences about the sample distribution medians (Ott and Longnecker 2001). Data analyses were conducted using the UNIVARIATE procedure in SAS® version 9.2 (SAS 2007). To compare species composition between the mature and regenerating stands two separate analyses were used within each site class. The first analysis compared the species composition in the regenerating stands considering all crown positions to that of all stems ≥ 1.5 in dbh in the mature stands. The second analysis considered only stems in the upper canopy (dominant and codominant) crown positions in the regenerating stands to that of all stems ≥ 1.5 in dbh in the mature stands. All analyses were conducted using the mean species composition expressed as a proportion from each sample stand for each species group to reduce the impact of variable stand ages on comparison analyses. Therefore, species composition proportions reported in the statistical analysis in Tables 3.5 and 3.6 may not be numerically equivalent to proportions computed from the stand summaries of stems per acre provided in Tables 3.2 and 3.3.

RESULTS

Overstory basal area of the mature stands was similar across both site classes, averaging 100 ft^2/ac in the subxeric stands and 115 ft^2/ac in the submesic stands (Table 3.2). Oaks comprise the largest proportion of basal area in the mature stands on both site classes, making up about 72% of the basal area in mature subxeric stands, but only about 29% in mature submesic stands. Maples were second behind oaks in basal area on both site classes, and comprised about 26% of the basal area in mature submesic stands but only 14% in mature subxeric stands. Stand densities ranged from 412 stems per acre in the mature subxeric stands to 372 stems per acre in the mature submesic stands (Table 3.2). Maples had the most stems per acre in mature stands of both site classes comprising 40% of all stems in the subxeric and 34% in the submesic stands. Oaks were over twice as numerous in the subxeric compared to the submesic stands, with 118 stems per acre in the mature subxeric stands, but only 48 stems per acre in the mature submesic stands. Black cherry was not present in the mature subxeric stands, and pioneer and yellow-poplar groups were limited as well. In contrast, yellow-poplar and black cherry each comprised about 10% of the basal area in mature submesic stands (Table 3.2).

Advance reproduction averaged just over 6500 stems per acre in the mature subxeric stands, and over 7000 in the submesic stands (Table 3.3). The midstory species group is the most common group of advance reproduction in large and medium size classes in mature stands on both site classes. Maples become more common in small and germinant size classes. Both maples and midstory species make up the bulk of all advance reproduction (≈70%) and dominate the large advance reproduction in mature stands on both site classes. The midstory group makes up about 49% of all 498 stems of large advance reproduction in mature subxeric stands and about 47% of all 589 stems of large advance reproduction in mature submesic stands. Maples were about 27% of the large advance reproduction in mature subxeric stands and about 30% in the mature submesic stands. Large oak advance reproduction was limited, averaging only 39 stems (≈8%) in mature subxeric stands and 24 stems (≈4%) in mature submesic stands. Advance reproduction of pioneer and yellow-poplar were limited in both site classes. The few conifers present as advance reproduction were mostly large hemlocks (*Tsuga spp.*). Black cherry was rare in the mature subxeric stands, and although more common in mature submesic stands, was limited to the small and germinant size classes.

Adequate regeneration occurred following clearcutting on both the subxeric and submesic sites, with an average of 3436 stems per acre and 5158 stems per acre respectively (Table 3.4). There were 1666 stems per acre in the upper canopy (dominant and codominant crown classes) of the regenerating subxeric stands and 1955 stems per acre in the upper canopy of regenerating submesic stands. Maples were the most common group in the lower canopy positions in both subxeric (≈26%), and submesic regenerating stands (≈25%). Maples were also the most common group in the upper canopy of regenerating subxeric stands (≈30%), but pioneer species were the most numerous in the upper canopy of the regenerating submesic stands (≈25%). Oaks were the second most numerous species in the upper canopy of the regenerating subxeric stands, with 380 stems per acre, or about 23% of all upper canopy stems. Oaks were less common in the upper canopy of the regenerating stands on the submesic sites, with only 129 stems per acre or about 7% of the upper canopy. Yellow-poplar exhibited similar numbers of stems per acre in the upper canopy of regenerating stands in both site classes, but was slightly more numerous in submesic stands. Although black cherry, pioneer, and yellow-poplar were virtually nonexistent in the mature subxeric stands they had a larger representation in the regenerating subxeric stands. Conifers were nearly absent in stands of both site classes.

Comparisons of species composition for each species group between the mature and regenerating stands on both site classes are displayed in Table 3.5. In this analysis, stems of all crown positions in the regenerating stands were compared to all stems ≥ 1.5 in dbh in the mature stands. Compared to mature stands, the black cherry, pioneer, and yellow-poplar species groups were significantly greater in proportion in regenerating stands while maples made up a significantly smaller proportion on both site classes. Despite the significant increase from mature subxeric stands, black cherry only comprised 2% of total stand proportion in regenerating subxeric stands. The difference in proportion from the mature to the regenerating subxeric stands was greatest for yellow-poplar which increased on average from 0 to 12% of stand proportion. There were no significant differences in proportion between the mature stands and regenerating stands for other species groups on subxeric sites. More significant changes were found for submesic stands. On submesic sites, conifers, maples, and other overstory groups made up a significantly smaller proportion in regenerating stands than mature stands, but maples were nominally the group of greatest proportion in regenerating stands. In contrast, black cherry, pioneer, and yellow-poplar species groups are all significantly greater in regenerating submesic stands and collectively made up about 45% of stand proportion. Pioneer species displayed the greatest differences between the mature and regenerating submesic stands increasing by an average of 16% of stand proportion.

Because the upper canopy of regenerating stands is often considered to provide the greatest insight into future species composition, statistical analyses were conducted to compare the species composition of all stems ≥ 1.5 in dbh in the mature stands to the upper canopy species composition of the regenerating stands on each site class (Table 3.6). On subxeric sites, this analysis showed that the proportions of the midstory, pioneer, and yellow-poplar species groups were significantly different in regenerating stands compared to mature stands. Both yellow-poplar and pioneer species were significantly greater in the upper canopy of regenerating stands on subxeric sites compared to the mature stands. The midstory group had a significantly smaller representation in the upper canopy of the regenerating stands compared to their proportion of all stems in the mature stands on subxeric sites. On submesic sites, black cherry, pioneer, and yellow-poplar were all significantly greater in the upper canopy of regenerating stands and collectively made up about 56% of the upper canopy stems. Pioneer species displayed the greatest increase from the mature to regenerating stands on submesic sites. Maples and midstory species were significantly fewer in the upper canopy of the regenerating stands compared to mature species composition on submesic sites. Conifer species were significantly fewer in regenerating submesic stands to nearly nonexistent levels. Oaks did not experience significant differences on either site class.

The mean proportion of upper canopy stems of sprout origin for all eight species groups are presented in Table 3.7 for both the subxeric and submesic site classes. Most of the upper canopy maples and oaks in both site classes are of sprout origin. Sprout origin reproduction is also a considerable component of upper canopy reproduction for the midstory, other overstory, and submesic black cherry. On average, all upper canopy yellow-poplar reproduction in subxeric stand is of seed origin either from sources stored in the forest floor or disseminated post harvest.

DISCUSSION

The mature stands in both site classes were dominated by oaks in terms of basal area (Table 3.2), but maples were the most abundant species group (Table 3.4). Similar to past research, the more shade-tolerant species groups, including both maples and midstory species, dominate advance reproduction across both site classes as shown in Table 3.3 (Bowersox and Ward 1972, Trimble 1973). Following clearcutting, these typically slower growing species are expected to be outcompeted by more aggressive shade-intolerants (McGee and Hooper 1975), with the exception of red maple, which is typically competitive (Tift and Fajvan 1999). This is due, in part, to the high sprouting propensity of maples (Table 3.7). In fact, red maple is widely recognized as a species increasing in abundance and importance throughout its natural range (Fei and Steiner 2007), and has shown to regenerate successfully in clearcuts (Loftis 1989) and across a variety of site qualities (Hilt 1985). However, Oswalt and Turner (2009) did not estimate large increases in red maple populations throughout the Appalachians. Although maple was statistically smaller in proportion in regenerating stands compared to mature stands in both site classes (Table 3.5), on average, maples nominally made up the greatest proportion of all stems in regenerating stands of both site classes. Given their shade tolerance and density, the presence of maples is expected to persist through development. The majority of the midstory group, however, is already occupying the lower canopy of the regenerating stands (Table 3.4).

The species composition of regenerating stands across this study is similar to other reported studies. Following clearcutting, previously oak dominated stands are often initially dominated by early successional species such as yellow-poplar, black locust, cherries, and sweet birch when seed sources are available (Beck and Hooper 1986, Trimble 1973, Hilt 1985). The dominance of pioneer species in the upper canopy of regenerating submesic stands suggests that these stands may be developing similarly to the mixed pathway described by Gould et al. (2005). The increased presence of yellow-poplar in this study may be attributable to geography and would likely necessitate an additional pathway for stands farther south (McGee and Hooper 1975). However, the developmental pathways described by Gould et al. (2005) are designated as such according to, amongst other things, stand stocking, which was not calculated in this study.

Black cherry, yellow-poplar, and pioneer species groups were significantly greater in proportion in the regenerating stands on both subxeric and submesic site classes compared to mature stands (Table 3.5). The pioneer species, which are comprised of short-lived species, are expected to be only a minor component later in the rotation of the regenerating stands. The increased status of yellow-poplar, however, is expected to be a lasting one considering the duration of superior height growth (Doolittle 1958), and relative longevity compared to typical rotation lengths. Black cherry is expected to persist as well. These species were infrequent as advance reproduction, with the exception of black cherry germinants, particularly in submesic stands (Table 3.3). Many species, including black cherry have shown greater tolerances to shade early in development compared to larger specimens (Marquis 1990). These early successional species produce ample seed regularly, and can successfully regenerate from seed sources stored in the forest floor prior to harvest and dispersed post harvest. This successful reliance on sexual reproduction is obvious considering the low proportion of sprout origin upper canopy reproduction from these species in the regenerating stands (Table 3.7). Apart from black cherry in the submesic stands, at least 75% of the upper canopy reproduction for black cherry, pioneer, and yellow-poplar was of seed origin. Seed from some of these species, particularly yellow-poplar and pin cherry, can remain viable for several years in the forest floor (Burns and Honkala 1990). Mean sprout origin reproduction proportion for black cherry and yellow-poplar in the submesic stands (Table 3.7) is likely higher than in the subxeric stands due to the greater occurrence of these species prior to harvest (Table 3.2).

The influence of site quality on species composition has long been recognized (Carvell and Tryon 1961, Doolittle 1958, Weitzman and Trimble 1957). Oak advance reproduction was most abundant in subxeric mature stands (Table 3.3), but even on these sites, large oak advanced reproduction is limited to only 39 stems per acre, well below the recommended 433 stems by Sander et al. (1976) for successful oak regeneration. The high proportion of oaks that were of sprout origin in the upper canopy of the regenerating stands on both site classes is likely a reflection of inadequate advance reproduction (Table 3.7). While a numerical lack of advance reproduction is seldom reported in the Appalachians (Cook et al. 1998), inadequate size is often cited as contributing to the displacement of oak dominance following harvest of any kind (Sander 1972, Loftis 1990b, Steiner et al. 2008). Without adequate advance reproduction, oaks and other shade intermediate species with slower initial growth rates are often less successful at regenerating except on sites of poorer quality (Bey 1964, Roach and Gingrich 1968, Sander 1972). Oaks were indeed of greater proportion of the upper canopy in subxeric regenerating stands than in submesic regenerating stands (Table 3.6). This is to be expected according to previous studies (Ross et al. 1986, Hilt 1985, Elliot et al. 1997). Our results for upper canopy oaks were somewhat more optimistic than reports from the Southern Appalachians (Beck and Hooper 1986), but are in line with Hilt (1985). Hilt (1985) found that oaks made up approximately 30% of the upper canopy on medium quality sites, and about 10% on good quality sites in clearcuts across Indiana, Kentucky, and Ohio. This is similar to our subxeric and submesic figures for oaks respectively; however, oaks only averaged 19% of the upper canopy in subxeric stands in this study (Table 3.6).

Although stand means were slightly lower in the complete stand analysis and upper canopy analysis for oaks in regenerating stands compared to mature stands of both site classes (Tables 3.5, 3.6), the lack of statistical difference was contradictory to what was expected based on other works (Loftis 1989, Beck and Hooper 1986, Johnson et al. 2002). While these results are encouraging, the longevity of these stems is not certain. In the Southern Appalachians, upper canopy red oak at age 20 is expected to be about half as numerous as at age eight (Loftis 1990a). In Connecticut, only about 44% of codominant red oak stems at stand age 25 are expected to remain so to age 55 (Ward and Stephens 1994). This indicates potential for significant mortality of oak stems that were in the upper canopy of the regenerating stands. Hilt (1985) found that oak reproduction is generally below 30% of the upper canopy regardless of site quality through the first 15 yrs of development, after which oaks dominance begins to be expressed where it occurs. Oaks are expected to be a strong component moving forward in subxeric regenerating stands. In all likelihood, oak will play a reduced role as the regenerating submesic stands mature compared to that of previous rotations. Additional management activities such as precommercial release treatments may improve the survival of existing upper canopy oak stems through stem exclusion (Ward 2009) and are often suggested (Elliot et al. 1997, Roach and Gingrich 1968). However, the success of these treatments is not guaranteed (Trimble 1974, Smith and Lamson 1983, Heitzman and Nyland 1991).

The greater success of oak regeneration following clearcutting that was observed in this study has been observed by others. Kabrick et al. (2008) found that in Missouri, red oaks only regenerated successfully following clearcutting compared to single-tree selection, group selection, and single-tree/group selection combination systems. Poor oak regeneration is often reported following one of two scenarios: clearcutting on high quality sites (Beck and Hooper 1986, Trimble 1973, Elliot et al. 1997) and partial harvesting in the presence of a dense shade-tolerant understory (Della-Bianca and Beck 1985, Schuler 2004, Trimble 1965). While aggressive shade-intolerants, primarily yellow-poplar, typically dominate clearcuts on high quality sites, shade-tolerant maples are often favored by partial harvesting. As a result, partial harvesting systems are often less successful at regenerating desirable species than even-aged systems in central hardwood forests on all but the highest quality sites.

There is growing concern over the impacts of partial harvesting systems that are currently being applied, particularly diameter-limit harvesting (Kenefic and Nyland 2006, Miller and Kochenderfer 1998, Schuler 2004). Fajvan et al. (1998) found that 80% of timber harvests in West Virginia were some form of diameter-limit harvest. Recent research has shown that partial harvesting practices, including deferment and shelterwood harvests, reduce stump-sprouting of upland oak in the southern Appalachians compared to clearcutting (Atwood et al. 2008). This was also observed in the Missouri Ozarks (Dey et al., 2008). Stump-sprouts are the most reliable forms of advance reproduction (Table 3.7) and are important sources of oak regeneration in the Southern Appalachians (Cook et al. 1998). Harvesting practices that inhibit stump-sprouting make successful oak regeneration increasingly unlikely without intensive management.

CONCLUSIONS

Clearcutting oak dominated stands on subxeric and submesic sites on the Appalachian Plateau in West Virginia appears to have successfully regenerated stands with numerous commercial species. In areas where large clearcuts are undesirable, group selection openings greater than about a half acre in size can mimic the regeneration of larger clearcuts (Trimble 1973, Smith 1981, Dale et al. 1995). The increased light levels in the bordering uncut stands resulting from these openings has also been observed to allow existing oak reproduction to develop successfully (Loftis 2004). Species composition in strip clearcuts is also comparable to results from this and other studies of larger clearcuts (Brashears et al. 2004).

Our results suggest that the future identity of stands regenerating following clearcut harvests will likely differ from previous rotations. More mesophytic, shade-intolerant species and maples are the dominant species groups in many regenerating stands at this point in stand development. Temporal shifts in species composition are expected during stand development. Although the current dominance of pioneer species is expected to be short-lived, the increased role of black cherry and yellow-poplar will likely remain throughout the rotation. Oaks appear to have successfully regenerated on the subxeric sites and will likely be a major component as these stands mature. The future for oaks is more uncertain on the submesic sites. Given the apparent inadequacy of oak advance reproduction found in mature stands of both site classes, the species composition of the regenerating stands is not surprising. Oaks will likely assume a smaller role as the clearcuts mature, particularly on the submesic sites, but are still a species to manage for following clearcutting through the second decade of stand development, possibly beyond.

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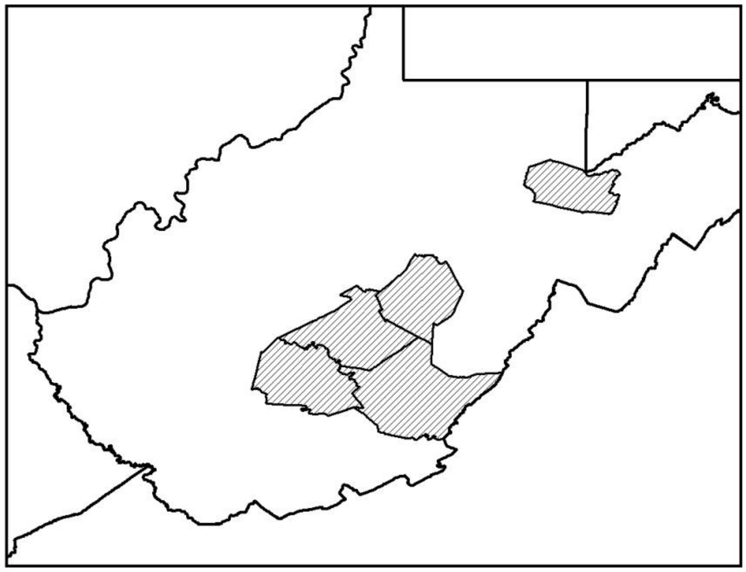
FIGURES

Figure 3.1. Location map of the study area on the Appalachian Plateau in West Virginia. Shaded areas represent counties in which sample stands were located.



TABLES

Table 3.1. Species groupings used in this study on the Appalachian Plateau in West Virginia.

Group	Species Included
Black Cherry	black cherry (*Prunus serotina* Ehrh.)
Conifers	e. white pine (*Pinus strobus* L.), hemlock (*Tsuga spp*.), red spruce (*Picea rubens* Sarg.)
Maples	red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.)
Midstory	Am. chestnut (*Castanea dentata* (Marsh) Borkh.), Am. beech (*Fagus grandifolia* Ehrh.), Am. holly (*Ilex opaca* Ait.), blackgum (*Nyssa sylvatica* Marsh.) dogwood (*Cornus spp*.), e. hophornbeam (*Ostrya virginiana* (Mill.) K. Koch.) sassafras (*Sassafras albidum* (Nutt.) Ness.), serviceberry (*Amelanchier spp*.), sourwood (*Oxydendrum arboretum* (L.) DC.), striped maple (*Acer pensylvanicum* L.)
Oaks	black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), northern red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.)
Other Overstory	ash (*Fraxinus spp*.), basswood (*Tilia spp*.), cucumbertree (*Magnolia acuminata* L.), Fraser magnolia (*Magnolia fraseri* Walt.), hickory (*Carya spp*.), yellow buckeye (*Aesculus octandra* Marsh.), yellow birch (*Betula alleghaniensis* Britton.)
Pioneer	Am. sycamore (*Platanus occidentals* L.), bigtooth aspen (*Populus grandidentata* Michx.), black locust (*Robinia psuedoacacia* L.), pin cherry (*Prunus pensylvanica* L.f.), sweet birch (*Betula lenta* L.)
Yellow-poplar	yellow-poplar (*Liriodendron tulipifera* L.)

Table 3.2. Mean composition of all 41 mature stands sampled on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes.

Species Group	Subxeric (n=9)				Submesic (n = 32)			
	BA		TPA		BA		TPA	
	Mean	SE ±	Mean	SE ±	Mean	SE ±	Mean	SE ±
	…(ft^2/ac)…		…(stems/ac)…		…(ft^2/ac)…		…(stems/ac)…	
Black Cherry	0	0	0	0	11	4	18	6
Conifers	3	2	12	10	5	2	20	8
Maples	14	3	166	27	30	3	128	11
Midstory	6	2	85	26	9	1	65	9
Oaks	72	7	118	15	33	5	48	9
Other Overstory	4	2	26	15	12	2	49	10
Pioneer	1	1	4	4	4	1	15	5
Yellow-poplar	0	0	1	1	11	2	29	7
Total	100		412		115		372	

Table 3.3. Mean species composition of advance reproduction in all 41 mature stands sampled on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes. Large (≥ 4ft tall), Medium (≥2ft. – 4ft tall), Small (< 2ft tall), Germinant (newly germinated seedlings).

Species Groups	Subxeric (n = 9)					Submesic (n = 32)				
	Advance Reproduction Size				Total	Advance Reproduction Size				Total
	Large	Medium	Small	Germinant		Large	Medium	Small	Germinant	
	…(Stems/ac)…									
Black Cherry	0	0	0	6	6	3	9	113	549	674
Conifers	31	2	0	0	33	19	0	3	1	23
Maples	134	47	315	2184	2680	176	72	579	2028	2855
Midstory	244	170	619	790	1823	278	233	558	1074	2143
Oaks	39	113	520	892	1564	24	54	368	456	902
Other Overstory	46	51	101	169	367	58	38	135	114	345
Pioneer	4	0	11	50	65	13	4	5	13	35
Yellow-poplar	0	0	0	4	4	18	2	31	36	87
Total	498	383	1566	4089	6536	589	412	1792	4271	7064

Table 3.4. Mean species composition of all 41 regenerating stands sampled on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes. Lower canopy values are for stems classified as suppressed and intermediate crown positions. Upper canopy values are for stems classified as codominant and dominant crown positions.

Species Group	Subxeric (n = 9)					Submesic (n = 32)				
	Lower Canopy		Upper Canopy		Total	Lower Canopy		Upper Canopy		Total
	TPA	SE ±	TPA	SE ±		TPA	SE ±	TPA	SE ±	
					…(Stems/ac)…					
Black Cherry	38	29	45	38	83	526	308	331	140	857
Conifers	16	10	0	0	16	1	1	7	4	8
Maples	458	59	498	159	956	818	125	300	59	1118
Midstory	398	87	101	54	499	635	101	316	154	951
Oaks	385	108	380	173	765	181	33	129	30	310
Other Overstory	107	39	146	42	253	219	36	133	30	352
Pioneer	157	139	283	256	440	448	73	488	134	936
Yellow-poplar	211	87	213	82	424	375	76	251	49	626
Total	1770		1666		3436	3203		1955		5158

Table 3.5. Mean species composition comparison across all 41 paired stands on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes. Mean values are calculated from individual stand proportions for each species group. P values less than 0.05 indicate significant differences about the distribution medians between mature and regenerating stands as calculated by the Wilcoxon Signed Rank test.

Species Groups	Subxeric (n = 9)			Submesic (n = 32)		
	Mature	Regenerating	P Value	Mature	Regenerating	P Value
	…(%)…			…(%)…		
Black Cherry	0	2	0.0313	5	8	0.0458
Conifers	3	1	0.5000	5	0	0.0039
Maples	39	29	0.0547	37	24	0.0055
Midstory	22	15	0.5703	18	17	0.7011
Oaks	29	22	0.2500	12	8	0.0706
Other Overstory	5	11	0.5469	13	8	0.0428
Pioneer	2	8	0.0156	4	20	<0.0001
Yellow-poplar	0	12	0.0039	7	17	0.0095
Total	100	100		100	100	

Table 3.6. Mean upper canopy species composition comparison across all 41 paired stands sampled on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes. Mean values for are calculated from individual stand proportions for each species group. P values less than 0.05 indicate significant differences about the distribution medians between mature and regenerating stands as calculated by the Wilcoxon Signed Rank test. Stem composition values in the mature stands consider all stems ≥ 1.5 in dbh. Stem composition values for the regenerating stands consider only dominant and codominant stems.

Species Groups	Subxeric (n = 9)			Submesic (n = 32)		
	Mature	Regenerating	P Values	Mature	Regenerating	P Values
	…(%)…			…(%)…		
Black Cherry	0	3	0.1250	5	11	0.0359
Conifers	3	0	0.5000	5	0	0.0078
Maples	39	31	0.2500	37	16	<0.0001
Midstory	22	5	0.0117	18	9	0.0041
Oaks	29	19	0.3008	12	9	0.2787
Other Overstory	5	17	0.1484	12	10	0.1028
Pioneer	2	9	0.0313	4	25	<0.0001
Yellow-poplar	0	16	0.0156	7	20	0.0004
Total	100	100		100	100	

Table 3.7. Mean proportion of upper canopy reproduction from sprout origin in all 41 regenerating stands on the Appalachian Plateau in West Virginia classified into subxeric and submesic site classes.

Species Group	Subxeric	Submesic
	……..(%)……..	
Black Cherry	19	44
Conifers	0	0
Maples	93	76
Midstory	43	41
Oaks	83	83
Other Overstory	45	61
Pioneer	10	17
Yellow-poplar	0	25

4. Predicting Regeneration in Appalachian Hardwood Stands Using the REGEN Expert System

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ABSTRACT

The REGEN regeneration prediction model is an expert system developed to predict species composition at the onset of stem exclusion after clearcutting using preharvest stand conditions. REGEN predictions are calculated using competitive rankings established for up to five advance reproduction size classes for encoded species. These rankings, and other stochastic parameters are contained in modular REGEN knowledge bases (RKBs). To expand REGEN applicability into hardwood stands in the Virginia and West Virginia Appalachians, we developed RKBs for four moisture regimes (xeric, subxeric, submesic, mesic). We tested model results using the subxeric and submesic RKBs with data from 48 paired sample stands, each consisting of one mature hardwood stand located adjacent to a regenerating stand that was clearcut within the past 20 yrs. All observed tree species were placed into one of eight species groups: 1) black cherry, 2) conifers, 3) maples, 4) midstory, 5) oaks, 6) other overstory, 7) pioneer, 8) yellow-poplar. On average, the REGEN model predicted the proportion of trees in each group to within 4% of the measured value. One standard deviation of the model error was typically within about 20% of the measured values. Across all 48 paired stands, the model was found to explain 32% (R^2 = 0.32) of the variation in species composition in regenerating stands. Only predictions for the other overstory and yellow-poplar species groups were statistically different from measured populations. Our results suggest that the REGEN expert system provides reasonable predictions of future species composition following clearcut in mixed Appalachian hardwood stands.

INTRODUCTION

The mixed hardwood forests of the Appalachians are some of the most complex forests in the United States. The intricate climate, geology, and topography of the Appalachians interact to create diverse forest communities. The land use history and disturbance regimes across the region further increase the complexity of these forests. Over 20 commercial species are commonly found in the Appalachians, often occurring in mixed stands (Miller and Kochenderfer 1998). These species vary in shade tolerance, growth rates, and regeneration strategies (Burns and Honkala 1990). Following clearcutting, shade-intolerant species such as black cherry (*Prunus serotina* Ehrh.) and yellow-poplar (*Liriodendron tulipifera* L.), and other early successional species can regenerate vigorously from seed, both recently dispersed and stored in the forest floor. In contrast, shade-tolerant species such as maples (*Acer spp.*) and intermediate-tolerant oaks (*Quercus spp.*) rely on advance reproduction to compete successfully following overstory removal. Only larger advance reproduction or stump-sprouts from these slower growing species can avoid being overtopped by faster growing intolerants following clearcutting (Sander 1972), unless site factors offer an ecological advantage to these species (Johnson et al. 2002). Site productivity, primarily determined by moisture availability, is indeed a significant factor influencing species composition and regeneration potential in the Appalachians (McNab 1988). Many of the naturally occurring species assemblages in the region are delineated by moisture availability. Smith (1994) describes four forest types in the Southern Appalachians where changes in species composition among these forest types primarily occur along a moisture gradient, ranging from xeric, subxeric, submesic, to mesic moisture regimes.

Given these diverse species assemblages, it is difficult to reliably predict future species composition following harvest. Following the acceptance of initial floristics (Egler 1954), the development of upland oak stocking guides (Gingrich 1967), and the recognition of the impact of advance reproduction size on the success of oak regeneration (Sander 1972), a number of models were developed to assess regeneration based on preharvest stand characteristics. Probabilistic models and resulting management guidelines were initially developed to evaluate regeneration potential in oak dominated forests (Sander et al. 1976). Methods for evaluating regeneration have been published for the Missouri Ozarks (Sander et al. 1984), Southern Bottomlands (Johnson 1980), the Central Appalachians (Steiner et al. 2008) and the Alleghenies (Marquis et al. 1992).

These models were intended to serve as management tools for practicing silviculturists and forest managers. Other models have been published that are more focused on quantitative output (McQuilkin 1975, Loftis 1990, Gould et al. 2006). Rather than assessing the adequacy of regeneration, these models provide a numerical output of expected successful regeneration. Loftis (1990) and McQuilkin (1975) developed single species models for oaks. Similar models have been developed solely to quantify contributions from stump-sprouting as well (Dey et al. 1996, Gould et al. 2007). Most of these tools are limited to oak management. Rogers and Johnson (1998) summarize several approaches used to model oak dominated ecosystems. Multi-species, regional predictive models are available in some areas (Dey 1991, Waldrop et al. 1986), but these types of models are not available for all regions.

Interest in a multi-species, regional predictive model for the Southern Appalachians fostered the development of the REGEN model (Loftis 1989). The REGEN model is an expert system designed to predict species composition at the onset of stem exclusion following clearcutting. REGEN is a competition based model that uses numerical rankings of species competitiveness following clearcutting in conjunction with existing stand characteristics to generate predictions. The objectives of this study were to: 1) Adapt the REGEN model to hardwood forests in the Appalachians of Virginia and West Virginia and 2) Compare predictions of species composition produced by REGEN using a paired stand approach.

METHODS

This study was conducted in the Appalachians of Virginia and West Virginia using a paired stand sampling approach. This approach utilized sample sites containing a mature hardwood stand free from known recent disturbance adjacent to a regenerating stand of similar site characteristics (aspect, slope, topographic position) that was harvested via clearcut within the past 20 yrs. This approach assumes that the two stands were once contiguous and of similar composition and productivity. Further, we assume that if any mature stand were harvested now it would regenerate in a similar fashion to its paired regenerating stand. A total of 48 paired stands were located in Virginia and West Virginia (Fig. 4.1). Forty-five of the 48 paired stands were located within the Appalachian Plateau Physiographic Province, while the remaining three were located in the Ridge and Valley Province (Fenneman 1938). Because of the complex assemblages of species that occur across this area, and for the purposes of data analysis and presentation, we created 8 species groups: 1) black cherry, 2) conifers, 3) maples, 4) midstory, 5) oaks, 6) other overstory, 7) pioneer, and 8) yellow-poplar (Table 4.1). Species groups are composed of either a single species that is numerous throughout the area or a collection of species that are expected to occupy similar stand structural positions.

Mature stands were sampled between May and September, 2008 using a systematic grid with a plot spacing of 165 ft and 264 ft. The distance from the stand boundary to the first plot was randomly determined. Mature stands were sampled using 0.004 ac reproduction plots installed at a density of one plot per acre in each mature stand, with a maximum of 20 plots. At each plot, the dbh of stems ≥ 1.5 in were measured and advance reproduction was tallied by species and height class. Overstory basal area was measured with a 10 BAF prism. Regenerating stands were sampled at a density of one plot per acre using 0.001 ac plots unless stands had developed such that plots were frequently unpopulated. In this case, 0.004 ac plots were established throughout the stand. In the regenerating stands, regeneration was tallied by species, stem origin (seed or sprout), and crown class (dominant, codominant, intermediate, suppressed). Advance reproduction from the mature stand inventories was scaled up to represent 0.01 ac to meet the input requirements of the REGEN computer program which are described later.

To ensure similar site productivity between paired mature and regenerating stands slope, aspect, and landscape position were used to estimate site index using the Forest Site Quality Index (Meiners et al. 1984). This methodology estimates site index based on moisture retention potential and provides relative estimates of site quality throughout the region in areas of similar rainfall. However, because these estimates may be misleading when comparing sites in regions with different rainfall amounts, paired stands were also classified into site classes based on indicator species as proposed by McNab et al. (2002). In this ecological classification system, certain species serve as indicators of moisture and nutrient availability and provide insight into relative site quality. We applied the species moisture weights from this methodology to a list of species present at each mature stand to classify sites into one of four moisture regimes: xeric, subxeric, submesic, and mesic. All stands in our study fell within subxeric or submesic regimes with 38 paired stands in the submesic regime and ten paired stands in the subxeric regime.

The mature stands examined in this study were dominated by oaks and maples. Mean basal area was 118 ft^2 per acre with about 370 trees per acre ≥ 1.5 in dbh (Table 4.2). Maples made up the greatest proportion of trees per acre, but midstory and oak species were also common. In regenerating stands maples and pioneer species were the most numerous in the upper canopy (dominant and codominant), while maples and midstory species were the most numerous in the lower canopy positions (intermediate and suppressed) (Table 4.3). Mature subxeric stands were dominated by oaks with nearly 75% of the total basal area per acre (Table 4.2). Oaks and maples were the most numerous species in the subxeric regenerating stands (Table 4.3). Oaks also dominated submesic stands, but the proportion of basal area was much less than in subxeric stands (Table 4.2). Pioneer species made up the greatest proportion of upper canopy stems in the regenerating submesic stands (Table 4.3).

Boucugnani (2005) describes the development of the computer adaptation of REGEN and provides documentation of the underlying framework of the model. The following summary highlights the prediction process and associated data requirements. In order to generate predictions in REGEN, a survey of advance reproduction prior to harvest is required. Advance reproduction is categorized into five species-size combinations, which are defined as: germinant (newly germinated seedlings), small seedlings (< 2 ft tall), medium seedlings (2-4 ft tall), large seedlings (≥ 4 ft tall), and potential stump-sprouts (trees > 4 ft tall and ≥ 2 in dbh). REGEN also allows for the probabilistic establishment of stump-sprouts, root-suckers, and new seedlings following harvest using constant or logistic parameters combined with multiple runs of the input data. Prior to the competitive selection process, each plot is stochastically populated with stump-sprouts, root-suckers, and new post harvest seedlings in addition to the existing advance reproduction using expert user established probabilistic parameters. To identify potential stump-sprouts that are expected to produce a sprout, the outcome of the constant or logistic probabilistic parameters is determined for each simulation run. The establishment of new post harvest seedlings is calculated in a similar manner for species that are expected to regenerate in this way. Root-suckering is also handled similarly; however, REGEN requires that advance reproduction of a particular species must be present in the plot before root-suckers of that species are added into the regeneration pool. The number of stems and establishment probability for new seedlings and root-suckers that are to be added to the regeneration pool is defined by the expert user.

Each species-size-source combination is given a competitive ranking ranging from 1 to 8 decreasing in competiveness. Individuals ranked 1 will outcompete those ranked 2; individuals ranked 2 will outcompete those ranked 3, and so forth. Competition is simulated at the plot level, and future upper canopy species composition is predicted based on the relative competitive rankings of the regeneration pool in each sample plot. REGEN populates each prediction plot by identifying up to six "winning" stems based on competitive rank in a 0.01 acre plot. A loop is established in which individuals ranked 1 are selected first. If the threshold of six is not met, the selection process moves on to individuals ranked 2, then 3, and so forth until all six "winning" stems have been selected. In the case of ties for the selection of the final "winning" stem, each equally ranked individual is selected proportionally (e.g., if there are five individuals of equal rank, each one is selected as 0.2 of an individual). This fragmentation is resolved when "winning" stems per plot are scaled to stems per acre in the summary output. On plots where stump-sprouts are chosen, fewer "winning" stems are added to compensate for the greater space requirements of stump-sprouts. If one stump-sprout is selected, only three additional individuals will be selected. If two stump-sprouts are selected, only one additional individual is selected. If three or more stump-sprouts are selected, the top two are chosen and the remaining "winning" stems are selected proportionally using the tiebreaker logic described earlier. The stochastic element permits numerous runs of input data and allows summary statistics to be provided for model output.

A REGEN Knowledge Base (RKB) contains the competitive rankings and probabilistic parameters used to process input data. RKBs are modular, allowing REGEN to be adapted to different scenarios by creating custom RKBs. This also allows for multiple RKBs to be used in the same stand. To adapt REGEN to the Appalachians of Virginia and West Virginia, we created four preliminary RKBs in an attempt to capture species variability resulting from site productivity differences associated with moisture availability. The four RKBs were designed to predict regeneration in xeric, subxeric, submesic, and mesic moisture regimes. Because all paired stands fell in either the subxeric or submesic moisture regimes, only those two RKBs were field tested. The initial rankings and parameters for these four RKB's were based on data from the literature, including silvical characteristics (Burns and Honkala 1990), reported species composition following clearcutting from several authors (e.g., Beck and Hooper 1986, Ross et al. 1986, Loftis 1989), and site productivity interactions (Doolittle 1958).

Beck and Hooper (1986) found that early successional species such as yellow-poplar, black locust, and sweet birch along with red maple made up the majority of free to grow stems 20 yrs post harvest in the Southern Appalachians. Ross et al. (1986) report a favorable density of oak regeneration relative to other species in the more xeric types of four forest types as well as the relative competitiveness between classes of oak advance reproduction in southwest Virginia. Loftis (1989) reports on the species composition of nine clearcuts in the Southern Appalachians and proposes the conceptual foundation and initial subjective rankings of the REGEN model. Stump-sprouting, root-suckering, and new seedling establishment probabilities were initially taken from the literature when available, particularly the silvics manual (Burns and Honkala 1990), but these values often were the results of empirical trials in different forest types and climates (e.g. Michigan, Ontario, U.S. coastal plain). Doolittle's (1958) comparison of site index curves provides insight into potential competitive capacity and interactions with site productivity for several common species and form the foundation of the competitive relationships among species across moisture regimes for our rankings. The information from these sources and others was modified to fit the REGEN framework and rankings were assigned based on the experience of the authors. Preliminary model results based on the advance reproduction survey from the mature stands using the initial rankings (predicted) were compared to the upper canopy species composition of developing stands (measured). Based on these intermediate results, competitive rankings for each species in each RKB were amended accordingly. Probabilities and parameters were also amended according to the results of preliminary model runs. The revised rankings and results presented in this document represent the highest level of accuracy obtained after several iterative trials of amendments to the initial RKBs. The final RKBs developed for the four moisture regimes are presented in Tables 4.4 and 4.5. Complete rankings and parameters for each of the four RKBs are provided in Appendices B-E. Because an independent data set was not available, the data collected for calibration of the initial RKBs was used to assess the performance of REGEN.

Stump-sprouts are considered the most competitive source of regeneration for a species when applicable, and rankings subsequently decrease for smaller size classes. Although the competition within a species (large vs. small seedling) is straightforward, distance between size class rankings must also allow for competitive relationships among species to be relatively stable across size classes. Because these rankings are designed to predict upper canopy species at the onset of stem exclusion, species that may be numerous in the lower canopy and may possibly ascend into the upper canopy in later stages of development are not necessarily given a high rank. Conversely, pioneer species, which are expected to be numerous, but ultimately short lived in the upper canopy, are ranked highly. Generally, more mesic species such as basswood decrease in rank as moisture availability decreases, while xeric species such as Virginia pine increase in rank. Sweet birch and yellow-poplar are expected to be strong competitors and are given a rank of 1 in all moisture regimes except for xeric. Black locust and eastern white pine are also among the most competitive species across all moisture regimes. Red maple sprouts were considered very competitive across all four moisture regimes. Oaks, as a group, are among the most competitive species in the xeric and subxeric RKBs and decrease as moisture increases. Chestnut and scarlet oaks are more competitive in the xeric and subxeric regimes and decrease as moisture increases, while northern red oak becomes increasingly competitive up to the submesic RKB.

The primary model output evaluated was the predicted species composition expressed as a proportion of the total stand. Only comparing proportions allows predictions from the REGEN model to be compared to the measured species composition of regenerating stands which vary in age, density, and development up to the stem exclusion phase. Tests for normality indicated that the data did not fit a normal distribution. Further analyses were conducted using non-parametric tests. These analyses were conducted using SAS® version 9.2 software using the UNIVARIATE procedure (SAS 2007). To asses overall performance of the model, mean values of predicted species composition from the REGEN model based on advance reproduction from mature stands was compared to mean values of measured species composition from regenerating stands for all 48 paired stands. A test was conducted for significant differences in sample distribution medians between the measured and predicted proportions for each species group from each of the 48 paired stands. The Wilcoxon Signed Rank test, a nonparametric analog to a paired *t* test, was conducted to test for differences between measured and predicted values for species groups (Ott and Longnecker 2001, SAS 2007). To test the model for site specific performance, the measured regenerating species composition was plotted against the REGEN model output across all 48 paired stands and eight species groups (n = 384) using the REG procedure in SAS (SAS 2007). To test site specific performance for each species group individually, a regression analysis was conducted for only the measured and predicted proportions of that species group across paired stands (n = 48).

RESULTS

Using the RKBs we developed for the Appalachians of Virginia and West Virginia, the REGEN model appeared to provide reasonable predictions of mean species composition of regenerating stands after clearcutting (Fig. 4.2). Across all 48 paired stands, mean species composition predicted by the REGEN model was within 4% of the measured species composition for all 8 species groups used in this study. Mean differences between measured and predicted populations indicate that generally black cherry, conifers, maples, pioneer, and yellow-poplar species groups are slightly overpredicted. Midstory, oaks, and other overstory species groups are generally underpredicted. Tests for differences in population distributions indicate that among species groups, only the other overstory and yellow-poplar measured distributions are statistically different than their predicted distributions at an α threshold of 0.05 (Table 4.6). To assess the overall spread of the error from the model predictions a box and whisker plot was created (Fig. 4.3). On average, across all 48 paired stands, one standard deviation of the model error for a species group is generally not more than about ± 20%. The range of model error is broader indicating possible outliers.

The species composition comparisons for both the subxeric and submesic site classes separately are displayed in Figure 4.4. The predictions on the ten subxeric sites were, on average, within about 6% of the measured values, with the greatest discrepancies occurring in the maples and yellow-poplar species groups. The predictions for the 38 submesic sites were within about 4% of the measured values on average. To further investigate the spread of the model error for the RKBs individually, box and whisker plots were created for the subxeric and submesic sites (Fig. 4.5). The range of model error from the subxeric RKB appeared to be smaller than the submesic on average, with the exception of yellow-poplar on subxeric sites which tended to be underpredicted to a greater extent. However, it is possible that this reduced error spread of the subxeric RKB may be an artifact of fewer subxeric sample sites rather than superior performance compared to the submesic RKB. On average, one standard deviation of the model error for a species group is generally not more than ± 20% for both RKBs, with the exception of subxeric yellow-poplar which was within about ± 24%.

To investigate site specific performance, a linear regression analysis was conducted plotting the measured proportions against the predicted proportions for all 8 species group across all 48 paired stands for all data points (n = 384) (Fig. 4.6). This regression was found to be highly significant ($P < 0.0001$). The coefficient of determination indicates that the REGEN model predictions explain 32% ($R^2 = 0.32$) of the variation in species composition in regenerating stands across both moisture regimes. The subxeric RKB explains 42% ($R^2 = 0.42$) and the submesic RKB explains 29% ($R^2 = 0.29$) of the variation in regenerating stands of those moisture regimes, respectively. The analysis of the model residuals, which plot the model error (predicted – measured) against the measured values, suggests that the model consistently underpredicts future composition when a group occupies greater than about 30% of a stand (Fig. 4.7). In both the regression and residual plots, the subxeric and submesic RKB data points appear to be randomly distributed. The species composition comparison for each individual stand is provided in Appendix A.

Individual regression analysis for each species group indicates a highly significant regression for all species groups except the midstory group (Fig. 4.8). The model explains the greatest amount of variation for black cherry (R^2= 0.45), and over 25% of the variability in individual species composition in the regenerating stands for three other species groups: 39% (R^2= 0.39) for oaks, 30% (R^2= 0.30) for other overstory, and 28% (R^2= 0.28) for the pioneer species group.

Along with the overall species composition output, REGEN reports the source size class (sprout, large, medium, small, germinant) of each winning stem per plot. Given the importance of stump-sprouts to regeneration in the Appalachians, the sprout ratio for winning stems in the predicted populations was compared to the sprout ratio in measured stands. Tests indicate that mean predicted distributions for proportions of winning stems of sprout origin are significantly different from measured distributions of sprout origin regeneration for the black cherry, midstory, and pioneer species groups (Fig. 4.9).

DISCUSSION

The competitive rankings and moisture delineations for the Appalachians of Virginia and West Virginia that we incorporated into RKBs for the REGEN model appear to provide reasonable predictions of species composition following clearcutting (Fig. 4.2). The apparent success and potential for this model to predict regeneration is likely largely attributable to its design. The underlying REGEN framework is not a collection of regressions and probabilistic parameters, although these are incorporated. Rather, REGEN is more explanatory in design, and is built on a foundation of fundamental ecological and silvicultural concepts. It has long been recognized that certain species possess characteristics that allow them to flourish following disturbance of a particular magnitude (Egler 1954). The manipulation of these traits to favor desirable species is the foundation of regeneration silviculture. Shade-intolerant species typically dominate regeneration following clearcutting when present, unless site conditions provide an ecological advantage to other species (Johnson et al. 2002). Shade intermediate and shade tolerant species are typically slower growing following complete overstory removal and rely on stump-sprouts and disturbance to buildup larger advance reproduction for successful regeneration (Roach and Gingrich 1968, Sander 1972, Johnson et al. 2002). Reports of species of similar function regenerating successfully following clearcutting on stands of similar site quality and disturbance history (Trimble 1973, Brashears 2004, Gould et al. 2005), along with accepted theories of stand development (Egler 1954, Oliver and Larson 1996) indicate that a ranking of competitiveness for a given situation should be feasible. These rankings could be considered a numerical approximation of a species ability to capture growing space following a given disturbance. This ranking also describes the competitive relationship amongst species, and essentially evaluates the suitability of a given species to a particular silvicultural system.

A numerical ranking of regeneration potential has been used successfully to evaluate bottomland hardwood regeneration adequacy for red oaks and green ash (Johnson 1980, Johnson and Deen 1993, Belli et al. 1999). Their methodology numerically scores regeneration potential based on the size and quantity of advance reproduction, as well as the contribution from stump-sprouts. Smaller sources of advance regeneration are assigned lower scores than larger sources. Stump-sprouting potential is considered by assigning small overstory trees the largest score and decreasing scores for increasing sizes. This method is not so far removed from the underlying theory behind the regeneration evaluations for oak by Sander et al. (1976, 1984), Steiner et al. (2008), and the model by Loftis (1990), that larger stems of advance reproduction are usually older, and have more mature root systems. Following release from the overstory, these stems have increased capital to capture site resources, even if the main stem is destroyed during harvest

(Larsen and Johnson 1998). Therefore, larger stems of advance reproduction, and especially stump-sprouts, are likely to be the most competitive forms of regeneration following harvest (Sander 1972). The recognition of the advantages of the more mature root systems of larger advance reproduction and stump-sprouts adds to the explanatory function of REGEN.

The REGEN model differs from most regeneration models developed for hardwoods in that it provides a quantitative estimate of future species composition rather than an evaluation of regeneration adequacy or estimates for individual species or species group success. While tools such as these indeed provide insight into regeneration potential, typically for oak, the major flaw in most is the lack of explicit consideration for the composition of competing vegetation. That is, competition is often assumed constant. These models and evaluations certainly serve as useful tools when the primary species of interest is oak but, understandably, fall short of providing more complete stand assessments of regeneration as this is not their intended function. Ideally, a regeneration model would not only provide reliable estimates for species of current value but would also be robust, providing sufficient information to capitalize on emerging or unexpected markets for species that historically have not been of great value, or are currently non-commercial. The REGEN model shows potential to provide adequate information to meet a variety of management scenarios. Given the temporal instability of species composition in regenerating hardwood stands, and uncertainty associated with using regeneration models that do not specifically target the Appalachians of Virginia and West Virginia, this model may potentially provide the greatest insight into future species composition for local forest managers.

Other published regeneration models for Appalachian hardwoods have been found to explain a greater amount of variation in their respective targets than what this model has achieved (Loftis 1990, Gould et al. 2006). Loftis (1990) explained 52% of the variation for the height of northern red oak stems at age 8 in North Carolina. Gould et al. (2006) explained about 61% of the variation in third decade seed origin oak stocking in Pennsylvania. These models however, are focused solely on oak management, are derived from more extensive data sets, and only target certain components of natural regeneration. Our comparison of mean species composition between measured and predicted populations across all paired stands in this study (Fig. 4.2) is encouraging due to a lack of statistical difference for all species groups except other overstory and yellow-poplar (Table 4.6). Waldrop et al. (1986) also experienced difficulty modeling early successional species, particularly yellow-poplar, when testing the FORET model (Shugart and West 1977), and developing the FORCAT model for the Cumberland Plateau of Tennessee. Our yellow-poplar predictions are also likely confounded by the inconsistencies of its presence and importance in the northern portions of this study, which tend to be transitional forests between central, Allegheny, and northern hardwoods (Braun 1950, Stout 1991). The species in the other overstory group were relatively rare, which confounded efforts to assess competitiveness in this more miscellaneous species group.

Although species groups were used in our analyses, REGEN provides predictions for individual species. Therefore, the model performance for some species within a group may be better than others. For example, within the maples group, the model appears to perform better, on average, for sugar maple which was within about 1% of the measured values than red maple which was within about 2%. One standard deviation of model error for sugar maple was typically within about ± 6%, whereas for red maple it was ± 17%. The mean model predictions for the maples group, which consisted of red and sugar maple, as a whole, were found to be within about 3% of the measured values overall (Fig 4.2), with a standard deviation of ± 17% (Fig. 4.3). The species groupings were used to facilitate data analysis and presentation and, for the most part, were constructed of species that are expected to occupy similar positions in a mature forest. Therefore, species even within a group such as the other overstory group, which contains a more miscellaneous assortment of species, should all occupy similar positions in the canopy of an Appalachian hardwood stand near a typical rotation age. Thus, while the model may perform better or worse for some individual species within a group, the group as a whole should perform similarly to our results.

REGEN would likely provide a more accurate portrayal of regeneration tendencies for a large ownership than for a single stand at this time. Across all 48 paired stands, individual stand R^2 values ranged from 0.00-0.98 which indicates tremendous potential, but highlights that predictions for any given stand must always be subject to an experienced forester's greater judgment (App. A). Part of this range of individual stand results could be due to the sampling approach taken. While we see no reason that the assumptions made using this paired stand approach are unwarranted, the history of any stand was subject to the best available knowledge of the local forest manager. Therefore, we cannot account for all factors that may have influenced stand development including drought, frost, ice, browsing, or any otherwise stochastic events that may have impacted species composition. One standard deviation of the model error was usually within about 20% for a species group (Fig. 4.3). The regression analysis revealed a highly significant relationship between the measured and predicted values (Fig. 4.2), but the R^2 value of 0.32 indicates room for improvement. The potential to improve these RKBs without additional field data is limited however. The poor results in the regression analysis for the midstory group (Fig. 4.8), is likely due to the current developmental stage of the regenerating stands. The canopy position of this species group is in a state of flux as many stems of these species are already being relegated to lower canopy positions as found in Table 4.3.

For probabilistic modeling purposes, long-term trials conducted across the study region would be ideal. In spite of the large amount of literature detailing the effects of clearcutting on regeneration, there are few works that follow the progress of stand development to stem exclusion and include detailed characteristics of preharvest advance reproduction. This information would likely contribute a measurable improvement to the current model. However, species that are often the most successful following clearcutting have limited reliance on advance reproduction. Therefore, the greatest potential for improvements would likely come from modeling efforts to establish the probability for early successional species to attain upper canopy status from seed origin reproduction. Improvements in this area could perhaps remedy the lack of sensitivity for species occupying greater than 30% of future species composition (Fig. 4.7) and improve the accuracy of yellow-poplar predictions (Table 4.6). These are highly stochastic events however, and modeling attempts would likely be complex and inconsistent given the transitional tendency of the forests in much of the study region. Nonetheless, empirical results from studies such as these often can, and should be incorporated into the REGEN model as they become available. This would provide a more quantitative estimate of the competitive relationship amongst species and attempt to begin explaining greater amounts of the stochastic elements of regeneration dynamics.

CONCLUSION

Results of this study indicate that the REGEN model can be adapted to predict regeneration of various communities. REGEN can be adapted to new regions quickly based on knowledge of local regeneration ecology, and improved gradually as research becomes available.

The detailed description of advance reproduction required by REGEN is likely more time consuming in the field compared to other regeneration evaluations that utilize simpler metrics. Still, the REGEN methodology is straightforward and could likely be implemented into periodic stand evaluations with limited increases in labor, especially if an advance reproduction tally is already included in assessments for stands nearing rotation age. REGEN has the potential to be a useful tool in regeneration silviculture and should assist in identifying stands that may be candidates for preharvest manipulation or future ameliorative treatments to meet management objectives. Given the stochastic nature of Appalachian hardwood regeneration however, all REGEN predictions should be subject to an experienced manager's greater judgment. Rankings and probabilistic parameters should be continually evaluated as additional information becomes available. Future validation using an independent data set will provide greater insight into the accuracy and range of applicability of the REGEN model.

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FIGURES

Figure 4.1. Location of sample sites in Virginia and West Virginia. Shaded areas represent counties in which sample stands were located.

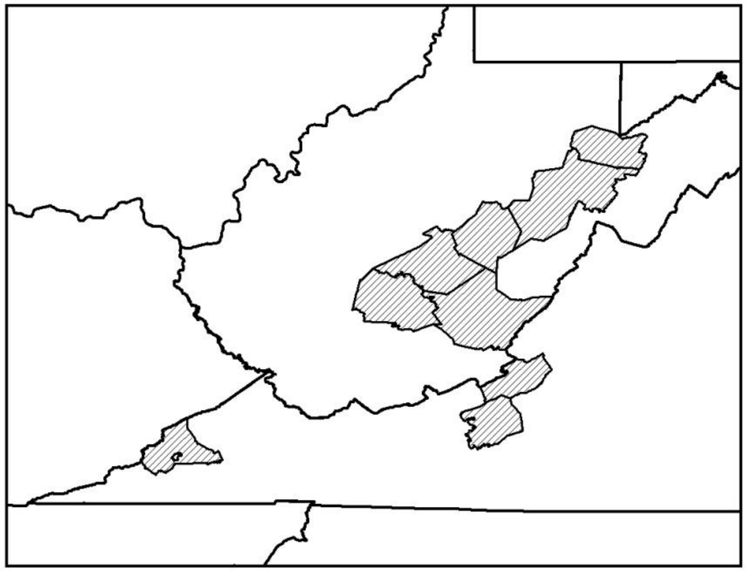


Figure 4.2. Comparison of mean values for measured and predicted species composition in regenerating stands following clearcutting in 48 stands in Virginia and West Virginia.

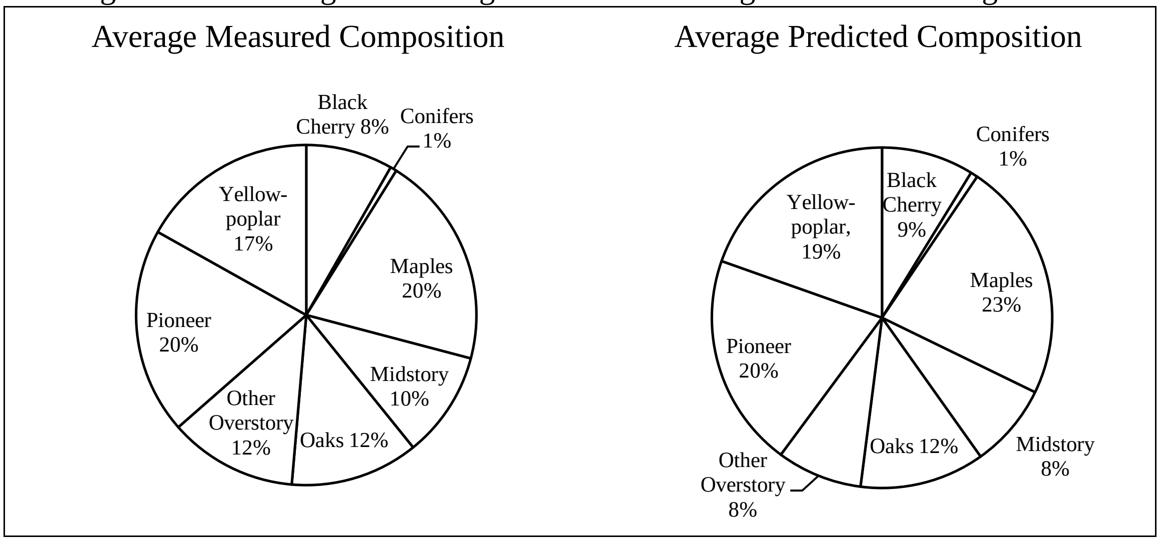


Figure 4.3. Summary of model error spread for each species group in 48 stands in Virginia and West Virginia. Model error was calculated as predicted – measured. Data points represent the mean error for a species group, open bars represent ± one standard deviation from the mean for each species group, vertical lines represent the range of errors for each species group.

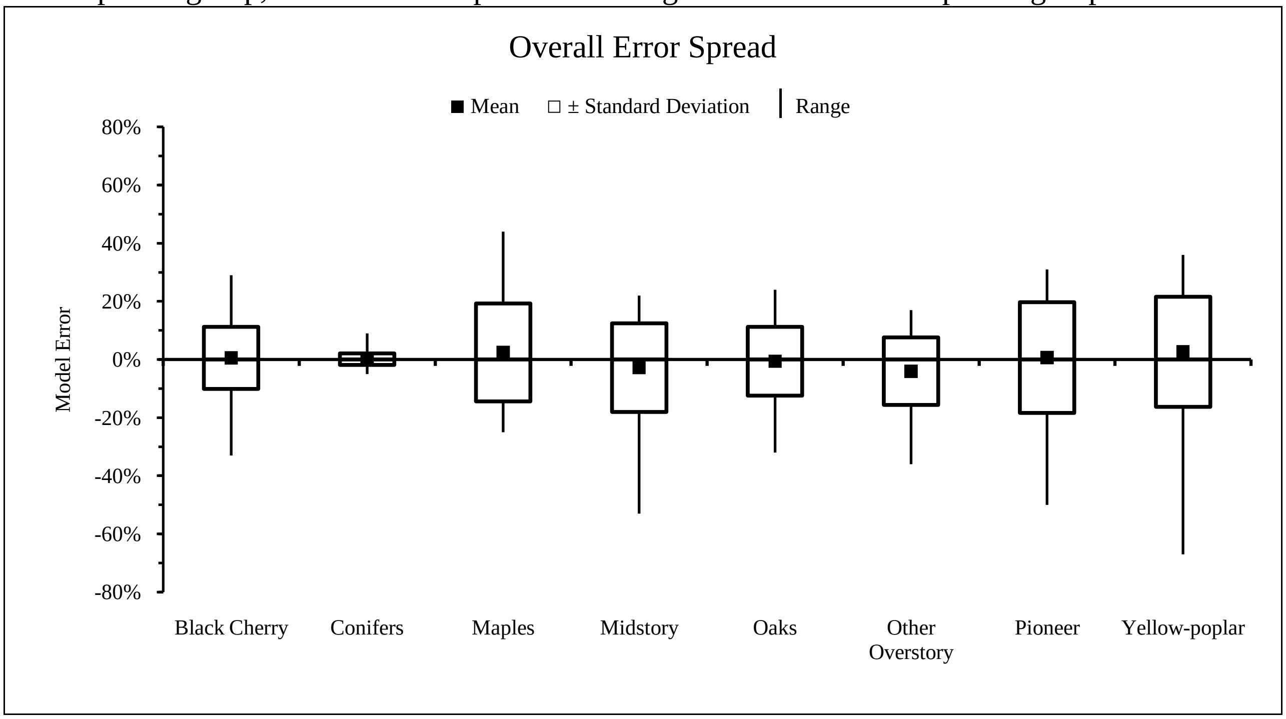


Figure 4.4. Comparison of mean values for measured and predicted species composition by site class in regenerating stands following clearcutting in 48 stands in Virginia and West Virginia. Subxeric sites are the top two charts, submesic sites are the bottom two charts.

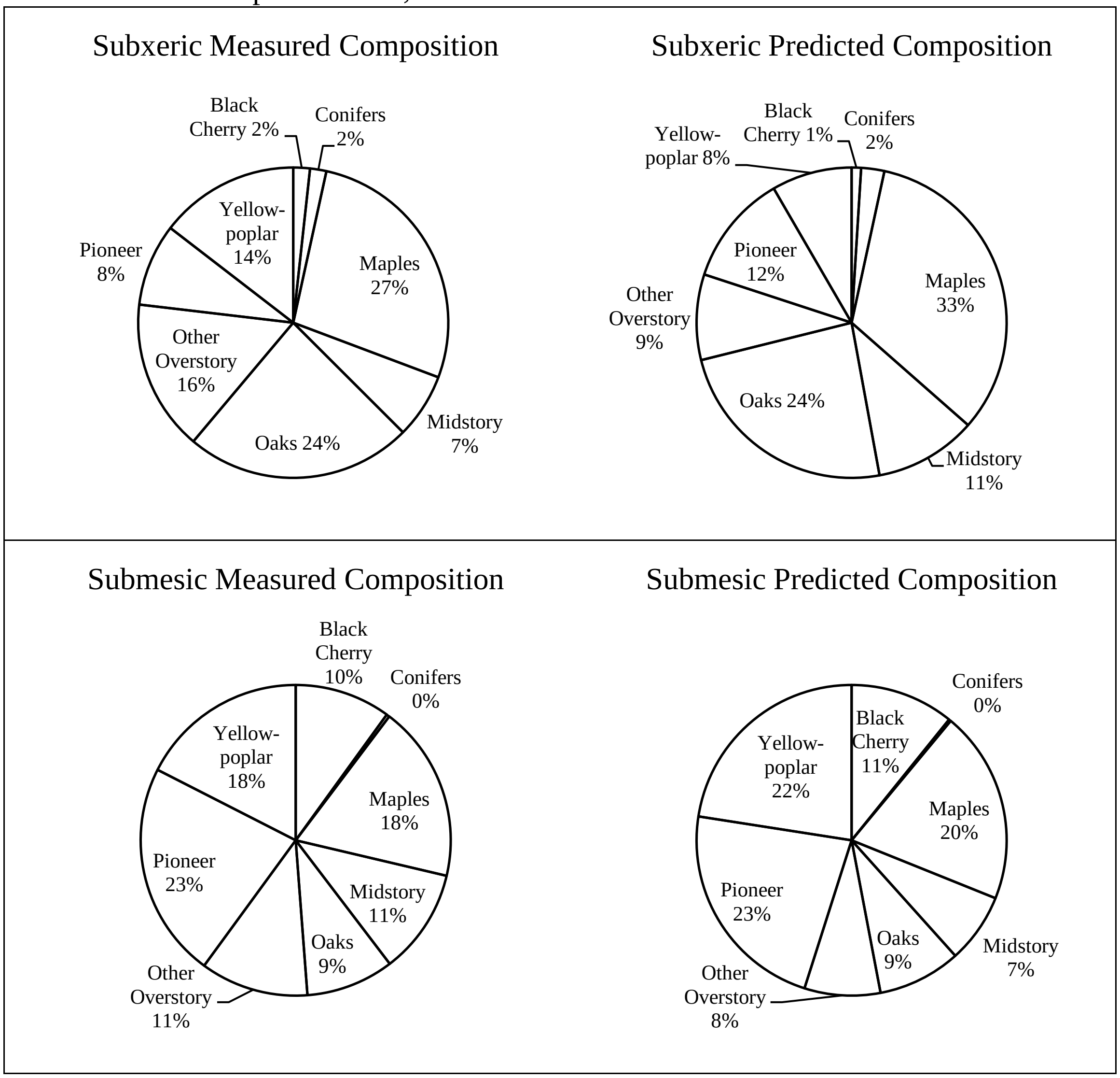


Figure 4.5. Summary of model error spread for each species group by site class in 48 stands in Virginia and West Virginia. Model error was calculated as predicted – measured. Data points represent the mean error for a species group, open bars represent ± one standard deviation from the mean for each species group, vertical lines represent the range of errors for each species group. Data from subxeric sites are displayed in the top graph, submesic sites data are in the bottom graph.

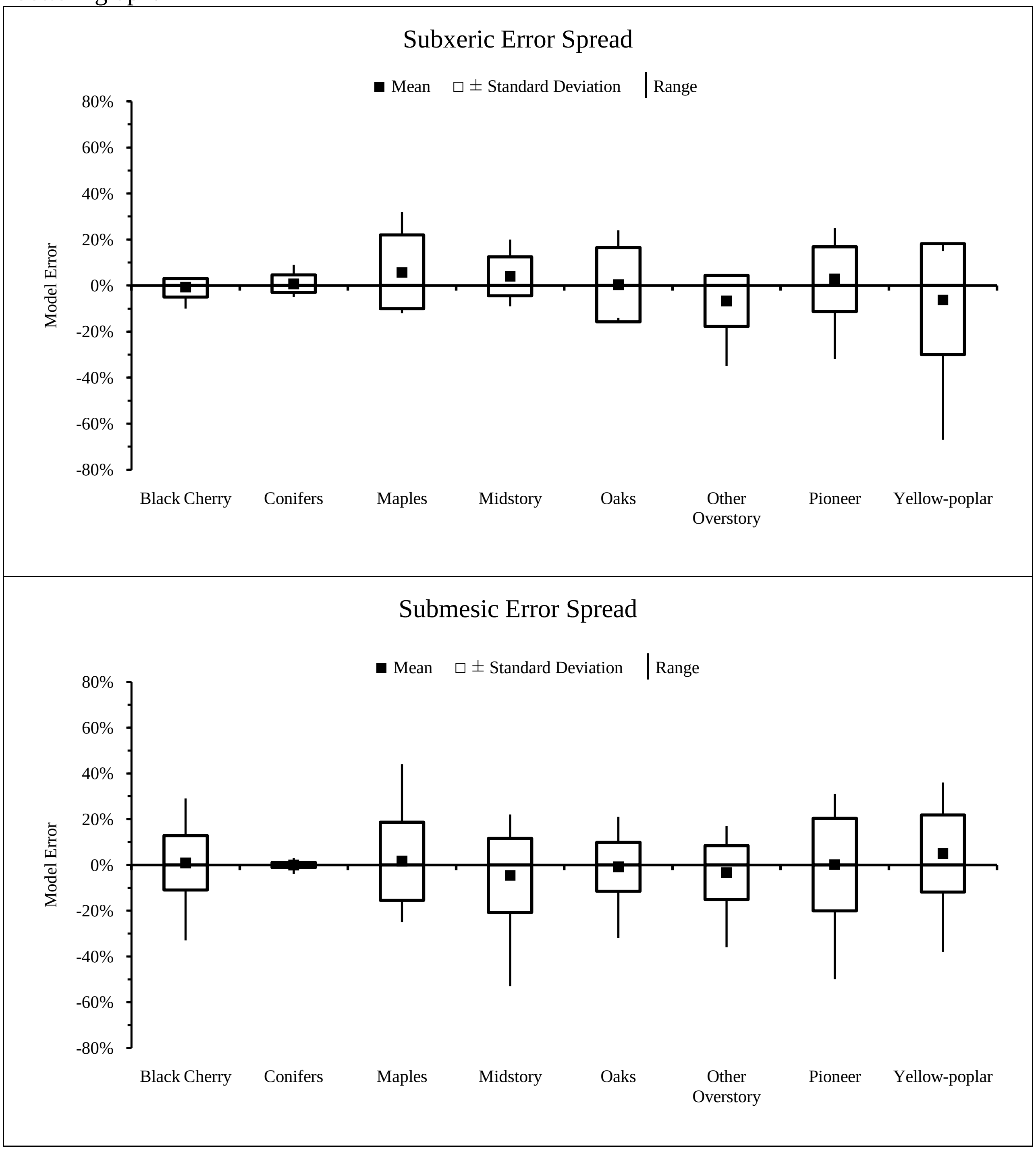


Figure 4.6. Regression analysis comparing measured vs. predicted values of the percentage of regeneration in each species group at 48 sites in Virginia and West Virginia. Values on the Y-axis are the predicted values for each species group on each stand based on the advance reproduction survey in the mature stand. Values on the X-axis are the measured values for each species group on each stand based on the inventory of dominant and codominant stems in the developing stands.

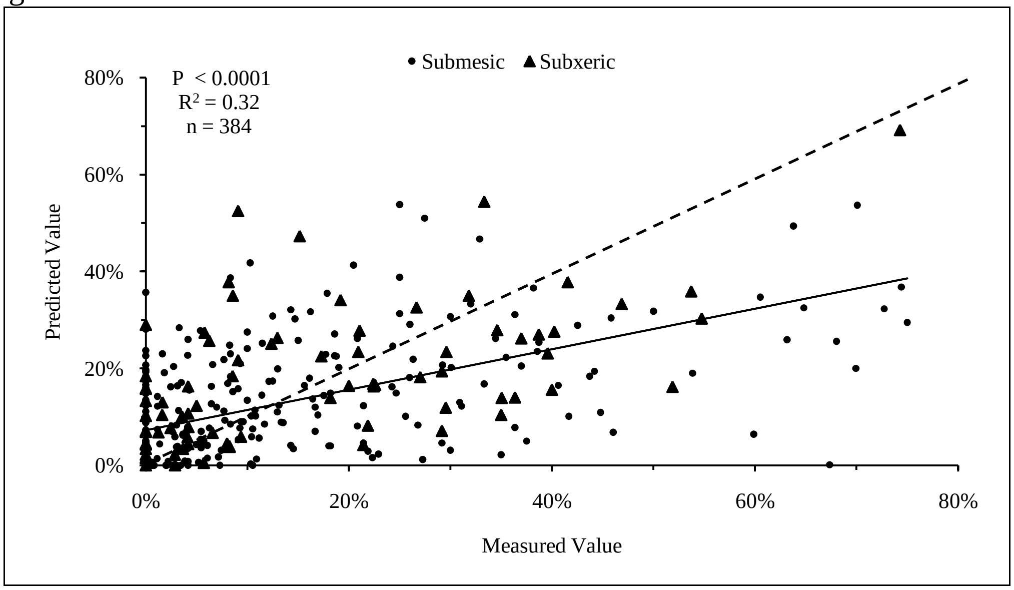


Figure 4.7. Residual analysis for all species groups and sample stands in Virginia and West Virginia. Values on the Y-axis are the model error (predicted – measured) and values on the X-axis are the measured values associated with the model error.

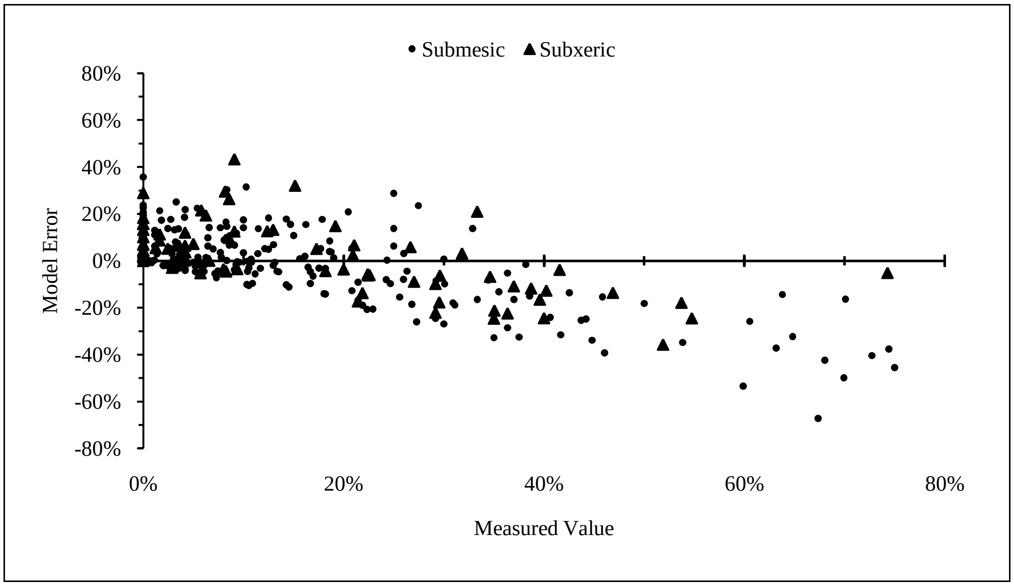


Figure 4.8. Regression analysis for each species group across all sample stands in Virginia and West Virginia. Values on the Y-axis are the predicted values on each stand based on the advance reproduction survey in the mature stand. Values on the X-axis are the measured values on each stand based on the inventory of dominant and codominant stems in the regenerating stands.

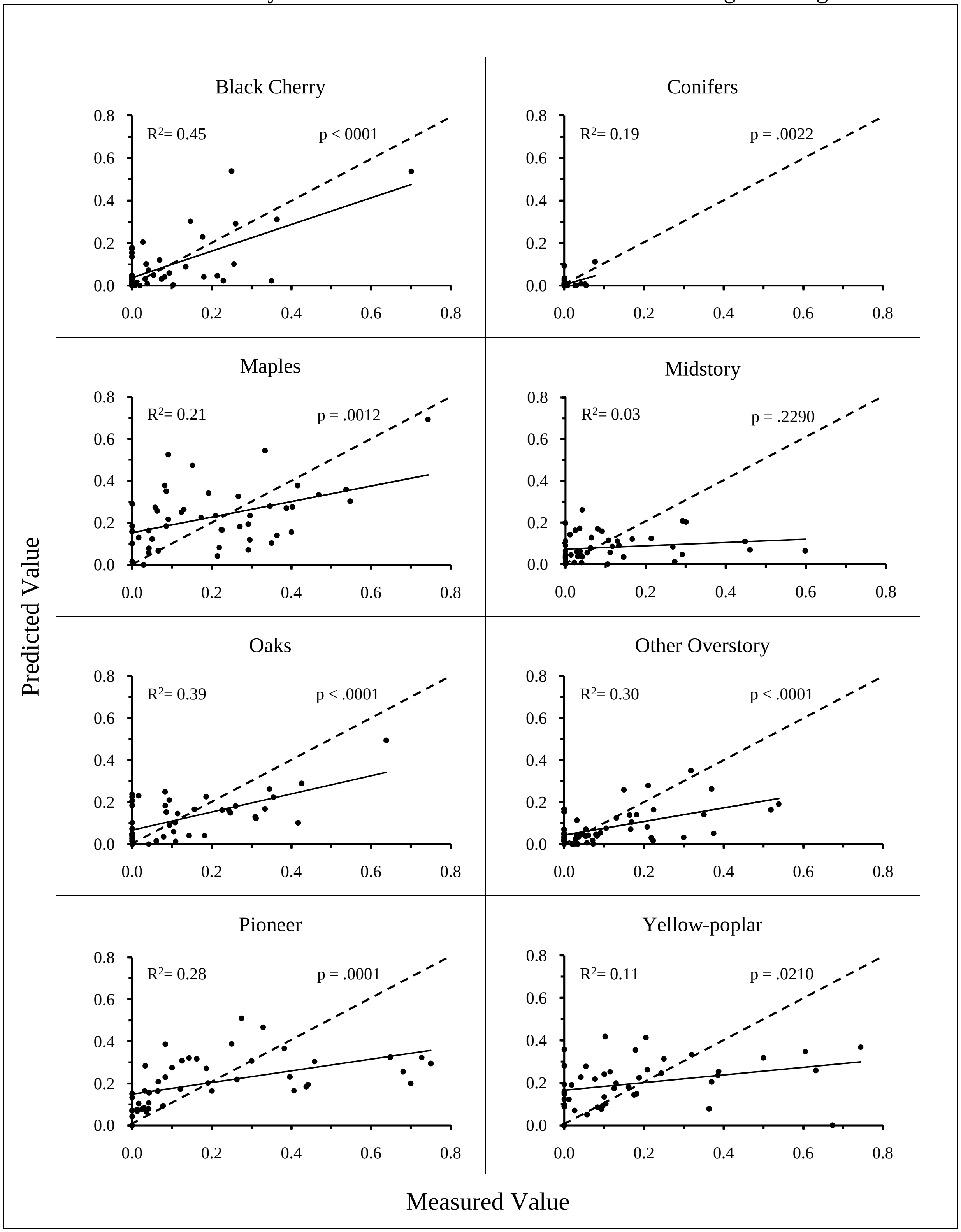
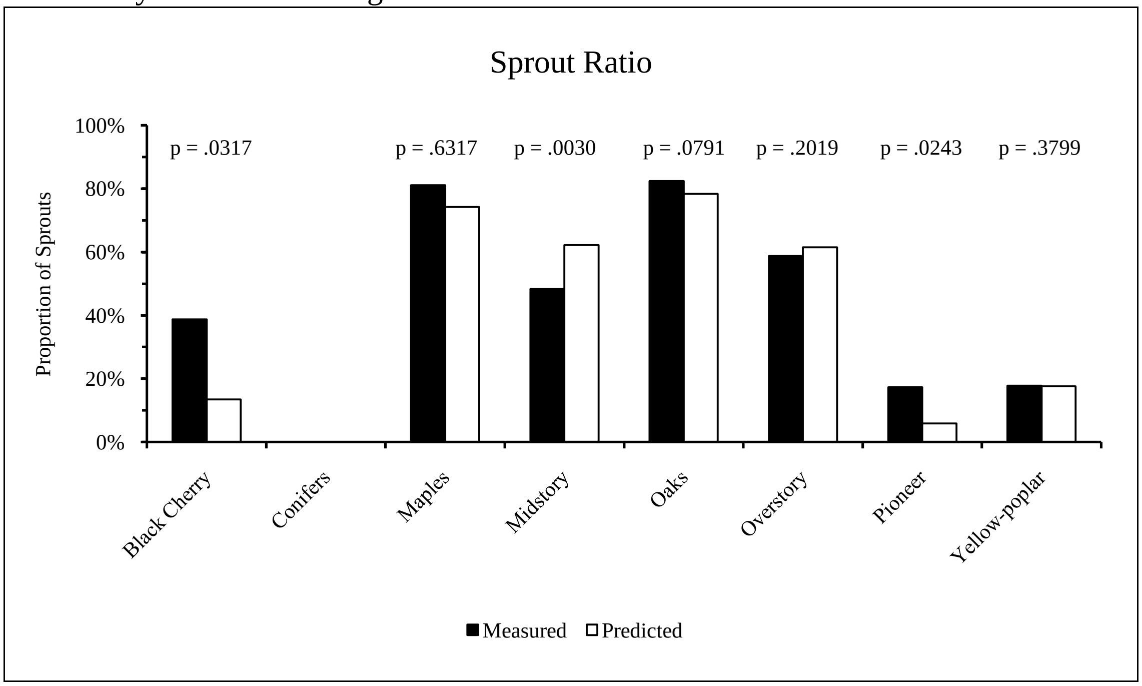


Figure 4.9. Comparison of measured and predicted proportion of stump sprouts in species groups in 48 regenerating stands in Virginia and West Virginia. The Y-axis represents the proportion of dominant and codominant stems that were of sprout origin. P values less than 0.05 indicate significant differences about the distribution medians between measured and predicted samples as calculated by the Wilcoxon Signed Rank test.



TABLES

Table 4.1. Species groupings used in this study in Virginia and West Virginia.

Group	Species
Black Cherry	black cherry (*Prunus serotina* Ehrh.)
Conifers	e. white pine (*Pinus strobus* L.), hemlock (*Tsuga spp.*), pitch pine (*Pinus rigida* Mill.), red spruce (*Picea rubens* Sarg.), shortleaf pine (*Pinus echinata* Mill.), Table Mountain pine (*Pinus pungens* Lamb.), Virginia pine (*Pinus virginiana* Mill.)
Maples	red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.)
Midstory	Am. chestnut (*Castanea dentata* (Marsh.) Borkh.), Am. beech (*Fagus grandifolia* Ehrh.), Am. holly (*Ilex opaca* Ait.), blackgum (*Nyssa sylvatica* Marsh.), dogwood (*Cornus spp.*), e. hophornbeam (*Ostrya virginiana* (Mill.) K. Koch.), sassafras (*Sassafras albidum* (Nutt.) Ness.), serviceberry (*Amelanchier spp.*), sourwood (*Oxydendrum arboretum* (L.) DC.), striped maple (*Acer pensylvanicum* L.)
Oaks	black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), n. red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.)
Other Overstory	ash (*Fraxinus spp.*), basswood (*Tilia spp.*), cucumbertree (*Magnolia acuminata* L.), Fraser magnolia (*Magnolia fraseri* Walt.), hickory (*Carya spp.*), yellow buckeye (*Aesculus octandra* Marsh.), yellow birch (*Betula alleghaniensis* Britton)
Pioneer	Am. sycamore (*Platanus occidentals* L.), bigtooth aspen(*Populus grandidentata* Michx.), black locust (*Robinia psuedoacacia* L.), pin cherry (*Prunus pensylvanica* L.f.), sweet birch (*Betula lenta* L.)
Yellow-poplar	yellow-poplar (*Liriodendron tulipifera* L.)

Table 4.2. Composition of mature sample stands in Virginia and West Virginia.

Species Group	Overall (n = 48)				Subxeric (n = 10)				Submesic (n = 38)			
	BA		TPA		BA		TPA		BA		TPA	
	Mean	SE ±	Mean	SE ±	Mean	SE ±	Mean	SE ±	Mean	SE ±	Mean	SE ±
	…(ft^2/ac)…		…(stems/ac)…		…(ft^2/ac)…		…(stems/ac)…		…(ft^2/ac)…		…(stems/ac)…	
Black Cherry	8	3	12	4	0	0	0	0	10	3	15	5
Conifers	4	1	16	6	3	2	10	9	5	2	17	7
Maples	26	3	130	10	13	3	149	29	30	3	125	10
Midstory	10	1	71	8	6	2	85	23	11	2	67	8
Oaks	47	5	67	9	73	6	128	16	41	6	51	8
Other Overstory	10	1	43	7	3	1	24	13	12	2	48	8
Pioneer	3	1	12	3	1	1	4	3	4	1	14	4
Yellow-poplar	10	2	21	5	0	0	1	1	12	2	26	6
Totals	118		372		99		401		125		363	

Table 4.3. Composition of regenerating sample stands in Virginia and West Virginia. Lower canopy values include all stems in the suppressed and intermediate crown positions. Upper canopy values include all stems in the dominant and codominant crown positions.

Species Group	Overall				Subxeric (n = 10)				Submesic (n = 38)			
	Lower Canopy		Upper Canopy		Lower Canopy		Upper Canopy		Lower Canopy		Upper Canopy	
	TPA	SE ±	TPA	SE ±	TPA	SE ±	TPA	SE ±	TPA	SE ±	TPA	SE ±
	…(stems/ac)…											
Black Cherry	382	207	250	96	35	26	40	34	473	260	305	119
Conifers	6	3	5	3	23	12	2	2	1	1	6	4
Maples	1009	141	437	90	555	110	456	148	1129	171	432	107
Midstory	888	149	331	111	547	168	171	85	978	181	373	139
Oaks	667	226	252	61	878	502	516	206	611	255	183	52
Other Overstory	308	76	185	34	96	36	132	40	364	93	199	42
Pioneer	399	68	417	104	141	125	264	230	467	76	457	117
Yellow-poplar	403	66	235	37	190	80	192	77	458	79	246	42
Total	4062		2112		2465		1773		4481		2201	

Table 4.4. Competitive rankings for common species following clearcut in xeric and subxeric moisture regimes in the Appalachians of Virginia and West Virginia. Sp = stump-sprout, L = large seedling, M = medium seedling, S = small seedling, G = germinant.

Rank	Xeric	Subxeric
1	Chestnut oak Sp, Scarlet Oak Sp, Sourwood Sp, Virginia Pine L	Black locust Sp, Chestnut oak Sp, Red maple Sp Scarlet Oak Sp, Sweet birch Sp, White Pine L, Yellow-poplar Sp
2	Black Oak Sp, Chestnut Oak L, Pitch pine L, Red maple Sp, Shortleaf pine L, Table Mt. pine L, White pine L	Black cherry Sp, Black locust L, Black oak Sp, Cucumbertree Sp, Fire cherry Sp, Sweet birch L, White oak Sp, White pine M, Yellow-poplar L
3	Black locust Sp, Black oak L, Blackgum Sp, Hickory Sp, N red oak Sp, Sassafras Sp, Scarlet oak L, Sourwood L, Table Mt. pine M, Virginia pine S, White oak Sp, White pine M	Black locust M, Chestnut oak L, Cucumbertree L, Fire cherry L, Hickory Sp, N red oak Sp, Scarlet oak L, Sweet birch M, Yellow-poplar M
4	Black locust L, Chestnut oak M, Pitch pine S, Red maple L, Scarlet oak M, Shortleaf pine S, Sourwood M, Table Mt. pine S, Virginia pine G, White oak L, White pine S	Black cherry L, Black locust S, Black oak L, Fire cherry M, Red maple L, Sourwood Sp, Sweet birch S, Virginia pine L, White pine S, Yellow-poplar S
5	Black locust M, Black oak M, Blackgum L, Chestnut oak S, Hickory L, Ironwood Sp, N red oak L, Pitch pine G, Red maple M, Sassafras L, Scarlet oak S, Serviceberry Sp, Shortleaf pine G, Sourwood S, Table Mt. pine G, White oak M, White pine G	Ash Sp, Black cherry M, Black locust G, Chestnut oak M, Dogwood Sp, Fire cherry S, Ironwood Sp, N red oak L, Pitch pine L, Scarlet oak M, Shortleaf pine L, Sweet birch G, Table Mt. pine L, White oak L, White pine G, Yellow-poplar G
6	Black cherry Sp, Black locust S, Black oak S, Blackgum M, Chestnut oak G, Dogwood Sp, Hickory M, N red oak M, Red maple S, Sassafras M, Scarlet oak G, Sourwood G, White oak S, Yellow-poplar Sp	Basswood Sp, Beech Sp, Black cherry S, Black oak M, Cucumbertree M, Fire cherry G, Fraser magnolia Sp, Hickory L, Ironwood L, Sassafras Sp, Serviceberry Sp, Sourwood L, Striped maple Sp, Virginia pine M
7	Ash Sp, Beech Sp, Black cherry L, Black oak G, Blackgum S, Dogwood L, Fire cherry Sp, Hickory S, Ironwood L, N red oak S, Red maple G, Sassafras S, Serviceberry L, Sweet birch Sp, White oak G	Ash L, Basswood L, Beech L, Blackgum Sp, Buckeye Sp, Dogwood L, Fraser magnolia L, Hemlock L, Ironwood S, Pitch pine M, Sassafras L, Serviceberry L, Shortleaf pine M, Striped maple L, Sugar maple Sp, Table Mt. pine M
8	Ash L, Basswood Sp, Beech L, Black cherry M, Black locust G, Blackgum G, Buckeye SP, Cucumbertree Sp, Dogwood M, Fire cherry L, Fraser magnolia Sp, Hemlock L, Hickory G, Ironwood M, N red oak G, Sassafras G, Serviceberry M, Striped maple Sp, Sugar maple Sp, Sweet birch L, Yellow birch Sp, Yellow-poplar L	Ash Sp, Basswood Sp, Black cherry G, Black oak S, Blackgum L, Buckeye L, Chestnut oak S, Cucumbertree S, Dogwood M, Fraser magnolia M, Hemlock M, Hickory M, Ironwood S, N red oak M, Red maple M, Scarlet oak S, Serviceberry M, Sourwood M, Striped maple M, Sugar maple L, Virginia pine S, White oak M, Yellow-birch Sp

Table 4.5. Competitive rankings for common species following clearcut in submesic and mesic moisture regimes in the Appalachians of Virginia and West Virginia. Sp = stump-sprout, L = large seedling, M = medium seedling, S = small seedling, G = germinant.

Rank	Submesic	Mesic
1	Basswood Sp, Black cherry Sp, Black locust Sp, Fire cherry Sp, Sweet birch Sp, Yellow-poplar Sp	Basswood Sp, Black cherry Sp, Fire cherry Sp, Sweet birch Sp, Yellow-poplar Sp
2	Basswood L, Black cherry L, Black locust L, Fire cherry L, N red oak Sp, Sweet birch L, White pine L, Yellow-poplar L	Ash Sp, Black cherry L, Black locust Sp, Cucumbertree Sp, Fire cherry L, Sugar maple Sp, Sweet birch L, White pine L, Yellow birch Sp, Yellow-poplar L
3	Black locust M, Black oak Sp, Fire cherry M, Red maple Sp, White pine M, Yellow-poplar M	Ash L, Basswood L, Black cherry M, Fire cherry M, Red maple Sp, Sweet birch M, Yellow-poplar M
4	Ash Sp, Basswood M, Black cherry M, Black locust S, Chestnut oak Sp, Fire cherry S, Scarlet oak Sp, Sweet birch M, White oak Sp, White pine S, Yellow-poplar S	Beech Sp, Black cherry S, Black locust L, Black oak Sp, Buckeye Sp, Cucumbertree L, Dogwood Sp, Fire cherry S, Fraser magnolia Sp, Hemlock L, Hickory Sp, N red oak Sp, Striped maple Sp, Sugar maple L, Sweet birch S, White pine M, Yellow birch L, Yellow-poplar S
5	Ash L, Black locust G, Cucumbertree Sp, Fire cherry G, Hickory Sp, N red oak L, Striped maple Sp, Sweet birch S, White pine G, Yellow birch Sp, Yellow-poplar G	Ash M, Basswood M, Beech L, Black cherry G, Black locust M, Buckeye L, Chestnut oak Sp, Cucumbertree M, Dogwood L, Fire cherry G, Red maple L, Scarlet oak Sp, Sugar maple M, Sweet birch G, White oak Sp, Yellow birch M, Yellow-poplar G
6	Ash M, Basswood S, Beech Sp, Black cherry S, Black oak L, Blackgum Sp, Fraser magnolia Sp, Red maple L, Sassafras Sp, Scarlet oak L, Serviceberry Sp, Sourwood Sp, Sweet birch G, White oak L, Yellow birch L	Beech M, Black locust S, Black oak L, Buckeye M, Fraser magnolia L Hemlock M, Hickory L, N red oak L, Serviceberry Sp, Sourwood Sp, Striped maple L, Sugar maple S, White pine S, Yellow birch S
7	Ash S, Basswood G, Chestnut oak L, Cucumbertree L, Fraser magnolia L, Ironwood Sp, Serviceberry L, Sugar maple Sp, Yellow birch M	Black locust G, Blackgum Sp, Chestnut oak L, Cucumbertree S, Dogwood M, Fraser magnolia M, Hickory M, Ironwood Sp, Red maple M, Sassafras Sp, Scarlet oak L, Serviceberry L, Striped maple M, White oak L, White pine G, Yellow birch G
8	Ash G, Beech L, Black cherry G, Black oak M, Blackgum L, Buckeye Sp, Cucumbertree M, Dogwood Sp, Hemlock L, Hickory L, Ironwood L, N red oak M, Pitch pine L, Red maple M, Sassafras L, Scarlet oak M, Serviceberry M, Shortleaf pine L, Sourwood L, Striped maple L, Sugar maple L, Table Mt. pine L, Virginia pine L, White oak M, Yellow birch S	Ash S, Basswood S, Beech S, Black oak M, Blackgum L, Buckeye S, Cucumbertree G, Dogwood S, Fraser magnolia S, Hemlock S, Hickory S, Ironwood L, N red oak M, Pitch pine L, Red maple S, Sassafras L, Serviceberry M, Shortleaf pine L, Sourwood L, Striped maple S, Sugar maple G, Table Mt. pine L, Virginia pine L, White oak M

Table 4.6. Mean values for measured and predicted species composition based on individual stand proportions in regenerating stands following clearcutting in 48 stands in Virginia and West Virginia. P values less than 0.05 indicate significant differences about the distribution medians between measured and predicted samples as calculated by the Wilcoxon Signed Rank test.

Species Group	Measured	Predicted	P value
	……..(%)……..		
Black Cherry	8	9	0.3797
Conifers	1	1	0.7819
Maples	20	23	0.4060
Midstory	10	8	0.9419
Oaks	12	12	0.8012
Other Overstory	12	8	0.0397
Pioneer	20	20	0.1460
Yellow-poplar	17	19	0.0466
Total	100.00	100.00	

5. CONCLUSIONS

The results of these studies suggest that the identity of Appalachian hardwood stands may be changing as they transition from second to third growth forests following clearcut. This trend away from oak dominated forests has been forecast by many researchers on moderate to highly productive sites (Loftis and McGee 1993). Oaks appear to have successfully regenerated on subxeric sites. While temporal shifts in species composition are expected as stands develop following heavy disturbance, the increased presence of black cherry and yellow-poplar is expected to be a lasting one.

On our sites, there were no significant differences found for oaks in upper canopy proportion in the clearcut stands compared to the mature stands at this time. Without additional action however, the declining trend for oaks is expected to continue in submesic stands (Beck and Hooper 1986, Hilt 1985, Ward and Stephens 1994). In the successful cases of oak regeneration, research has shown that large advance reproduction along with vigorous stump-sprouting is the key to surviving the intense competition from other species following heavy disturbance (Loftis 1990b, Johnson et al. 2002, Sander et al. 1976). Given the composition of the advance reproduction beneath the mature stands, which was dominated by maples and midstory species, the species composition in the regenerating stands is not surprising. These species are typically not expected to regenerate aggressively after clearcutting with the exception of maple sprouts. The remaining species groups apart from the oaks were sparse as advance reproduction, leaving room for aggressive pioneer, black cherry, and yellow-poplar species to colonize following harvest. Oaks were only numerous in the smaller size classes and for this advance reproduction to continually develop either timely or regular preharvest disturbance is required (Loftis 1983a).

Paramount to the implementation of any silvicultural treatment is a reliable estimate of regeneration potential. There have been several guidelines and models developed for various parts of the United States to either assess regeneration potential, or predict regeneration (Dey 1991, Belli et al. 1999, Steiner et al. 2008). The results of a reliable regeneration model can help landowners determine if, in fact, there will be regeneration problems where anticipated, or warn of unexpected consequences of scheduled harvests. Our results suggest that the REGEN expert system framework can be adapted to fit the needs of managers in a variety of forest communities and has the potential to be a useful tool during the decision making process of regeneration silviculture. The RKBs developed for the Appalachians of Virginia and West Virginia were found to explain 32% ($R^2 = 0.32$) of the variation in species composition of developing stands in that area. Tests for differences in distributions between measured and predicted populations found that only the other overstory and yellow-poplar distributions were statistically different. In light of these findings, the RKBs appear to provide reasonable accuracy on average across the sample sites in the Appalachians of Virginia and West Virginia. Care should be taken when interpreting individual stand results however as the coefficient of determination (R^2) for individual stands ranged from 0.00 to 0.98. One standard deviation of the model error was typically within about ± 20% for a species group. Because REGEN is an expert system, it can be adapted quickly based on the expert user's knowledge of local regeneration ecology and improved gradually as additional research becomes available.

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7. APPENDICES

Appendix A. Measured and predicted proportions by species group and sample stand.

Stand	R^2	Black Cherry			Conifers			Maples			Midstory			Oaks			Other Overstory			Pioneer			Yellow-poplar		
		Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ
Submesic01	0.48	0.01	0.01	0.00	0.00	0.03	0.03	0.55	0.30	-0.25	0.46	0.06	-0.40	0.31	0.23	-0.09	0.08	0.04	-0.04	0.01	0.07	0.06	0.10	0.28	0.18
Submesic02	0.00	0.01	0.00	-0.01	0.00	0.00	0.00	0.06	0.27	0.21	0.46	0.07	-0.39	0.31	0.12	-0.19	0.04	0.03	-0.01	0.02	0.08	0.06	0.10	0.42	0.32
Submesic03	0.23	0.01	0.00	-0.01	0.00	0.00	0.00	0.17	0.23	0.06	0.30	0.20	-0.10	0.00	0.18	0.18	0.52	0.16	-0.36	0.00	0.07	0.07	0.00	0.16	0.16
Submesic04	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.25	0.13	0.27	0.08	-0.19	0.08	0.25	0.17	0.35	0.14	-0.21	0.00	0.13	0.13	0.18	0.14	-0.03
Submesic05	0.20	0.21	0.05	-0.17	0.00	0.00	0.00	0.09	0.35	0.26	0.00	0.03	0.03	0.09	0.15	0.07	0.03	0.02	-0.01	0.20	0.16	-0.04	0.39	0.24	-0.15
Submesic06	0.41	0.00	0.02	0.02	0.00	0.00	0.00	0.33	0.54	0.21	0.29	0.05	-0.25	0.33	0.17	-0.17	0.00	0.02	0.02	0.04	0.11	0.07	0.00	0.10	0.10
Submesic07	0.10	0.23	0.02	-0.21	0.00	0.00	0.00	0.00	0.16	0.16	0.04	0.26	0.22	0.10	0.06	-0.05	0.04	0.04	0.00	0.40	0.23	-0.17	0.19	0.23	0.04
Submesic08	0.98	0.26	0.29	0.03	0.00	0.00	0.00	0.00	0.02	0.02	0.04	0.01	-0.03	0.00	0.00	0.00	0.08	0.05	-0.03	0.30	0.31	0.01	0.32	0.33	0.01
Submesic09	0.72	0.07	0.12	0.05	0.00	0.00	0.00	0.00	0.16	0.16	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.07	0.07	0.19	0.27	0.08	0.74	0.37	-0.38
Submesic10	0.49	0.00	0.01	0.01	0.00	0.00	0.00	0.30	0.12	-0.18	0.00	0.00	0.00	0.18	0.04	-0.14	0.32	0.35	0.03	0.00	0.07	0.07	0.20	0.41	0.21
Submesic11	0.54	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.18	0.18	0.11	0.00	-0.11	0.08	0.04	-0.04	0.21	0.28	0.07	0.00	0.15	0.15	0.61	0.35	-0.26
Submesic12	0.73	0.00	0.02	0.02	0.00	0.00	0.00	0.23	0.17	-0.06	0.06	0.13	0.06	0.23	0.16	-0.06	0.03	0.11	0.08	0.06	0.16	0.10	0.39	0.25	-0.13
Submesic13	0.62	0.14	0.09	-0.05	0.03	0.00	-0.03	0.27	0.18	-0.09	0.05	0.05	0.00	0.11	0.10	-0.01	0.00	0.01	0.01	0.16	0.32	0.16	0.24	0.25	0.00
Submesic14	0.45	0.35	0.02	-0.33	0.00	0.02	0.02	0.05	0.12	0.07	0.00	0.05	0.05	0.00	0.05	0.05	0.00	0.15	0.15	0.10	0.28	0.18	0.50	0.32	-0.18
Submesic15	0.23	0.00	0.04	0.04	0.00	0.00	0.00	0.47	0.33	-0.14	0.00	0.09	0.09	0.16	0.17	0.01	0.22	0.03	-0.19	0.03	0.16	0.13	0.13	0.17	0.05
Submesic16	0.55	0.00	0.05	0.05	0.00	0.01	0.01	0.00	0.29	0.29	0.00	0.03	0.03	0.00	0.07	0.07	0.11	0.08	-0.03	0.26	0.22	-0.04	0.63	0.26	-0.37
Submesic17	0.35	0.26	0.10	-0.15	0.00	0.00	0.00	0.21	0.23	0.02	0.00	0.00	0.00	0.09	0.21	0.12	0.00	0.17	0.17	0.44	0.19	-0.25	0.00	0.10	0.10
Submesic18	0.28	0.36	0.31	-0.05	0.00	0.00	0.00	0.36	0.14	-0.22	0.03	0.04	0.01	0.06	0.02	-0.05	0.06	0.04	-0.02	0.12	0.17	0.05	0.00	0.28	0.28
Submesic19	0.25	0.00	0.14	0.14	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.04	0.04	0.00	0.04	0.04	0.15	0.26	0.11	0.75	0.30	-0.45	0.10	0.13	0.03
Submesic20	0.60	0.00	0.18	0.18	0.00	0.00	0.00	0.40	0.16	-0.24	0.04	0.06	0.03	0.11	0.01	-0.10	0.05	0.04	-0.01	0.38	0.37	-0.01	0.02	0.19	0.17
Submesic21	0.35	0.00	0.17	0.17	0.00	0.00	0.00	0.35	0.10	-0.25	0.00	0.06	0.06	0.00	0.00	0.00	0.30	0.03	-0.27	0.25	0.39	0.14	0.10	0.24	0.14
Submesic22	0.08	0.00	0.15	0.15	0.00	0.00	0.00	0.04	0.16	0.12	0.04	0.04	-0.01	0.04	0.00	-0.04	0.21	0.08	-0.13	0.46	0.30	-0.16	0.21	0.26	0.05
Submesic23	0.53	0.04	0.07	0.03	0.04	0.01	-0.03	0.29	0.19	-0.10	0.00	0.11	0.11	0.08	0.18	0.10	0.38	0.05	-0.33	0.13	0.31	0.18	0.08	0.09	0.00
Submesic24	0.03	0.00	0.04	0.04	0.00	0.01	0.01	0.29	0.07	-0.22	0.17	0.12	-0.05	0.42	0.10	-0.32	0.00	0.07	0.07	0.08	0.23	0.15	0.00	0.36	0.36

Appendix. A cont. Measured and predicted proportions by species group and sample stand.

Stand	R^2	Black Cherry			Conifers			Maples			Midstory			Oaks			Other Overstory			Pioneer			Yellow-poplar		
		Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ	Meas.	Pred.	Δ
Submesic25	0.62	0.00	0.03	0.03	0.00	0.01	0.01	0.09	0.22	0.13	0.09	0.16	0.07	0.00	0.05	0.05	0.09	0.05	-0.04	0.73	0.32	-0.41	0.00	0.16	0.16
Submesic26	0.86	0.00	0.02	0.02	0.05	0.01	-0.04	0.42	0.38	-0.04	0.12	0.09	-0.03	0.26	0.18	-0.08	0.00	0.05	0.05	0.03	0.08	0.05	0.13	0.20	0.07
Submesic27	0.00	0.05	0.05	-0.01	0.00	0.00	0.00	0.09	0.53	0.44	0.27	0.01	-0.26	0.31	0.13	-0.18	0.05	0.07	0.02	0.04	0.06	0.02	0.18	0.15	-0.03
Submesic28	0.29	0.09	0.06	-0.03	0.00	0.00	0.00	0.06	0.26	0.20	0.06	0.08	0.01	0.09	0.09	0.00	0.03	0.04	0.01	0.41	0.17	-0.24	0.25	0.31	0.06
Submesic29	0.15	0.04	0.10	0.07	0.00	0.00	0.00	0.21	0.04	-0.17	0.21	0.12	-0.09	0.14	0.04	-0.10	0.07	0.02	-0.05	0.14	0.32	0.18	0.18	0.36	0.18
Submesic30	0.70	0.08	0.04	-0.04	0.00	0.01	0.01	0.04	0.06	0.02	0.01	0.04	0.03	0.00	0.05	0.05	0.16	0.14	-0.02	0.33	0.47	0.14	0.37	0.21	-0.16
Submesic31	0.42	0.03	0.03	0.00	0.00	0.00	0.00	0.02	0.13	0.11	0.02	0.16	0.14	0.00	0.04	0.04	0.13	0.12	-0.01	0.68	0.26	-0.42	0.11	0.25	0.14
Submesic32	0.11	0.03	0.20	0.18	0.00	0.00	0.00	0.22	0.17	-0.05	0.02	0.01	-0.01	0.02	0.23	0.21	0.17	0.10	-0.07	0.44	0.18	-0.26	0.10	0.10	0.00
Submesic33	0.20	0.15	0.30	0.16	0.00	0.00	0.00	0.04	0.08	0.04	0.03	0.17	0.14	0.00	0.00	0.00	0.00	0.03	0.03	0.70	0.20	-0.50	0.08	0.22	0.14
Submesic34	0.06	0.18	0.04	-0.14	0.00	0.00	0.00	0.07	0.07	0.00	0.00	0.03	0.03	0.00	0.10	0.10	0.02	0.00	-0.02	0.07	0.21	0.14	0.03	0.07	0.04
Submesic35	0.85	0.07	0.03	-0.04	0.00	0.00	0.00	0.09	0.18	0.09	0.11	0.11	0.01	0.00	0.03	0.03	0.03	0.00	-0.03	0.04	0.16	0.12	0.04	0.23	0.19
Submesic36	0.00	0.25	0.54	0.29	0.00	0.00	0.00	0.22	0.08	-0.14	0.60	0.06	-0.53	0.00	0.00	0.00	0.07	0.00	-0.07	0.08	0.39	0.31	0.00	0.12	0.12
Submesic37	0.37	0.70	0.54	-0.16	0.00	0.00	0.00	0.30	0.23	-0.07	0.15	0.03	-0.11	0.00	0.00	0.00	0.22	0.02	-0.20	0.27	0.51	0.24	0.00	0.09	0.09
Submesic38	0.70	0.18	0.23	0.05	0.00	0.00	0.00	0.54	0.36	-0.18	0.45	0.11	-0.34	0.00	0.00	0.00	0.05	0.04	-0.01	0.19	0.20	0.01	0.00	0.19	0.19
Subxeric01	0.81	0.00	0.01	0.01	0.00	0.00	0.00	0.39	0.27	-0.12	0.08	0.17	0.09	0.35	0.22	-0.13	0.00	0.05	0.05	0.02	0.10	0.08	0.16	0.18	0.02
Subxeric02	0.09	0.00	0.03	0.03	0.03	0.00	-0.03	0.15	0.47	0.32	0.00	0.04	0.04	0.24	0.16	-0.08	0.18	0.14	-0.04	0.03	0.08	0.05	0.36	0.08	-0.29
Subxeric03	0.06	0.02	0.00	-0.02	0.00	0.04	0.04	0.08	0.38	0.30	0.00	0.20	0.20	0.00	0.23	0.23	0.22	0.16	-0.06	0.00	0.00	0.00	0.67	0.00	-0.67
Subxeric04	0.62	0.00	0.01	0.01	0.05	0.00	-0.05	0.19	0.34	0.15	0.00	0.04	0.04	0.25	0.15	-0.10	0.37	0.26	-0.11	0.04	0.08	0.04	0.10	0.09	-0.01
Subxeric05	0.98	0.00	0.01	0.01	0.00	0.00	0.00	0.74	0.69	-0.05	0.03	0.06	0.03	0.11	0.15	0.03	0.06	0.01	-0.05	0.00	0.04	0.04	0.06	0.05	-0.01
Subxeric06	0.33	0.04	0.01	-0.03	0.08	0.11	0.03	0.35	0.28	-0.07	0.00	0.02	0.02	0.00	0.24	0.24	0.54	0.19	-0.35	0.00	0.07	0.07	0.00	0.09	0.09
Subxeric07	0.64	0.01	0.01	0.00	0.00	0.00	0.00	0.27	0.33	0.06	0.13	0.09	-0.04	0.34	0.26	-0.08	0.17	0.07	-0.10	0.08	0.09	0.01	0.00	0.15	0.15
Subxeric08	0.66	0.10	0.00	-0.10	0.00	0.09	0.09	0.40	0.28	-0.12	0.01	0.14	0.13	0.43	0.29	-0.14	0.03	0.00	-0.03	0.01	0.07	0.06	0.01	0.12	0.11
Subxeric09	0.53	0.00	0.02	0.02	0.00	0.00	0.00	0.13	0.26	0.13	0.13	0.11	-0.02	0.00	0.21	0.21	0.00	0.00	0.00	0.65	0.33	-0.32	0.09	0.08	-0.02
Subxeric10	0.75	0.00	0.00	0.00	0.01	0.00	-0.01	0.03	0.00	-0.03	0.29	0.21	-0.09	0.64	0.49	-0.14	0.00	0.02	0.02	0.03	0.28	0.25	0.00	0.00	0.00
$\bar{x}$	0.44	0.08	0.09	0.01	0.01	0.01	0.00	0.22	0.24	0.02	0.12	0.10	-0.02	0.14	0.14	0.00	0.12	0.07	-0.05	0.20	0.20	0.00	0.12	0.15	0.04

Appendix B. Rankings and parameters for the Xeric REGEN Knowledge Base.

Xeric	Advance Reproduction					New Seedlings			Root-Suckers			Stump-Sprouting		
	Sprouts	Large	Medium	Small	Germinants	Rank	# Stems	Est. Prob.	Rank	# Stems	Est. Prob.	Est. Prob.	Logistic1	Logistic 2
ash	7	8										0.7		
basswood	8											0.8		
beech	7	8							8	4	0.1	0.5		
black cherry	6	7	8									0.7		
black locust	3	4	5	6	8	8	4	0.2	8	4	0.2	0.7		
black oak	2	3	5	6	7	8	3	0.3					3.153339	-0.2053537
blackgum	3	5	6	7	8				8	6	0.3	0.6		
buckeye	8											0.5		
chestnut oak	1	2	4	5	6	7	3	0.3					2.462946	-0.0878581
cucumbertree	8											0.8		
dogwood	6	7	8									0.8		
fire cherry	7	8										0.8		
Fraser magnolia	8											0.5		
hemlock		8												
hickory	3	5	6	7	8							0.6		
ironwood	5	7	8									0.8		
n red oak	3	5	6	7	8	8	3	0.3					3.111055	-0.1076234
pitch pine		2	3	4	5									
red maple	2	4	5	6	7								4.044538	-0.1786859
sassafras	3	5	6	7	8				8	6	0.3			
scarlet oak	1	3	4	5	6	7	4	0.3					3.852062	-0.2178389
serviceberry	5	7	8									0.5		
shortleaf pine		2	3	4	5									
sourwood	1	3	4	5	6							0.8		
striped maple	8											0.7		
sugar maple	8												2.325832	-0.2418001
sweet birch	7	8											3.396065	-0.5270089
Table Mt. pine		2	3	4	5									
Virginia pine		1	2	3	4									
white oak	3	4	5	6	7	8	3	0.3					2.34028	-0.299584
white pine		2	3	4	5									
yellow birch	8											0.5		
yellow-poplar	6	8										0.9		

Appendix C. Rankings and parameters for the Subxeric REGEN Knowledge Base.

Subxeric	Advance Reproduction					New Seedlings			Root-Suckers			Stump-Sprouting		
	Sprouts	Large	Medium	Small	Germinants	Rank	# Stems	Est. Prob.	Rank	# Stems	Est. Prob.	Est. Prob.	Logistic1	Logistic 2
ash	5	7	8									0.7		
basswood	6	7	8									0.8		
beech	6	7							8	6	0.2	0.5		
black cherry	2	4	5	6	8	8	15	0.3				0.7		
black locust	1	2	3	4	5	7	6	0.3	7	6	0.2	0.7		
black oak	2	4	6	8									3.153339	-0.2053537
blackgum	7	8							8	3	0.1	0.6		
buckeye	7	8										0.5		
chestnut oak	1	3	5	8									2.462946	-0.0878581
cucumbertree	2	3	6	8								0.8		
dogwood	5	7	8									0.8		
fire cherry	2	3	4	5	6	8	20	0.2				0.8		
Fraser magnolia	6	7	8									0.5		
hemlock		7	8											
hickory	3	6	8									0.6		
ironwood	5	6	7	8								0.8		
n red oak	3	5	8										3.111055	-0.1076234
pitch pine		5	7											
red maple	1	4	8										4.044538	-0.1786859
sassafras	6	7	8						8	2	0.2			
scarlet oak	1	3	5	8									3.852062	-0.2178389
serviceberry	6	7	8									0.5		
shortleaf pine		5	7											
sourwood	4	6	8									0.8		
striped maple	6	7	8									0.7		
sugar maple	7	8											2.325832	-0.2418001
sweet birch	1	2	3	4	5	7	20	0.2					3.396065	-0.5270089
Table Mt. pine		5	7											
Virginia pine		4	6	8										
white oak	2	5	8										2.34028	-0.299584
white pine		1	2	4	5	5	2	0.3						
yellow birch	8											0.5		
yellow-poplar	1	2	3	4	5	6	20	0.3				0.9		

Appendix D. Rankings and parameters for the Submesic REGEN Knowledge Base.

Submesic	Advance Reproduction					New Seedlings			Root-Suckers			Stump-Sprouting		
	Sprouts	Large	Medium	Small	Germinants	Rank	# Stems	Est. Prob.	Rank	# Stems	Est. Prob.	Est. Prob.	Logistic1	Logistic 2
ash	4	5	6	7	8							0.7		
basswood	1	2	4	6	7							0.8		
beech	6	8							8	10	0.3	0.5		
black cherry	1	2	4	6	8	8	20	0.4				0.7		
black locust	1	2	3	4	5	8	25	0.4	7	6	0.4	0.7		
black oak	3	6	8										3.153339	-0.2053537
blackgum	6	8							8	3	0.1	0.6		
buckeye	8											0.5		
chestnut oak	4	7											2.462946	-0.0878581
cucumbertree	5	7	8									0.8		
dogwood	8											0.8		
fire cherry	1	2	3	4	5	7	20	0.3				0.8		
Fraser magnolia	6	7										0.5		
hemlock		8												
hickory	5	8										0.6		
ironwood	7	8										0.8		
n red oak	2	5	8										3.111055	-0.1076234
pitch pine		8												
red maple	3	6	8										4.044538	-0.1786859
sassafras	6	8							8	6	0.2			
scarlet oak	4	6	8										3.852062	-0.2178389
serviceberry	6	7	8									0.5		
shortleaf pine		8												
sourwood	6	8										0.8		
striped maple	5	8										0.7		
sugar maple	7	8											2.325832	-0.2418001
sweet birch	1	2	4	5	6	7	20	0.2					3.396065	-0.5270089
Table Mt. pine		8												
Virginia pine		8												
white oak	4	6	8										2.34028	-0.299584
white pine		2	3	4	5	8	3	0.3						
yellow birch	5	6	7	8								0.5		
yellow-poplar	1	2	3	4	5	7	30	0.3				0.9		

Appendix E. Rankings and parameters for the Mesic REGEN Knowledge Base.

Mesic	Advance Reproduction					New Seedlings			Root-Suckers			Stump-Sprouting		
	Sprouts	Large	Medium	Small	Germinants	Rank	# Stems	Est. Prob.	Rank	# Stems	Est. Prob.	Est. Prob.	Logistic1	Logistic 2
ash	2	3	5	8								0.7		
basswood	1	3	5	8								0.8		
beech	4	5	6	8					8	10	0.3	0.5		
black cherry	1	2	3	4	5	7	20	0.4				0.7		
black locust	2	4	5	6	7	8	15	0.3	8	5	0.3	0.7		
black oak	4	6	8										3.153339	-0.2053537
blackgum	7	8							8	3	0.1	0.6		
buckeye	4	5	6	8								0.5		
chestnut oak	5	7											2.462946	-0.0878581
cucumbertree	2	4	5	7	8							0.8		
dogwood	4	5	7	8								0.8		
fire cherry	1	2	3	4	5	6	20	0.3				0.8		
Fraser magnolia	4	6	7	8								0.5		
hemlock		4	6	8										
hickory	4	6	7	8								0.6		
ironwood	7	8										0.8		
n red oak	4	6	8										3.111055	-0.1076234
pitch pine		8												
red maple	3	5	7	8									4.044538	-0.1786859
sassafras	7	8							8	3	0.1			
scarlet oak	5	7											3.852062	-0.2178389
serviceberry	6	7	8									0.5		
shortleaf pine		8												
sourwood	6	8										0.8		
striped maple	4	6	7	8								0.7		
sugar maple	2	4	5	6	8								2.325832	-0.2418001
sweet birch	1	2	3	4	5	6	25	0.3					3.396065	-0.5270089
Table Mt. pine		8												
Virginia pine		8												
white oak	5	7	8										2.34028	-0.299584
white pine		2	4	6	7	8	3	0.3						
yellow birch	2	4	5	6	7	8	15	0.2				0.5		
yellow-poplar	1	2	3	4	5	6	30	0.4				0.9		

Appendix F. Mean importance values by species and site class in mature and regenerating stands on the Appalachian Plateau in West Virginia. Importance values were calculated as the mean of plot frequency and stem density both expressed as a proportion for each species.

Species	Mean Importance Values			
	subxeric (n=9)		submesic (n=32)	
	mature	harvested	mature	harvested
Am chestnut	0.00	0.02	0.00	0.00
Am holly	0.01	0.00	0.00	0.00
ash	0.00	0.05	0.01	0.03
aspen	0.00	0.00	0.00	0.00
basswood	0.00	0.00	0.01	0.03
beech	0.01	0.01	0.10	0.08
black cherry	0.00	0.05	0.05	0.14
black locust	0.00	0.03	0.01	0.04
black oak	0.08	0.13	0.03	0.04
blackgum	0.07	0.05	0.01	0.04
buckeye	0.00	0.00	0.00	0.00
chestnut oak	0.12	0.13	0.04	0.03
cucumber	0.00	0.19	0.03	0.03
dogwood	0.00	0.01	0.00	0.01
fire cherry	0.00	0.00	0.00	0.11
Fraser mag	0.00	0.00	0.03	0.02
hemlock	0.01	0.00	0.05	0.00
hickory	0.06	0.08	0.05	0.03
ironwood	0.00	0.00	0.01	0.03
n red oak	0.03	0.08	0.02	0.05
red maple	0.39	0.45	0.17	0.19
sassafras	0.02	0.09	0.02	0.03
scarlet oak	0.06	0.08	0.02	0.02
serviceberry	0.01	0.04	0.01	0.03
sourwood	0.12	0.05	0.03	0.03
spruce	0.00	0.01	0.00	0.00
striped maple	0.00	0.08	0.03	0.09
sugar maple	0.00	0.00	0.21	0.16
sweet birch	0.02	0.10	0.03	0.20
sycamore	0.00	0.00	0.00	0.00
white oak	0.07	0.06	0.04	0.01
white pine	0.03	0.01	0.00	0.00
yellow birch	0.00	0.00	0.01	0.02
yellow-poplar	0.00	0.20	0.08	0.26
Total	1.12	2.02	1.10	1.74