Oak Regeneration After Clearcutting on Steep Slopes in the Ridge and Valley Province of Southwest Virginia

by

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INTRODUCTION

There is a natural tendency to view Appalachian upland oak forests as stable and enduring by virtue of their vast extent. However, these forests are relicts of an association whose single most important species, American chestnut (*Castanea dentata* (Marsh.) Borkh.), was eliminated suddenly, within the lifetime of most of the present dominant individuals. The post-blight forests of the 1980's, shaped in addition by extensive clearcutting and high-grading early in this century, are transitional ecosystems whose present makeup may change under various management options. Increased fire control, whole-tree harvesting, and shorter rotations will further alter conditions for replacement of present stands from the environments which produced them. Although regeneration problems are seen in a different light under current emphasis on fiber and energy production, rapid reestablishment of individuals well-suited to management objectives remains a vital concern. The development of dependable silvicultural techniques for regenerating oaks has been identified as the most pressing research need in eastern hardwood forests (McLintock, 1979). Knowledge of natural replacement processes on upland oak sites of marginal commercial productivity must keep pace with the increased utilization likely to be made of such sites.

Oaks combine several attributes desirable from various management perspectives. When grown in dense stands, tree form is good and the wood produced highly valuable. Oaks are abundant mast producers and provide favorable habitat for many wildlife species. They are relatively disease-resistant, and maintain steady growth for many years. Because of their longevity, the forest manager has great latitude in the choice of rotation length. Furthermore, regeneration costs are avoided and rapid reoccupation of the site with oaks is assured when harvest coincides with appropriate structure and composition in both overstory and understory.

Seedlings which germinate after removal of an oak overstory have little chance of survival to maturity (McGee and Hooper, 1970). Replacement of oak depends primarily on two sources---sprouts from dormant buds at the base of cut stems ("stump sprouts") and individuals which had been present in the understory of the previous stand ("advance regeneration"). Stump sprouts are more likely to attain early dominance than advance regeneration stems, since fast-growing sprouts of chestnut oak (*Quercus prinus* L.) or northern red oak (*Quercus rubra* L.) commonly average 4-5 m in height within five years. Advance regeneration of these species rarely exceeds 3 m within the same period (Wendel, 1975; McGee, 1975). Despite their rapid early growth, stump sprouts have traditionally been considered a less desirable form of oak reproduction because of their high incidence of butt rot and poor form. However, low stump heights (Lamson, 1976), forest fire control, and high initial densities associated with modern forestry practices minimize these problems; a recent U.S. Forest Service guide (Sander et al., 1976) draws no distinction in quality between advance regeneration and sprout origin stems. European coppice experience suggests that the initial growth advantage of sprouts may not persist for more than about 40 years (Daniel et al., 1980).

The question of which stumps or which advance regeneration stems will provide the most vigorous post-harvest shoot growth is of considerable practical importance. Stands could be cut when an adequate number of vigorous oak stems were projected in the new stand. In addition, silvicultural treatments could be applied which would bring the uncut stand toward a proper structure and composition. Most attempts at projecting future stem growth have examined the relationship between stump diameter and sprout production (Johnson, 1977;Wendel, 1975;Johnson, 1979), or original "seedling" size and subsequent shoot elongation (Sander, 1972). In the case of advance regeneration, larger individuals generally grow faster, while it is the smaller stumps which are more dependable sprout producers. In addition to their implications for forest management, such studies help to clarify the ecological strategies of the oaks. Of special interest are the relative contributions of seedlings and sprouts to the perpetuation of oaks, and how these roles might shift with changes in stand age or site quality, or among different oak species.

This study attempts to develop predictive models for shoot growth of stump sprouts and advance regeneration stems. Whereas similar studies to date have considered either seedling or stump sprout development alone, useful comparisons can be drawn by conducting parallel investigations of these two forms of oak reproduction. This study extends research reported in the literature to drier, less productive sites than hitherto examined, and investigates the effect of site directly in the models. Factors not considered in most other studies, such as age, recent growth increment, and root collar diameter are included as independent variables. Although growth response is only measured over a two-year period, the permanent nature of the plots allows easy resampling in the future. An examination of several older clearcuts is also included to assess the persistence of the early growth advantage exhibited by stump sprouts.

The following objectives were thus established:

1. To investigate the effects of site quality, type of regeneration, and the interaction between these two factors on height and biomass increment of oak regeneration during the first two growing seasons after harvest on steep slopes in the Ridge and Valley Province.

2. To develop models for predicting the early post-harvest growth and frequency of stump sprouts, and the growth of advance reproduction stems of black, scarlet, and chestnut oaks on steep slopes in the Ridge and Valley Province of southwestern Virginia from characteristics measurable prior to overstory removal.

3. To determine the effect of time since clearcutting on the relative size of stems of advance regeneration and stump sprout origin.

The first two objectives were met by measuring certain variables on tagged trees and advance regeneration stems before or immediately following harvest, then recording periodic shoot growth two years later. The third objective involved measurements on paired sprout and seedling origin stems in older clearcuts near the primary study area.

MATERIALS AND METHODS

The primary study area, in which the two-year development of oak stems was examined (Objectives #1 and #2), was located in the Ridge and Valley Physiographic Province at midslope (760 m elevation) on the southeast face of Potts Mountain, a northeast-southwest- trending ridge in Craig County, Virginia. Parent materials are nutrient-poor Silurian sandstones and shales (Butts, 1933) which form mostly coarse-textured, shallow, heavily leached soils of the typic Dystrochrept, and typic and arenic Hapludult soil groups (Morin, 1978). Slopes are steep, generally 30-40 percent. Annual precipitation in nearby Newcastle, Virginia averages 965 mm, and is evenly distributed throughout the year. The frost-free season on Potts Mountain is about 160 days.

The second growth forests on Potts Mountain are typical of those found on thousands of hectares of the more exposed mountain slopes in the Appalachians (Braun, 1950). Oak species such as chestnut, scarlet (_Q. coccinea_ Muenchh.) and black (_Q. velutina_ Lam.) are overstory dominants on most midslope positions, while pitch pine (_Pinus rigida_ Mill.) is prominent on south-facing spur ridges. Red maple (_Acer_ rubrum L.), yellow-poplar (Liriodendron tulipifera L.), and northern red oak become important in the upper reaches of coves. Blackgum (Nyssa sylvatica Marsh.) and dogwood (Cornus florida L.) are important understory tree species on a variety of sites. An ericaceous shrub layer, dominated by mountain laurel (Kalmia latifolia L.), huckleberry (Gaylussacia baccata (Wang) K. Koch), and blueberries (Vaccinium spp.) is especially well-developed on the drier sites. Herbaceous species and tree seedlings are most abundant where this shrub layer is lacking or of less influence (McEvoy et al., 1980).

Potts Mountain sites were divided into four easily recognizable types on the basis of vegetation composition and structure, as follows: (1) mixed hardwood, with overstory consisting of a variety of relatively mesic species; shrub stratum poorly developed and the herb layer well-developed and diverse, but largely devoid of ericads; (2) mixed oak, with overstory predominantly oak and ericaceous understory discontinuous; (3) mixed oak-pine, characterized by an overstory mostly of oaks, but with scattered pine, and a well-developed shrub component dominated by Kalmia, Gaylussacia, and Vaccinium and (4) mixed pine, with overstory dominated by pines, oaks in a slightly subordinate position, and a heavy shrub layer predominantly of ericads and bear oak (Quercus ilicifolia Wang.) (McEvoy et al., 1980).

The older stands used to determine the relative size of stems of different origin at different stand ages (Objective #3) were located either south of the primary study area on Potts Mountain or on adjacent ridges (Table 1). All were within 70 km of the primary area, on similar sandstone parent material, and at a comparable midslope position. All stands but one were on the southeast face of the NE-SW trending ridges. Vegetation composition was similar to either the mixed oak or mixed oak-pine types on the main study area.

As part of a cooperative research effort between Virginia Polytechnic Institute and State University, the Westvaco Corporation, and the U.S. Forest Service, nine 40 x 40 m plots were established in the fall of 1977 to provide a permanent record of the vegetational changes associated with whole-tree harvesting. The plots were situated within three non-contiguous compartments totaling 61 ha and extending over 5.3 km distance (Figure 1). Of the nine plots, eight were used in the investigation of oak regeneration development, along with two smaller plots (400 m^2 and 800 m^2) established in the summer of 1978. The locations of these ten plots were chosen to include the entire range of growing conditions within the study area. One plot was representative of the mixed hardwood vegetation type, while mixed oak,

Table 1: Location of study areas within the Ridge and Valley Physiographic Province in southwestern Virginia.

Study Area Number	Time Since Clearcut (as of 1980)	Elevation	Aspect	Location Description
1 (Main study area)	2 years	760 m	SE	Along USFS Rd. intersecting State Rt. 311, 8 miles west of Newcastle, Va. and 1 mile west of USFS Rt. 604.
2	5 years	800 m	SE	1/4 mile west of State Rt. 311 along USFS road that intersects Rt. 311, 1/2 mile west of main study area.
3	5 years	600 m	SE	Above USFS Rt. 604 about 5 miles SW of State Rt. 311.
4	5 years	675 m	SE	Above USFS Rt. 604 about 4 miles SW of State Rt. 311.
5	12 years	615 m	SE	Above USFS Rt. 630, 1 mile from its intersection with State Rt. 621 and about 10 miles east of US 460.
6	17 years	770 m	NW	East of State Rt. 601, about 1 mile from its intersection with State Rt. 632, near the Craig-Giles line in Craig County.
7	12 years	770 m	W	Across Rt. 601 from Study Area 6.
8	11 years	860 m	S	East of State Rt. 613, 1/2 mile north of Kire, Va.
9	28 years	920 m	S	East of Mill Creek, Giles County, about 3 miles south of Narrows, Va. Accessible by foot along Mill Creek.

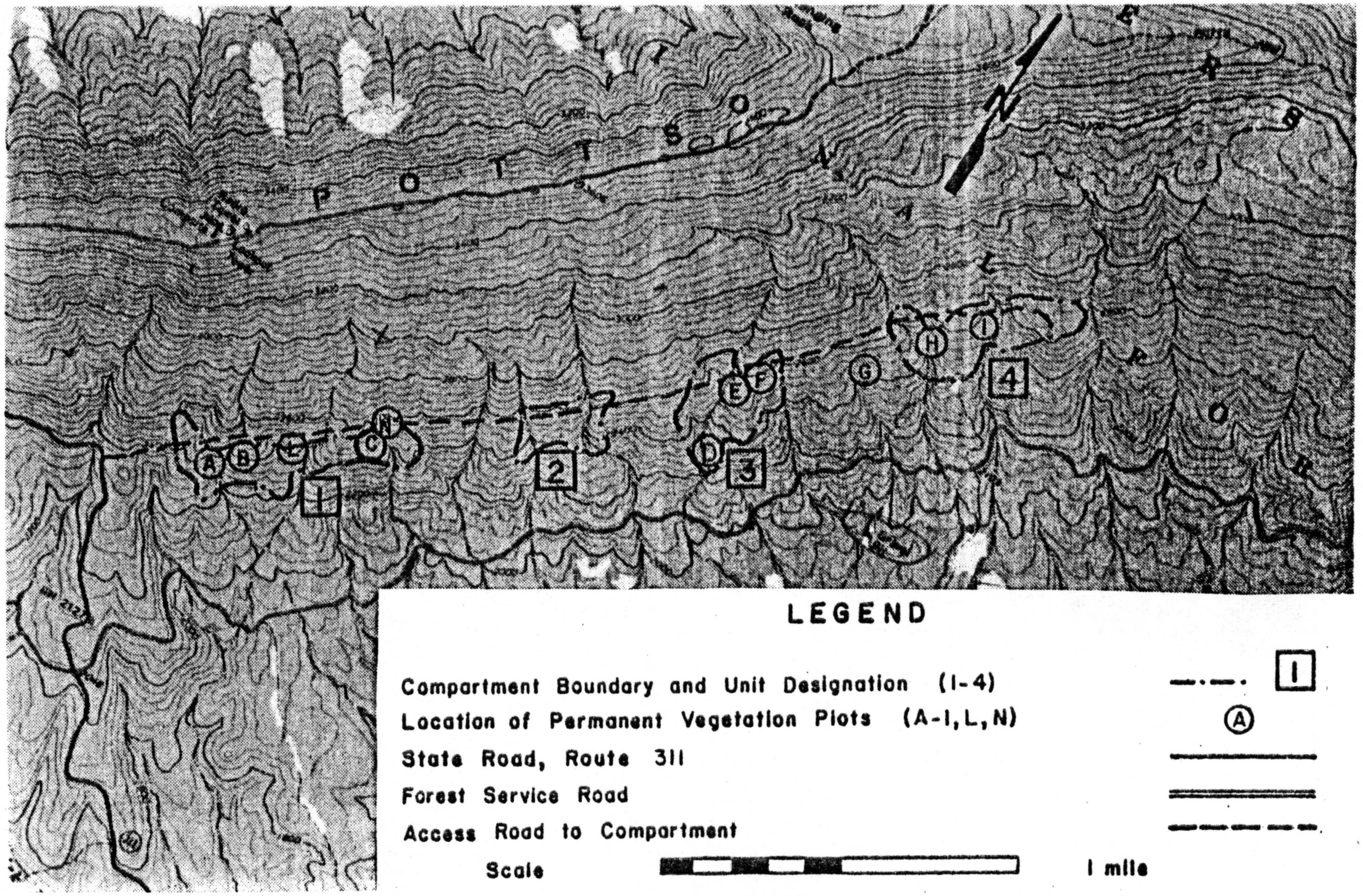

Figure 1: Location of plots within main study area (Potts Mountain, Craig Co., Va.) (from U.S.G.S., Potts Creek quadrangle, Va:W.Va.). Plot D is mixed hardwood vegetation type; plots A, F, and I are mixed oak; plots C, L, and N are mixed oak-pine; and plots B, E, and H are mixed pine. Compartment 2 and plot G were uncut.

mixed oak-pine, and mixed pine vegetation types were each represented by three plots.

The classification of stands according to vegetation composition produced groups which also differed in terms of site productivity. Table 2 shows that when three separate indices of productivity are applied to the four vegetation types, a gradient of increasing growth potential is revealed, ranging from mixed pine, mixed oak-pine, mixed oak, to mixed hardwood. This sequence is hypothesized to represent a gradient of decreasing moisture stress. Cluster analysis of the nine original plots according to various structural attributes (foliage density profile, stand basal area, canopy cover within several height strata, etc.) also produced groups which were similar to those formed on the basis of composition (McEvoy et al., 1980). Thus, classification according to vegetation type was used to stratify the oak data into biologically meaningful units for statistical analysis.

At the time of plot establishment all oak stems greater than 5 m in height were identified, tagged at the base, and located on a coordinate grid. Total height and crown length were recorded for each tree. Between August, 1978 and March, 1979 all stems greater than 1.5 m in height were cut back to within fifteen cm of ground level, and removed from

Table 2: Productivity indices for the four vegetation types occurring in the main study area, Potts Mountain, Craig Co., Va. Values are from 8 of the 9 plots in the main study area.

Vegetation Type	No. of Stands Represented	Forest Site Quality Index[1]	Site Index[2]	Basal Area Incr./Tree[3] (cm^2)
Mixed pine	3	5.3	37	46
Mixed oak-pine	1	8.0	49	44
Mixed oak	3	9.3	59	65
Mixed hardwood	1	14.0	71	67

[1]Based on aspect, slope percent, and slope position. High value indicates high potential productivity (Wathen, 1977).

[2]Based on total height for upland oaks at age 50 (Olson, 1959).

[3]Growth increment during 1968-1978 for stems (of all species) which were alive and taller than 5 m at the time of sampling.

the plots. Removal was by a commercial cable logging system, except in isolated, relatively flat areas where rubber-tired skidders were utilized. Shortly after each area was cleared, age at stump height, inside-bark diameter, and radial growth over the past ten years were determined for each tagged oak. Diameter was recorded as the average of two perpendicular measurements, while radial growth represented the mean of two typical radii on opposite sides of the stump. Estimates of age were considered to be within two years of true stem age.

The schedule of cutting was such that all plots except one (Area I---Figure 1) were cut during the dormant season. Oak stumps in that area (harvested on August 15) resprouted in September and October, but all sprouts were killed by frost before winter.

In the fall of 1980, at the end of the second growing season after harvest, each oak stump was relocated and sprout growth assessed. Diameter of each sprout was measured 3 cm above ground level, as well as height of the tallest three sprouts from each stump. At about the same time sprouts of black, scarlet, and chestnut oaks spanning a wide range of sizes were collected outside the study plots. After height and diameter measurements were made on these sprouts in the field, leaves and stems of each individual were bagged separately, dried (65 C), and weighed. Biomass regressions were developed from these data for each species-vegetation type combination in order that biomass production could be estimated non-destructively for each tagged stump.

Statistical analysis of stump sprout response was directed at answering two questions: (1) Which stumps sprout?, and (2) Which stump characteristics are associated with vigorous sprouting? Stumps which failed to produce any sprouts were omitted from the analysis of sprout vigor.

Two analytical techniques were used to distinguish between those stumps that sprouted and those that did not. The Wilcoxon Rank Sum procedure was used to test the hypothesis that no differences exist in measured tree characteristics between sprouting and nonsprouting stumps. The decision level for all statistical tests in this and other sections of this dissertation was $\alpha = .05$. Discriminant function analysis (Guertin and Bailey, 1970) was applied to the two classes of stumps in order to determine how well sprouting and non-sprouting stumps could be differentiated on the basis of tree and site variables.

Sprout production data were treated in three basic ways:

1. Effects of species and vegetation type were tested by an analysis of covariance (ANACOVA) procedure.

2. In order to identify the tree attributes associated with vigorous sprouting, the Rank Sum test was used to test for differences in sprouting characteristics among several levels of the various tree variables.

3. Least squares regression analysis was used to arrive at prediction models for sprout production. Sprout data were stratified into species-vegetation type combinations, and no combination which contained fewer than fifteen stumps was considered.

Advance Regeneration Development

After the harvesting operation was completed in each of the ten study areas, the plots were divided into 10 x 10 m cells. At the four corners of each cell, each oak advance regeneration stem within one or two $1m^2$ quadrats (depending on the density of oak individuals in the plot) was mapped, tagged, measured, and classified as seedling, seedling sprout, or stump sprout. Where means and ranges are presented for various facets of size or growth of several categories of oak advance regeneration they are based on these 352 randomly sampled individuals. Means are presented in the text to one decimal place beyond the level of precision of the original measurement. Because a wider range of sizes was needed in order to develop regression equations broader in applicability, the two largest advance regeneration stems greater than 30 cm in height in each cell were also sampled. The regression analyses and analyses of covariance include these additional large individuals and are thus based on a total sample of 518 oak stems.

Seedlings were defined as individuals whose stem had never died back and resprouted, seedling sprouts had resprouted from the base of stems less than 5 cm in diameter, and stump sprouts had originated from larger stems. Root collar diameter, stem diameter 2 cm above ground level, and stem height were recorded. Stem age, height growth during the last two years, and height growth during the first two years of stem life were determined assuming terminal bud scars marked the passage of one year. A preliminary sample of small oak individuals indicated that aging by terminal bud scars gave estimates within two years of those obtained by sectioning at the base in 75 percent of all cases. In most of the remaining instances, counting bud scars gave an underestimate of stem age because of dieback and subsequent resprouting. Root collar diameter was a reasonably good index of total age of the genet, as well as a measure of root size. Correlations between root age and root diameter ranged from r=.76 for chestnut oak to r=.66 for scarlet oak in a preliminary sample of 120 individuals.

At the end of the 1979 growing season, mortality or dieback/resprouting were recorded for tagged individuals. The number of 1979 growth flushes recognizable from terminal bud scars was recorded. Although no incidence of multiple flushing was observed among understory individuals in adjacent uncut stands, the increase in light, moisture, and nutrients expected in the clearcut area might stimulate bud elongation during the same season as bud formation.

In October, 1980, advance regeneration stems were remeasured. Final stem diameter was recorded, as well as two-year elongation of the leading shoot on each individual. Mortality, dieback, and number of flushes were recorded as before.

As in the previous section the analytical approach was to examine a relationship within several categories of experimental unit and ecosystem type. The central relationship was the effect of attributes representing initial size, age, and vigor of an oak individual on growth during the early years following harvesting. Whereas the experimental units in the first section were cut stems from trees taller than 5 m in height of three species of oak, the units in the second section were seedlings, seedling sprouts, or stump sprout advance regeneration. Like the stump sprouts, advance regeneration stems were also of three species, but were further divided into those which died back and resprouted during the two year period ("resprouts") and those which continued growing from the original leading shoot ("intact stems"). In this section the four vegetation types were grouped into two site quality classes in order to maintain enough individuals in each category to adequately describe the basic growth relationships. Accordingly, mixed hardwood and mixed oak types were combined into a "medium quality" category, and mixed oak-pine and mixed pine classed together as "low quality" sites. Multiple regression was again used to examine the relationships between advance regeneration parameters and growth response.

Analysis of advance regeneration data was divided into four parts:

1. <u>Comparison of growth variables among various categories of individuals</u>. Growth variables were height growth (measured directly), diameter growth (difference between initial and final values), and number of 1979 and 1980 flushes. The Wilcoxon Rank Sum test, a non-parametric test of location difference, was used in the analysis because in

most cases the variables were not normally distributed.

2. *Development of "best" prediction models.* A backwards stepwise regression procedure was used to decide which variables and interaction terms were most important in predicting height growth and diameter growth. Because of the problems which arise in multiple regression when independent variables are highly correlated (Gordon, 1968), a ridge regression technique was used to adjust the coefficients associated with each term (Gunst and Mason, 1980). Equations were developed only for seedling and seedling sprout stems, because of inadequate numbers of oak stump sprout advance regeneration.

3. *Comparison of growth equations among different categories of advance regeneration.* In order to compare models for different species or site quality classes, the independent variables involved must be the same. Applying principal component analysis (PCA), with the Varimax rotation method (Guertin and Bailey, 1970; Daultrey, 1976) to the advance regeneration parameters measured immedi-

ately after harvest gave a series of factors which were orthogonal to one another, thus avoiding the problem of multicollinearity alluded to above (Guertin and Bailey, 1978). Thus, in the models produced, the independent variables used to explain height or diameter growth were the first four factor scores obtained from PCA. Equations were tested for equality of regression coefficients. If the coefficients were not different between data sets, testing for a difference in intercept was comparable to analysis of covariance, with the four factors as covariates. If the difference in regression coefficients between two data sets was not equal to zero, coefficients for individual factors were tested for equality.

4. Effects of different independent variables on height and diameter growth. Comparative effects were indicated by the order of entry of the four factors mentioned above when a forward stepwise procedure was used to develop a prediction model. The effect of the individual factors was tested by comparing height and diameter growth for individuals scoring "high" in a factor vs. individuals classified as "low". Again, the non-parametric

Wilcoxon Rank Sum test was used because of non-normality in the distribution of factor scores.

Development of Seedling and Sprout Origin Stems beyond Age Two

In the summer of 1980 eight areas were located on Potts Mountain or nearby ridges which had been clearcut since 1950 (Table 1). Criteria used in the choice of study areas were that few residual trees had been left after harvest, that present vegetation fit into the mixed oak or mixed oak-pine categories, and that chestnut oak was a major component of the current stand. Three of the stands chosen were five years old, three were approximately twelve, and two were about seventeen and twenty-eight years old.

A modification of the point-centered quarter method (Mueller-Dombois and Ellenberg, 1974) was used to sample seedling and sprout origin chestnut oaks. Sample points were located by pacing randomly chosen distances along a transect. At each point, the nearest stem of each type was located within one randomly chosen quadrant of the four formed by the intersection of the transect and its perpendicular. In this section, sprout origin stems were those arising from stumps associated with the last cutting. Seedling origin stems were all single-stemmed chestnut oaks not included in the sprout origin category; i.e., seedlings and seedling sprouts. In all stands except the oldest, identification of sprout origin stems was based on the presence of the undecayed stump. In the 28 year-old stand identification was more difficult, and sometimes depended on characteristics such as multiple lower stems or stem form. Seedling origin stems were only considered if they were as old or older than the stand itself.

For the sprout origin stems, total height and diameter 1.4 m above ground level were measured on the tallest stem in the sprout clump. Distance from point to stump, diameter of stump, and number of major stems arising from the stump were also recorded. Height, diameter, and distance were also measured for the nearest seedling origin stem; age was estimated by felling the tree and counting annual rings at the base. Dominance class (Daniel, 1980) was recorded for individuals of both types.

Wilcoxon's Signed Rank test was used to examine the paired data for differences in height or diameter between seedling and sprout origin chestnut oaks. Data were divided into four stand age classes, and further subdivided into mixed oak or mixed oak-pine vegetation types.

Differences between the two vegetation types in sprout and seedling height and diameter were tested with Wilcoxon's

Rank Sum test both within stand and within the broader stand age classes.

Correlation analysis was employed to detect relationships between stump size or number of sprouts originating from a stump and size of the largest sprout. Correlations between seedling age and size parameters were also generated.

The effects of vegetation type and stem origin on density (Stems/ha=10,000/(mean distance (m))^2) were assessed within the five, twelve, and seventeen-year-old stands by the non-parametric (Wilcoxon) test of location difference. Too few individuals were sampled within the 28-year-old stand for valid density comparisons. For comparative purposes, density of chestnut oak stems of seedling and sprout origin in the main study area two years after cutting was extracted from the data collected during the annual vegetation sampling of the shrub stratum (stems 1-5 m in height), which took place in March,1981. A stratified random sampling design was employed, in which all stems were measured within 50% of eight 40 x 40m plots.

Several statistical packages were used in the data analyses. SAS was used for most analyses presented above (Helwig and Council, 1979). The paired data referred to in the last section were analyzed using the SGNRANK routine on the

VPI Nonparametric Statistics Package (Pirie, 1981). The ridge regression analysis was contained in the REGRESS program supplied by the Virginia Tech Statistics Department.

RESULTS

Stump Sprout Development

Sprout Frequency

The frequency of oak stumps for which at least one sprout was present after two years was highest (76 percent) for chestnut oak (Table 3). Sprout frequency also appeared to increase with decreasing site quality, with only 53 percent of oak stumps sprouting in the mixed hardwood vegetation type, in contrast to 79 percent in mixed pine.

Diameter, age, basal area increment during 1969-1978, and height for trees which did and did not produce sprouts were compared by species (Table 4). In all cases in which statistically significant differences occurred, the oaks which failed to produce sprouts were larger, older, and faster-growing during the ten years prior to harvest.

Given the apparent effects of site and tree attributes illustrated in Tables 3 and 4, one might reasonably expect to predict with some accuracy whether a cut stump will or will not sprout. Therefore, discriminant analysis using the four tree measures and a site quality class variable was performed for each species. The results for chestnut oak

Table 3: Percent of stumps within the main study area (Potts Mountain, Craig Co., Va.) which produced at least one stump sprout. Figures in parentheses represent numbers of stumps sampled.

Oak Species	Mixed Hardwood	Mixed Oak	Mixed Oak-Pine	Mixed Pine	Total
	Vegetation Type				
Chestnut	58 (24)	74 (193)	71 (115)	87 (111)	76 (443)
Scarlet	0 (1)	69 (48)	67 (84)	74 (120)	70 (253)
Black	40 (5)	44 (39)	86 (7)	73 (33)	58 (84)
Total	53 (30)	68 (280)	70 (206)	79 (264)	

Table 4: Comparison of four attributes of the parent tree for sprouting and non-sprouting stumps of chestnut, scarlet, and black oak in the main study area (Potts Mountain, Craig Co., Va.). Means (within species) followed by different letters differ at α = .05 level (Wilcoxon Rank Sum test).

	Basal Diameter Inside Bark (cm)	Age (yrs)	Basal Area Increment 1969-1978 (cm^2)	Height (m)
	Chestnut oak			
Trees whose stumps produced at least one sprout				
mean	16.6a	62.1a	55.0a	11.0a
range	(5.0-68.0)	(25-89)	(3.3-431)	(5.2-23.8)
Trees which did not produce sprouts				
mean	26.0b	90.7b	92.5b	12.9b
range	(5.6-65.0)	(30-215)	(6-634)	(5.5-30.2)
	Scarlet oak			
Trees whose stumps produced at least one sprout				
mean	16.4r	63.4r	60.6r	10.7r
range	(4.6-38.1)	(37-114)	(4.1-315)	(4.9-21.3)
Trees which did not produce sprouts				
mean	21.2s	66.2s	81.2s	11.9s
range	(5.8-54.0)	(35-82)	(6-377)	(5.2-21.6)
	Black oak			
Trees whose stumps produced at least one sprout				
mean	12.9x	57.3x	39.1x	9.7x
range	(5.8-27.3)	(35-82)	(4.5-155)	(5.2-15.8)
Trees which did not produce sprouts				
mean	21.0y	61.7x	92.4x	12.5y
range	(6.4-88.0)	(50-69)	(5.7-618)	(5.2-26.5)

were typical of the three species. The discriminant function classified 318 trees out of a total of 401 correctly into sprouting or non-sprouting categories; assuming that <u>all</u> stumps would sprout yielded 309 correct classifications, only nine fewer than the discriminant function. Thus, although sprouting and non-sprouting trees differ in mean values for several measurable characteristics, these characteristics provide little capability to predict sprouting behavior on an individual stump basis.

<u>Estimating Sprout Biomass from Sprout Dimensions</u>

Various measures of sprout size were used to predict leaf, stem, and total aboveground biomass for chestnut, black and scarlet oak.

The regression equations for estimating stem weight are of the form

$$\text{Stem weight} = a(\text{diameter})^b$$

was chosen, based on plots of the data, plots of residuals, and comparison of R^2 values with other models (Appendix 1). Inclusion of height as a predictor (independent) variable along with diameter added little to the fit. Diameters included in the samples ranged from 2 to 40 mm, and encompassed the range of sprout sizes encountered in the two-year-old stand. F tests indicated that equations representing the species-vegetation type combinations differed significantly and thus could not be combined into single equations for all species or for all vegetation types. Only one equation accounted for less than three-fourths of the variation in stem weight.

The log/log model for leaf weight as a function of diameter (Appendix 2) was selected over alternative models for the same reasons as for stem weight relationships. Because large individuals were sampled at a time in the fall when the sprouts no longer carried a full complement of leaves, these equations are based on a smaller range of diameters---2 to 20 mm---than those for stem weight. Again, F tests indicated that separate equations were required for each of the 11 species-vegetation type combinations represented in the study plots. The coefficients of determination (R^2) ranged from .54 to .90 for the leaf weight equations.

Estimates of total biomass were needed for stems as large as 4 cm in diameter. Since accurate leaf weights were not available for the larger individuals included in the stem weight equations, leaf weights for those individuals were estimated from the equations developed for the smaller sizes, and incorporated into the data base for the total biomass equations. Since leaf weight probably accounted for less than 30 percent of total biomass in individuals 2-4 cm in diameter (based on plots of leaf weight/stem weight ratio vs. diameter in the 2-20 mm range), errors caused by extrapolation of the leaf weight equations were unlikely to exceed 10 percent of total biomass. Such use of the leaf weight equations was considered acceptable because the absolute values pedicted by the total biomass equations were of less concern than the relative estimates in differentiating among stumps. Model form for the regression equations for total biomass (Table 5) was the same as for stem and leaf weight. However, because of the complications associated with the leaf component, R^2 values are not included.

Sprout Production

The three variables chosen to represent the production of each stump were total sprout biomass, height of the tallest sprout, and number of sprouts originating from the stump. Species appeared to differ in sprout production per stump (Table 6) in the same sequence as for probability of sprouting (Table 3), with all three production variables decreasing in the order chestnut oak, scarlet oak, and black oak. For instance, biomass production per stump ranged from

Table 5: Equations for predicting total aboveground biomass (dry weight) of oak stump sprouts within the main study area (Potts Mountain, Craig Co., Va.). Equations are based on a total sample of 411 sprouts, including 76 stems for which the leaf component was estimated.

Model: Total Biomass (g) = a (stem diameter, mm)^b

Oak Species	Vegetation Type	n[1]	a	b
Chestnut	Mixed hardwood	41	.207	2.40
Black	Mixed hardwood	16	.338	2.16
Chestnut	Mixed oak	51	.186	2.40
Scarlet	Mixed oak	51	.188	2.38
Black	Mixed oak	26	.238	2.35
Chestnut	Mixed oak-pine	39	.377	2.22
Scarlet	Mixed oak-pine	46	.474	2.14
Black	Mixed oak-pine	35	.287	2.28
Chestnut	Mixed pine	45	.231	2.34
Scarlet	Mixed pine	42	1.02	1.80
Black	Mixed pine	19	.336	2.20

[1] Number of stems sampled.

Table 6: Means for several oak sprout production variables by species and by vegetation type two growing seasons after clearcutting in the main study area (Potts Mountain, Craig Co., Va.). Only stumps which produced at least one sprout are included.

	Total Biomass g/stump	Average Height of Tallest Sprout per Stump (cm)	Sprout Density No./Stump	Stumps No./ha	Total Biomass kg/ha	Sprout Density No./ha
Species						
Chestnut oak	1490	174	18.8	240	360	4510
Scarlet oak	1240	124	12.7	130	160	1650
Black oak	950	110	10.1	30	30	300
Total	-	-	-	400	550	6460
Vegetation Type						
Mixed hardwood	1350	179	18.5	100	140	1850
Mixed oak	1530	178	17.7	400	610	7080
Mixed oak-pine	1150	122	17.8	510	590	9080
Mixed pine	1350	149	13.4	430	580	5760

almost 1.5 kg for chestnut oak to less than 1 kg for black oak, while sprout heights were 174 and 110 cm for chestnut and black oak, respectively. However, unlike sprouting probability, obvious trends for biomass or number of sprouts were not evident among vegetation types, although height of the tallest sprout was particularly high (nearly 180 cm) where site productivity was highest.

Because of the low density of oak stumps in the mixed hardwood vegetation type (Table 6), total biomass production per unit area for oak stump sprouts was lower in that type (140 kg/ha over the two year period) than in the mixed oak, mixed oak-pine, or mixed pine types, which all produced about 600 kg/ha. Furthermore, because of the high density of chestnut oak stumps, biomass production for that species was even more outstanding relative to black and scarlet oak when expressed on an areal basis than on a per stump basis. Total biomass accumulation for stump sprouts of the three oak species over the entire study area was 544 kg/ha over the two year period, or approximately one-fourth ton/ha/yr. per year.

In order to ascertain that the effects mentioned above were not the product of tree characteristics which differed among species or among vegetation types, analysis of covariance was performed. Preliminary tests had indicated that sprout production characteristics generally did not differ for a species among plots within a vegetation type. Such differences were significant only for scarlet oak in the mixed pine type and chestnut oak in the mixed oak type (Appendix 3). Therefore, vegetation type and species were the main effects being tested in the ANACOVA procedure, while diameter, age, height, and basal area increment were the covariates. Such an analysis assumes that the effects of the covariates do not differ among categories of the main variables. Therefore, F tests were first performed to detect differences in the slope coefficients (b's) for the model

$$\text{Sprout production variable} = a + b_1(\text{diameter} + b_2(\text{age}) + b_3(\text{height}) + b_4(\text{basal area increment})$$

among species within a vegetation type, and among types within a species. Differences in slope coefficients were found only among species in the mixed oak-pine type for the dependent variable Hmax (height of the tallest sprout). Therefore, this combination was excluded from the analysis of covariance which was employed to test for differences in adjusted means of production variables between species and vegetation type pairs (Table 7). The analyses indicated

Table 7: Comparisons of adjusted means[1] of stump sprout production variables among species within a vegetation type and among vegetation types within a species in the main study area (Potts Mountain, Craig Co., Va.). Comparisons listed are those pairs which differ at a comparisonwise decision level of $\alpha = .05$.

Species Differences

Vegetation Type	Production Variable	Species With Larger Adjusted Mean	Species With Smaller Adjusted Mean
Mixed oak	Hmax (height of tallest sprout)	Chestnut oak	Scarlet oak
		Chestnut oak	Black oak
	Num (number of sprouts per stump)	Chestnut oak	Scarlet oak
Mixed pine	Totbio (total biomass per stump)	Chestnut oak	Black oak
	Hmax	Chestnut oak	Scarlet oak
		Chestnut oak	Black oak
	Num	Chestnut oak	Black oak

Type Differences

Species	Production Variable	Type With Larger Adjusted Mean	Type With Smaller Adjusted Mean
Chestnut oak	Totbio	Mixed pine	Mixed hardwood
		Mixed pine	Mixed oak-pine
	Hmax	Mixed hardwood	Mixed oak-pine
		Mixed oak	Mixed oak-pine
		Mixed pine	Mixed oak-pine

[1]Adjusted for tree diameter, age, height, and basal area increment.

that, given similar tree characteristics, chestnut oak stumps had a production advantage over at least one of the other species on both poor and medium quality sites. For chestnut oak, differences in sprout production among vegetation types were present, with stumps in the mixed pine type exhibiting highest biomass production, while sprouts in the mixed oak-pine type were shortest. Differences among vegetation types were not present for scarlet or black oak.

The results reported above suggest that species of oak and vegetation types differ in their capacity for sprout production. Therefore, separate models of stump sprout production from characteristics of the parent tree were developed for each species-type combination. Stepwise regression techniques were used to remove variables which contributed little to the models; tree crown variables were eliminated entirely because of their generally low correlations with the measures of production. Final choice of model was based not only on the fit of the model to the data, but also on the ability of the model to predict, as expressed by the Press statistic (Allen, 1974). Except for black oak in the mixed pine vegetation type---for which the equation was based on only 24 observations---the proportion of the total variation in the production (dependent) variables accounted for by the "best" regression models was very

Table 8: "Best" regression models for predicting total biomass, maximum stem height and number of stems of stump sprouts from attributes of the parent stem two years after clearcutting on Potts Mountain, Craig Co., Va.

Oak Species	Vegetation Type	Dependent Variable[1]	Independent Variables[2]	n	R^2
Chestnut	Mixed oak	Totbio	Age, Age^2, Dia^2, Dia/Age	135	.13
		Hmax	Ht, Age, Dia^2, Dia^{2}xHt, Dia/BAI, Age^2	134	.20
		Num	Age, Ht, Age^2, BAI^2, Dia^2, Dia^{2}xHt	134	.23
	Mixed oak-pine	Totbio	Dia, Ht, BAI, Age^2, Dia^2, Dia^{2}xHt	77	.31
		Hmax	Age, Dia, Ht, BIA^2, Dia^2, Dia^{2}xHt	75	.23
		Num	BAI, Ht, Dia, BAI^2, Ht/Age, Dia/Age	81	.30
	Mixed pine	Totbio	Age, BAI, Ht, Age^2, Ht/Age, Dia^2	86	.34
		Hmax	Age, Age^2, Ht, BAI^2, Ht/Age, Dia, BAI	86	.24
		Num	Dia, Age, Age^2, Ht/Age	86	.25
Scarlet	Mixed oak	Totbio	Dia, Ht/Age, Dia^2, Dia^{2}xHt	32	.34
		Hmax	Age^2, Dia/Age, Dia^2, Dia, Dia^{2}xHt	32	.42
		Num	Age, Age^2, Dia, Dia^2	32	.31
	Mixed oak-pine	Totbio	BAI, Ht, Age^2, Ht/Age, Dia^2, Dia^{2}xHt	49	.24
		Hmax	Age, BAI, Age^2, Dia^2, Dia^{2}xHt	49	.33
		Num	Age, Ht, BAI^2, Ht/Age, Dia^2, Dia/BAI	49	.27
	Mixed pine	Totbio	Age, BAI, Dia, Ht^2, BAI^2, Dia/Age	81	.15
		Hmax	Dia, Age, Ht^2, Dia/Age	81	.11
		Num	Age, Age^2, Dia, Ht, Ht/Age, Dia/Age	81	.06
Black	Mixed pine	Totbio	Dia, Age^2, Dia/Age, Dia^{2}xHt, Dia/BIA	23	.71
		Hmax	Dia^2, BAI^2, Dia/Age, Dia^{2}xHt, Dia/BAI	23	.65
		Num	Dia, BAI, Dia/Age	24	.54

[1]Totbio=Total biomass/stump; Hmax=Height of tallest sprout/stump; Num=Number of sprouts/stump.

[2]Ht=Total tree height; Dia=Stump diameter inside bark; BAI=Basal area increment during 10 years before harvest; Age=Age at stump height.

low (Table 8). Because of the poor fit of most of the models, no attempt was made to compare equations developed from the different data sets, and the effects of the independent variables were examined further by a classification system described below.

Tree diameter, height, age, and basal area increment distributions for the combined chestnut, scarlet, and black oak data sets were divided into three nearly equal groups. Wilcoxon Rank Sum tests were then used to compare sprout production for stumps within the various groups of parent tree. Results for the combined data set (Table 9) were similar to those obtained for each species, or for each species-vegetation type combination. Stumps of the smaller trees, and the trees which grew most slowly during the last decade prior to harvest, produced the least biomass and the fewest sprouts after clearcutting. Stumps of the tallest trees produced the tallest sprouts. However, age appeared to have a negative impact on sprout production, especially sprout height.

Advance Regeneration Development

Condition of Advance Regeneration at Time of Harvest

The densities of oak advance regeneration immediately after overstory removal in the ten stands of the main study

Table 9: Means of sprout production variables from stumps on Potts Mountain, Craig Co., Va., classified into three levels of four attributes of the parent tree. Means, within variable groupings, followed by different letters differ at α=.05 level.[1] Means are based on data from chestnut, scarlet, and black oak.

Parent Tree Variable and Level	Sprout Production Variable: Total Biomass per Stump (g)	Height of Tallest Sprout per Stump (cm)	Number of Sprouts per Stump
Basal diameter inside bark			
< 11.0 cm	1130a	151a	11.6a
11.0-23.0 cm	1500b	153a	17.3b
> 23.0 cm	1420b	155a	21.8b
Height			
< 8.0 m	1130e	151e	11.9e
8.0-14.0 m	1400f	148e	16.3f
> 14.0 m	1600f	167f	22.0g
Age			
< 56 years	1300r	162r	14.7r
56-66 years	1440r	153s	16.5r
> 66 years	1200r	134s	18.0r
Basal area increment (1969-1978)			
< 16 cm²	1130x	151x	11.8x
16-79 cm²	1480y	154x	16.6y
> 79 cm²	1390y	154x	21.1z

[1]Wilcoxon Rank Sum test.

area (Table 10) reflect the effect of both species and vegetation type. Chestnut oak was the most abundant of the three species in all vegetation types. Total oak advance regeneration was greatest in the mixed oak type, where nearly 10,000 stems/ha were present, and least on the low quality mixed pine sites, where 1100 stems/ha were observed. Oaks were well-represented in the one mixed hardwood plot. However, 98 percent of the sampled individuals were true seedlings, which were generally less than 30 cm tall (Figure 2).

Several differences in height at the time of harvest among species and among types of advance regeneration (seedling, seedling sprout, and stump sprout) were found to be statistically significant. Chestnut oak seedling and stump sprout advance reproduction were significantly shorter than those of scarlet oak, while chestnut oak seedling sprouts were significantly shorter than both scarlet and black oak individuals of the same type. For all three species, sample means increased in the order seedlings < seedling sprouts < stump sprouts, although these differences were only statistically significant for chestnut oak (all categories) and scarlet oak (stump sprout height > seedling height). Perhaps the most revealing element in Figure 2 is the shortness of advance regeneration in all categories. Although sam-

Table 10: Number of oak advance regeneration individuals per hectare immediately after harvest in main study area (Potts Mountain, Craig Co., Va.). Number in parentheses is percentage of individuals in category which are true seedlings (seedlings/(seedlings + seedling sprouts + stump sprout advance regeneration)).

	Vegetation Type				
Species	Mixed Hardwood	Mixed Oak	Mixed Oak-Pine	Mixed Pine	Mean
Chestnut Oak	5160	8270	3250	780	3130(50)
Scarlet Oak	310	770	1320	220	620(51)
Black Oak	1250	450	530	100	360(52)
Total	6720 (98)	9490 (34)	5090 (51)	1100 (53)	

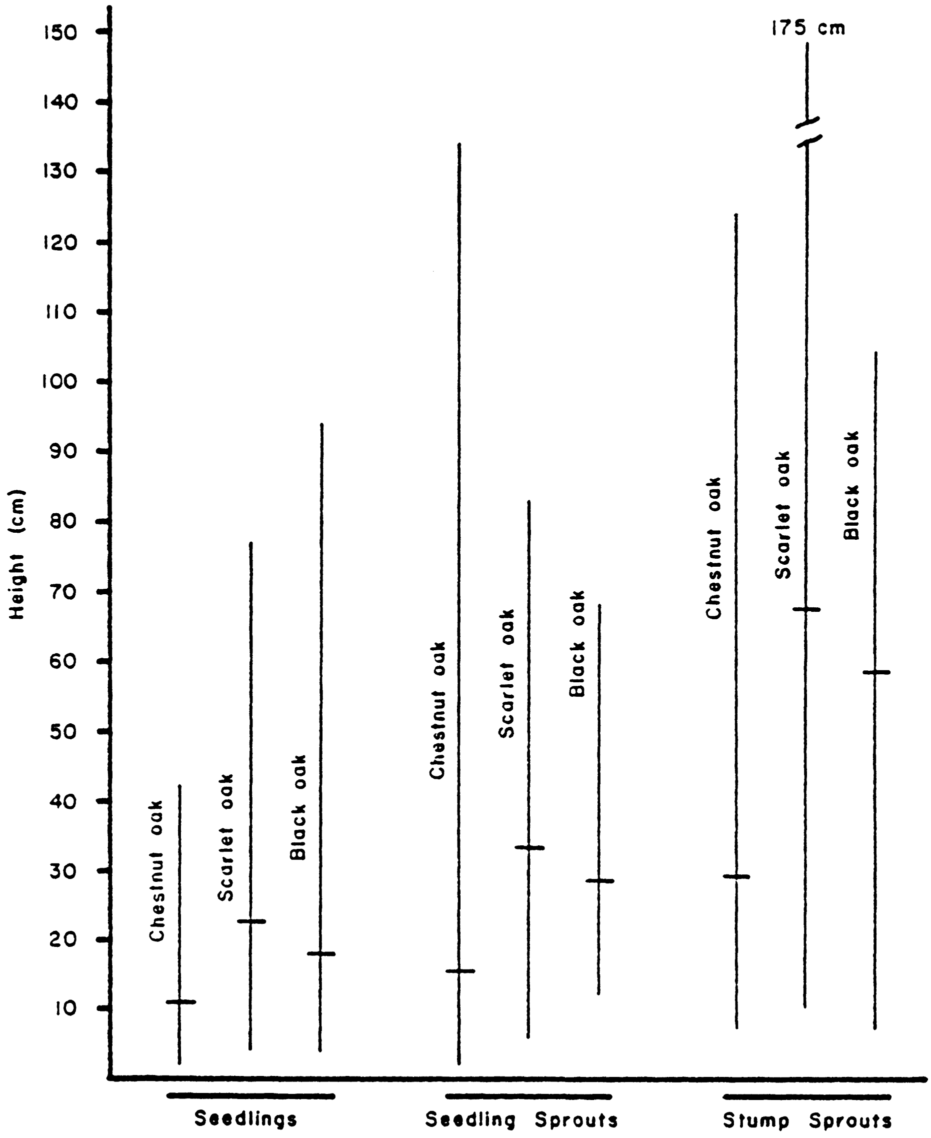

Figure 2: Mean (⊥) and range of heights for three categories of chestnut, scarlet, and black oak advance regeneration at time of harvest in the main study area (Potts Mountain, Craig Co., Va.).

pling occurred after the harvesting operation, in which all stems above breast height (1.4 m) were prescribed to be cut, few large understory oak individuals were present in pre-cut stands. A survey of the 1-5 m height stratum during the fall of 1977 (Sharik, unpublished data) revealed only 213 oak stems/ha taller than 1.4 m.

Survival and Resprouting

Of 352 oak stems randomly sampled at the time of harvest in the fall and winter of 1978-79, 9 percent had died, 33 percent had died back and resprouted from within 10 cm of ground level, and 58 percent maintained expansion of their original leader as of October, 1980. These proportions varied little among the three oak species, or among vegetation types. An effort was made to determine if individuals which died back and resprouted ("resprouts") differed in the characteristics which had been measured immediately after overstory removal from individuals which maintained normal growth ("intact stems"). Because of insufficient numbers of black and scarlet oaks in the study plots, this analysis was confined to seedling and seedling sprout chestnut oak individuals. The results indicated that resprouts were taller and older than intact stems at the time of harvest (Table 11). However, a discriminant function developed from the seven

Table 11: Means of variables measured immediately after harvest for resprout and intact chestnut oak seedling and seedling sprout advance regeneration in the main study area (Potts Mountain, Craig Co., Va.)

Category:	Resprout -- Individuals which had died back and re-sprouted within two years of harvest (n=80).	Intact -- Individuals whose original top was still alive two years after harvest (n=144).	Probability[1] that samples of two categories come from same population
Root diam. (mm) at root collar:	6.0	6 0	.48
Basal stem diam. (mm) 2 cm above ground:	3.8	3.2	.44
Height (cm):	15.5	11.9	.06
Age (yrs):	5.4	3.8	.002
Periodic height growth (cm) during 1977 & 1978 growing seasons:	5.4	6.0	.38
Periodic height growth (cm) during first two years of of stem life:	8.8	9.6	.39
Ratio of root diam. to basal stem Diam:	1.63	1.79	.66

[1]Test procedure: Wilcoxon Rank Sum.

measures of original size, age, and vigor listed in Table 11 failed to differentiate accurately between stems which continued growth and those which resprouted.

Shoot Growth Means

Species means for height and diameter growth of seedling, seedling sprout, and stump sprout advance regeneration during the two year post-harvest period (Table 12) indicated no case in which species within an advance regeneration type differed significantly in growth rate. On the other hand, scarlet oak stump sprout advance regeneration grew more rapidly in height and diameter than scarlet oak seedlings, and chestnut oak seedling sprouts increased more in diameter than seedlings of the same species. However, site quality, as estimated by vegetation type, had a strong effect on three measures of chestnut oak shoot growth (Tables 13 and 14). In all cases where differences between medium and low quality sites occurred, growth was more rapid in the higher quality areas. For example, intact seedlings grew twice as much in height on medium quality sites (15 cm) as on low quality sites (7 cm) (Table 13). The effect on height and diameter growth of intact stems appeared to be most pronounced for seedlings and seedling sprouts, less so for stump sprout advance regeneration. The effect of site

Table 12: Height and diameter growth of intact[1] advance regeneration of three oak species during the first two growing seasons following harvest on Potts Mountain, Craig Co., Va. Data for medium and low quality sites are combined. Range of values for each category is in parentheses.

Advance Regeneration Type	Chestnut oak	Scarlet oak	Black oak
	Species		
	Height Growth (cm)		
Seedling	12.4 (1-60) a[2] (x)[3]	8.8 (1-53) a (x)	10.4 (2-23) a (x)
Seedling Sprout	21.0 (2-109) a (x)	30.5 (9-52) a (xy)	17.4 (6-55) a (x)
Stump Sprout	23.8 (3-82) a (x)	30.6 (4-52) a (y)	12.0 (12-12) a (x)
	Diameter Growth (mm)		
Seedling	1.6 (0-4) a[2] (x)[3]	1.3 (0-5) a (x)	1.8 (0-4) a (x)
Seedling Sprout	2.7 (0-8) a (y)	5.0 (3-7) a (xy)	3.9 (0-10) a (x)
Stump Sprout	2.0 (0-9) a (xy)	5.3 (0-13) a (y)	5.0 (5-5) a (x)

[1]Individuals which continued to expand the original stem over the study period.

[2]Values within a row which are followed by the same letter (a or b) OUTSIDE of parentheses do not differ at $\alpha=.05$ (Wilcoxon Rank Sum Test).

[3]Values within a column which are followed by the same letter (x or y) INSIDE parentheses do not differ at $\alpha=.05$.

Table 13: Height and diameter growth and number of 1979 growth flushes for chestnut oak intact advance regeneration on sites of medium and low quality in the main study area (Potts Mountain, Craig Co., Va.) during the first two growing seasons following harvest. Range of values for each category is in parentheses.

Advance Regen. Type	Growth Variable	Site Quality Class: Medium Quality	Low Quality	Prob > Z[1]
Seedling	Height growth (cm)	15.8 (2-60)	7.1 (1-28)	.0002
	Diameter growth (mm)	1.9 (0-4)	1.1 (0-3)	.003
	No. of 1979 growth flushes	2.3 (1-4)	1.5 (1-3)	.0002
Seedling sprout	Height growth (cm)	28.2 (2-109)	13.5 (2-76)	.04
	Diameter growth (cm)	3.5 (0-8)	1.8 (0-6)	.01
	No. of 1979 growth flushes	2.0 (1-4)	1.8 (1-3)	.33
Stump sprout	Height growth (cm)	22.6 (3-82)	26.7 (9-46)	.51
	Diameter growth (mm)	2.0 (0-9)	2.0 (1-3)	.51
	No. of 1979 growth flushes	1.7 (1-3)	1.5 (1-2)	.78

[1]Probability that sample means in "medium" and "low quality" categories belong to the same population--Wilcoxon Rank Sum Test.

Table 14. Height and diameter growth and number of 1979 growth flushes for chestnut oak resprout advance regeneration on sites of low and medium quality in the main study area (Potts Mountain, Craig Co., Va.). Range of values for each category is in parentheses.

Advance Regen. Type	Growth Variable	Site Quality Class Medium Quality	 Low Quality	Prob > Z[1]
Seedling	Height growth (cm)	23.1 (6-50)	15.1 (3-38)	.03
	Diameter growth (mm)	4.8 (1-3)	3.7 (2-6)	.04
	No. of 1979 growth flushes	2.3 (1-3)	1.4 (1-2)	.003
Seedling sprout	Height growth (cm)	38.4 (2-144)	35.9 (8-109)	.93
	Diameter growth (cm)	6.6 (2-19)	5.2 (3-12)	.13
	No. of 1979 growth flushes	2.0 (1-4)	1.5 (1-2)	.04
Stump sprout	Height growth (cm)	113.2 (87-136)	30.7 (17-58)	.08
	Diameter growth (mm)	13.0 (9-17)	6.0 (4-10)	.12
	No. of 1979 growth flushes	2.4 (2-3)	1.7 (1-2)	.27

[1]Probability that sample means in "medium" and "low quality" categories belong to the same population--Wilcoxon Rank Sum Test.

quality on the number of 1979 growth flushes of intact advance regeneration is significant only in the seedling category. However, oak stems in clearcut areas of all types flushed more often than oaks in the understory of adjacent uncut stands, where casual observation revealed no instance of multiple flushing. The influences of site quality on growth response of chestnut oak resprouts (Table 14) were similar to those mentioned for intact stems, in that sites of higher quality supported greater shoot growth and more growth flushes than poor sites. However, unlike what had been observed for intact stems, resprout stump sprout advance regeneration growth was apparently affected by site quality, as were the number of growth flushes on resprouts from seedling sprout individuals.

The relative heights of stump sprout, seedling sprout, and seedling oak advance reproduction at the end of the study period (Figure 3) were unchanged from two years earlier (Figure 2). Advance regeneration stems were generally in an inferior position in the developing stand, with the tallest individuals (149 cm) similar in height to an average stump sprout leader (Table 6). Notably, two years after clearcutting, resprout chestnut oak stems were similar in stature to stems which had maintained normal shoot growth.

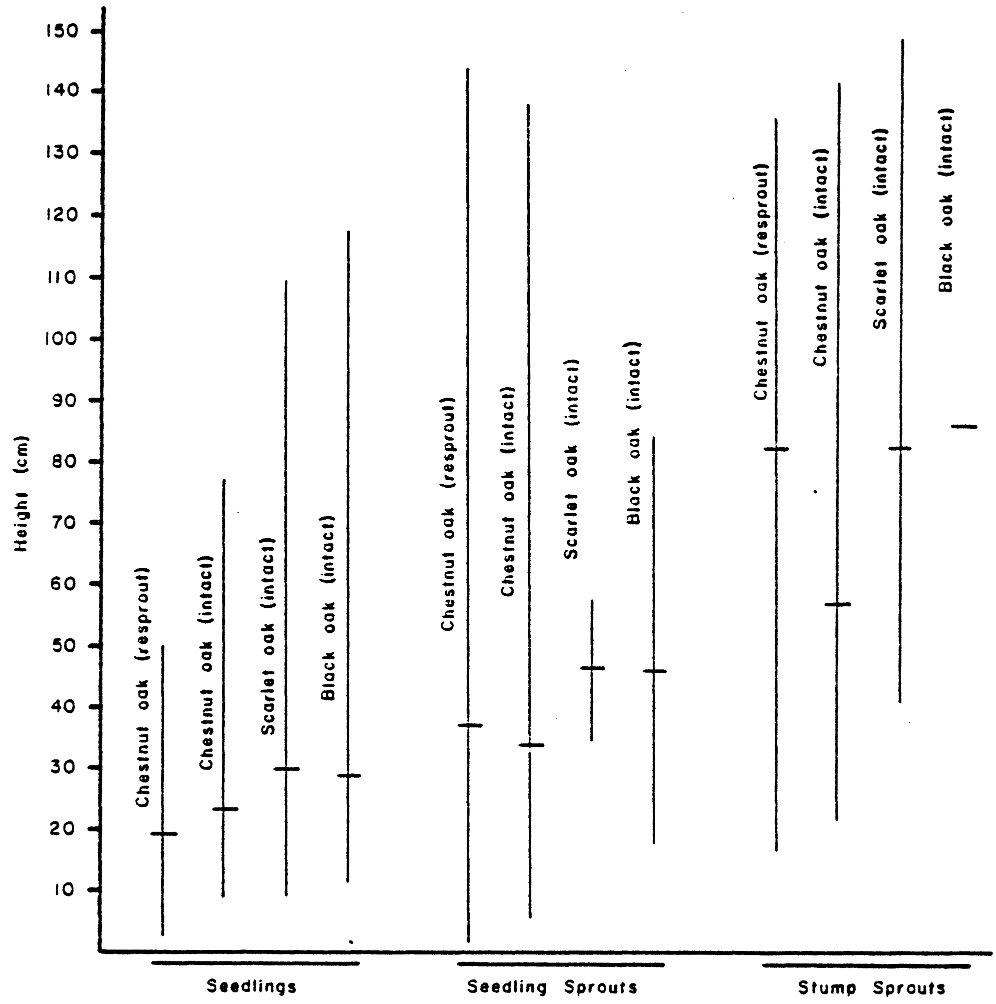

Figure 3: Mean (⊥) and range of heights for three categories of chestnut, scarlet, and black oak intact advance regeneration, and chestnut oak resprout advance regeneration two years after harvest in the main study area (Potts Mountain, Craig Co., Va.).

Prediction Equations for Height and Diameter Growth of Seedling and Seedling Sprout Advance Regeneration

The prediction equations derived for height and diameter growth of six categories of oak seedling and seedling sprout advance regeneration (Table 15) contained terms including root diameter in all twelve models, and stem diameter, height, and last two years' growth in all models but one. However, terms for first two years' height growth and age were absent from three and five equations, respectively. Coefficients of determination were consistently higher for the advance regeneration growth equations than for the corresponding stump sprout development models (Table 8). For chestnut oak the fit of the models was better for resprouting advance regeneration than for intact seedlings and seedling sprouts, except for height growth in the lower quality plots, where corresponding R^2's were equal. As with the "best" models for stump sprout growth, the proportion of variation accounted for by the models for intact black oak advance regeneration development exceeded the values for scarlet or chestnut oak.

Comparison of Growth Response among Various Categories of Advance Regeneration

Seven variables associated with the initial post-harvest measurements---root diameter, shoot diameter, shoot

Table 15: Prediction equations for height and diameter growth of seedling and seedling sprout advance regeneration on Potts Mountain, Craig Co., Va. Abbreviations: Htgr = cumulative height growth, 1979-1980; Diagr = cumulative diameter growth, 1979-1980; Diar = root diameter (mm), fall 1978; Dias = basal stem diameter (mm), 1978; Ht = height (cm), fall 1978; Age = age (yrs), 1978; Frst2 = Height growth (cm) during first two years of stem life; Last2 = height growth (cm), 1977-1978.

Oak Species	Resprout or Intact	Site Quality Class	Equation	R^2	n
Chestnut	Intact	Medium	$\mathrm{Htgr}=8.73+1.57\mathrm{Diar}+7.48\mathrm{Dias}-3.99(\frac{\mathrm{Diar}}{\mathrm{Dias}})+3.98(\frac{\mathrm{Diar}}{\mathrm{Dias}})^2+.35\mathrm{Ht}-2.05\mathrm{Age}-.13(\mathrm{Diar})^2$	.33	95
Chestnut	Intact	Medium	$\mathrm{Diagr}=1.16+.69\mathrm{Diar}-.17\mathrm{Age}-.27(\frac{\mathrm{Last2}}{\mathrm{Frst2}})-.02\mathrm{Diar}^2+.0003\mathrm{Dias}^2\mathrm{xHt}$	.41	95
Chestnut	Intact	Low	$\mathrm{Htgr}=1.95-3.29(\frac{\mathrm{Diar}}{\mathrm{Dias}})+.79\frac{\mathrm{Diar}^2}{\mathrm{Ht}}-.25\mathrm{Ht}+.64\mathrm{Age}-.24\mathrm{Last2}+.50\mathrm{Frst2}+7.00(\frac{\mathrm{Last2}}{\mathrm{Frst2}})+.13\mathrm{Dias}^2-.0001\mathrm{Dias}^2\mathrm{xHt}$	.82	47
Chestnut	Intact	Low	$\mathrm{Diagr}=-0.70+.0004\mathrm{Diar}+0.10(\mathrm{Diar}^2/\mathrm{Ht})+.11\mathrm{Age}+.45\mathrm{Ht}/\mathrm{Age}-.006\mathrm{Last2}-.002\mathrm{Diar}^2$	.40	48
Chestnut	Resprout	Medium	$\mathrm{Htgr}=-8.49+5.09\mathrm{Diar}+3.81(\mathrm{Diar}/\mathrm{Dias})+1.01(\mathrm{Diar}/\mathrm{Dias})^2-8.78(\mathrm{Diar}^2/\mathrm{Ht})+2.80\mathrm{Age}+21.9(\mathrm{Last2}/\mathrm{Frst2})-.0004(\mathrm{Dias}^2\mathrm{xHt})$	.70	50
Chestnut	Resprout	Medium	$\mathrm{Diagr}=2.58+.79\mathrm{Diar}+.19\mathrm{Dias}-.80(\mathrm{Diar}^2/\mathrm{Ht})+.95(\mathrm{Last2}/\mathrm{Frst2})+.005\mathrm{Dias}^2-.0001(\mathrm{Dias}^2\mathrm{xHt})$	.77	49
Chestnut	Resprout	Low	$\mathrm{Htgr}=1.25+1.18\mathrm{Diar}+7.16\mathrm{Dias}-17.1(\mathrm{Diar}/\mathrm{Dias})+7.1(\mathrm{Diar}/\mathrm{Dias})^2-.86(\mathrm{Diar}^2/\mathrm{Ht})-.20\mathrm{Ht}+2.04\mathrm{Last2}-13.02(\mathrm{Last2}/\mathrm{Frst2})$	.82	28
Chestnut	Resprout	Low	$\mathrm{Diagr}=1.11+.24\mathrm{Diar}+.55\mathrm{Dias}+.38(\mathrm{Diar}/\mathrm{Dias}^2-.42(\mathrm{Diar}^2/\mathrm{Ht})-.05\mathrm{Ht}+.11\mathrm{Frst2}-.96(\mathrm{Last2}/\mathrm{Frst2})+.02\mathrm{Dias}^2+.0007(\mathrm{Dias}^2\mathrm{xHt})$	.82	26
Scarlet	Intact	Combined	$\mathrm{Htgr}=.35+.71\mathrm{Diar}-.11\mathrm{Dias}-.48(\mathrm{Diar}/\mathrm{Dias})^2+.67(\mathrm{Ht}/\mathrm{Age})+.01\mathrm{Last2}+3.50(\mathrm{Last2}/\mathrm{Frst2})-.002\mathrm{Diar}^2$	.42	22
Scarlet	Intact	Combined	$\mathrm{Diagr}=1.00+.36\mathrm{Diar}-.52(\mathrm{Diar}^2/\mathrm{Ht})-1.31(\mathrm{Ht}/\mathrm{Age})+.80\mathrm{Last2}+.10\mathrm{Frst2}-.01\mathrm{Dias}^2$	.37	23

Table 15: Prediction equations for height and diameter growth of seedling and seedling sprout advance regeneration (continued).

Oak Species	Resprout or Intact	Site Quality Class	Equation	R^2	n
Black	Intact	Combined	$Htgr=4.36-.75Diar+3.06(Diar/Dias)-4.46(Diar/Dias)^2+4.01(Diar^2 x Ht)+.09Ht+1.05Last2-.008Dias^2-.0001(Dias^2 x Ht)$	.80	26
Black	Intact	Combined	$Diagr=.67-.06Dias+.62(Diar/Dias)-.41(Diar/Dias)^2+68(Diar^2/Ht)+.06Ht-.76(Last2/Frst2)-.01Diar^2+.00006(Dias^2 x Ht)$	.54	24

height, stem age, root diameter-shoot diameter ratio, height growth during 1977-78, and height growth during the initial two years of stem life---were reduced to four factors using principal component analysis. These four factors accounted for approximately 95 percent of the total variance contained in the variables included in the analysis. The rotated factor patterns for seedlings and seedling sprouts of all three oak species together, and for chestnut oak advance regeneration alone, were easily interpretable because of the relatively high loadings on specific variables (Table 16). Accordingly, for all three species, Factor 1 was designated "Old-Large Stems", Factor 2 "Large Root/Shoot", Factor 3 "Currently (1978) Vigorous", and Factor 4 "Initially Vigorous". For chestnut oak, the extracted factors appeared to have similar interpretations.

Using scores for the four factors described above as independent variables, equations predicting height and diameter growth were developed for several categories of seedlings and seedling sprouts (Table 17). The amount of variation explained by these equations (R^2) was somewhat lower than when the original independent variables and their interactions were used (Table 15). In order to more closely investigate the effect of species, site quality, and resprout vs. intact growth form on shoot response, the hypothesis

Table 16: Factor pattern (rotation method=Varimax) for first four factors extracted by principal component analysis for all oak seedlings and seedling sprouts, and for chestnut oak seedlings and seedling sprouts sampled immediately following the harvest in the main Potts Mountain study area. Abbreviations as in Table 15, plus Ratio = Diar/Dias.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
		All oaks		
Diar	.597	.616	.258	.306
Dias	.851	.029	.371	.275
Ht	.875	.030	.316	.278
Age	.930	.056	-.197	.002
Last2	.120	.094	.958	.156
Frst2	.218	.102	.161	.952
Ratio	-.029	.982	.032	.036
		Chestnut oak		
Diar	.742	.528	.230	.246
Dias	.867	-.032	.281	.304
Ht	.889	.019	.208	.333
Age	.888	.042	-.316	.013
Last2	.081	.064	.963	.142
Frst2	.296	.040	.147	.939
Ratio	.017	.994	.029	.005

Table 17: Coefficients for prediction equations for height and diameter growth of various categories of oak seedling and seedling sprout advance regeneration in the main study area (Potts Mountain, Craig Co., Va.). Independent variables are factor scores based on factor patterns reported in Table 16. Factor scores used to develop Equations 1-6 are from principal component analysis applied to all seedling and seedling sprouts sampled; factor scores for Equations 7-18 are derived from PCA of chestnut oak advance regeneration only. Abbreviations: Htgr = height growth (cm), 1979-1980; Diagr = diameter growth (mm), 1979-1980. Model: Dependent Variable = $b_0 + b_1F_1 + b_2F_2 + b_3F_3 + b_4F_4$, where F_1-F_4 = Factors 1 through 4 (see text for interpretations of factors).

Group No.	Equation No.	Oak Species	Site Quality Class	Intact or Resprout	Dependent Variable	Coefficients b_0	b_1	b_2	b_3	b_4	R^2
1	1	Chestnut	Combined	Intact	Htgr	23.2	3.8	3.2	7.6	3.8	.13
	2	Scarlet	Combined	Intact	Htgr	14.4	3.2	1.6	8.9	-1.2	.16
	3	Black	Combined	Intact	Htgr	20.9	1.7	19.1	8.2	-0.3	.49
2	4	Chestnut	Combined	Intact	Diagr	2.92	.30	.45	.47	.71	.18
	5	Scarlet	Combined	Intact	Diagr	2.62	.38	.00	.76	.10	.05
	6	Black	Combined	Intact	Diagr	3.85	.64	2.35	.62	.88	.24
3	7	Chestnut	Medium	Intact	Htgr	27.6	7.4	5.9	4.9	4.2	.15
	8	Chestnut	Low	Intact	Htgr	10.7	3.9	1.0	6.4	-2.2	.40
4	9	Chestnut	Medium	Intact	Diagr	3.32	.62	.41	.46	.59	.21
	10	Chestnut	Low	Intact	Diagr	1.66	.49	.34	.05	.26	.23
5	11	Chestnut	Medium	Resprout	Htgr	40.9	26.1	13.9	2.3	-0.9	.60
	12	Chestnut	Low	Resprout	Htgr	28.5	15.7	8.2	7.6	8.9	.77
6	13	Chestnut	Medium	Resprout	Diagr	7.08	2.46	1.42	0.37	0.87	.69
	14	Chestnut	Low	Resprout	Diagr	4.89	1.87	.21	.47	1.31	.74
7	15	Chestnut	Combined	Intact	Htgr	21.4	3.5	6.3	2.3	2.6	.14
	16	Chestnut	Combined	Resprout	Htgr	37.6	20.7	10.3	3.7	6.2	.54
8	17	Chestnut	Combined	Intact	Diagr	2.76	.29	.38	.33	.54	.18
	18	Chestnut	Combined	Resprout	Diagr	6.44	2.16	.84	.37	1.40	.63

was first tested that the slope coefficients ($b_1 - b_4$) did not differ within the following groups of equations: (1) intact stems of chestnut, scarlet, and black oak, unstratified by site quality (Eqs. 1,2,3 and 4,5,6); (2) intact chestnut oak individuals on medium and low quality sites (Eqs. 7,8 and 9,10); (3) resprout chestnut oaks on medium and low quality sites; (Eqs. 11,12 and 13,14); and (4) intact and resprout chestnut oak individuals unstratified by site quality (Eqs. 15,16 and 17,18) (Table 18). Four of the eight groups had at least one pair of slope coefficients which differed between equations. Both the statistical analyses and visual inspection of the equations revealed the much stronger positive influence of stem size-age (Factor 1) on chestnut oak resprout growth in the medium quality than in the low quality areas (Groups 5 and 6), and the uniformly higher magnitudes of all coefficients for resprout compared to intact chestnut oaks (Groups 7 and 8). For those groups of equations for which corresponding slope coefficients did not differ (Groups 1,2,3, and 4) differences in intercept were tested. The ANACOVA procedure indicated that both height and diameter growth were greater for intact chestnut oak stems on relatively good than on relatively poor sites, even after adjustment had been made for initial characteristics of the individuals (Factors 1 through 4). However, the ANA-

Table 18: Differences in corresponding coefficients within groups of equations listed in Table 17. Abbreviations: Htgr = height growth (cm), 1979-1980; Diagr = diameter growth (mm), 1979-1980.

Group	Equations	Oak Species	Site Quality Class	Intact or Resprout	Dependent Variable	H_0: No Differences in Slope Coefficients (b_1-b_4) Within Groups	Slope Coefficients Differing	H_0: No Difference in Intercepts (b_0) Within Group
1	1, 2, & 3	Chestnut Scarlet Black	Combined	Intact	Htgr	fail to reject	-	fail to reject
2	4, 5, & 6	Chestnut Scarket Black	Combined	Intact	Diagr	fail to reject	-	fail to reject
3	7 & 8	Chestnut	Medium, Low	Intact	Htgr	fail to reject	-	reject
4	9 & 10	Chestnut	Medium, Low	Intact	Diagr	fail to reject	-	reject
5	11 & 12	Chestnut	Medium, Low	Resprout	Htgr	reject	b_1, b_4	-
6	13 & 14	Chestnut	Medium, Low	Resprout	Diagr	reject	b_1, b_3	-
7	15 & 16	Chestnut	Combined	Intact, Resprout	Htgr	reject	b_1, b_2, b_3, b_4	-
8	17 & 18	Chestnut	Combined	Intact, Resprout	Diagr	reject	b_1, b_3, b_4	-

COVA procedure indicated that differences in intercepts among the three species were not statistically significant, as suggested previously by results reported in Table 12.

Effect of Characteristics of Oak Seedlings and Seedling Sprouts on Post-harvest Growth

The characteristics assessed and compared with respect to their effect on shoot growth were stem size-age, root-shoot ratio, stem vigor at time of harvest, and the original vigor of the stem, as represented by the factors described in the previous section. For chestnut oak, both intact and resprout individuals which grew most rapidly during the two years after harvest were originally older and larger than the slow-growers, on both moist and dry sites (Table 19). High vigor at the time of harvest, estimated by shoot elongation during the 1977-1978 period, was also associated with rapid post-harvest growth, especially of intact stems of all three species. Average root-shoot ratio did not differ statistically between fast and slow-growing stems for any categories tested.

The order of entry for the four factors when a forward stepwise regression procedure was applied confirms the importance of stem size-age and vigor on growth, and the lack of effect of root-shoot ratio (Table 20). Both Factor 1 (size-age) and Factor 3 (current vigor) entered either

Table 19: Comparison of seedlings and seedling sprouts ranked "high" vs. those ranked "low" in post-harvest height and diameter growth in the main study area (Potts Mountain, Craig Co., Va.), in terms of their characteristics at time of harvest (scores on Factors 1, 2, 3, and 4). Abbreviations: Htgr = height growth (cm), 1979-1980; Diagr = diameter growth (mm), 1979-1980.

Oak Species	Intact or Resprout	Site Quality Class	Growth Characteristic Ranked	Factor 1 "Size-Age"	Factor 2 "Root/Shoot"	Factor 3 "Current (1978) Vigor"	Factor 4 "Initial Vigor
Chestnut	Intact	Medium	Htgr	Hi>Lo[1]	n.s.[2]	Hi>Lo	n.s.
Chestnut	Intact	Medium	Diagr	Hi>Lo	n.s.	Hi>Lo	Hi>Lo
Chestnut	Intact	Low	Htgr	Hi>Lo	n.s.	Hi>Lo	n.s.
Chestnut	Intact	Low	Diagr	Hi>Lo	n.s.	n.s.	Hi>Lo
Chestnut	Resprout	Medium	Htgr	Hi>Lo	n.s.	Hi>Lo	n.s.
Chestnut	Resprout	Medium	Diagr	Hi>Lo	n.s.	n.s.	n.s.
Chestnut	Resprout	Low	Htgr	n.s.	n.s.	n.s.	n.s.
Chestnut	Resprout	Low	Diagr	Hi>Lo	n.s.	n.s.	n.s.
Scarlet	Intact	Combined	Htgr	n.s.	n.s.	Hi>Lo	n.s.
Scarlet	Intact	Combined	Diagr	n.s.	n.s.	n.s.	n.s.
Black	Intact	Combined	Htgr	n.s.	n.s.	Hi>Lo	n.s.
Black	Intact	Combined	Diagr	n.s.	n.s.	n.s.	n.s.

[1]i.e., individuals in this category of regeneration which ranked high in height growth were initially larger-older than individuals ranked low, at $\alpha = .05$ level.

[2]No statistically significant difference between "Hi's" and "Lo's" at $\alpha = .05$ level.

Table 20: Order of entry of Factors 1, 2, 3, and 4 (F1-F4) into the forward stepwise regression model[1] predicting height or diameter growth of oak stems two years following harvest in the main study area (Potts Mountain, Craig Co., Va.). Factor 1 represents shoot size-age, Factor 2 root-shoot ratio, Factor 3 pre-harvest vigor, Factor 4 initial vigor. Abbreviations: Htgr = height growth (cm) 1979-1980; Diagr = diameter growth (mm) 1979-1980. Model: Dependent variable = $b_0 + b_1F1 + b_2F2 + b_3F3 + b_4F4$.

Oak Species	Intact or Resprout	Site Quality Class	Dependent Variable	Factor Entering First	Factor Entering Second	Factor Entering Third	Factor Entering Fourth
Chestnut	Intact	Medium	Htgr	F4	F2	F1	F3
Chestnut	Intact	Medium	Diagr	F4	F3	F1	F2
Chestnut	Intact	Low	Htgr	F3	F1	F4	F2
Chestnut	Intact	Low	Htgr	F1	F2	F4	-
Chestnut	Resprout	Medium	Htgr	F1	F3	-	-
Chestnut	Resprout	Medium	Diagr	F1	F3	F4	F2
Chestnut	Resprout	Low	Htgr	F1	F3	F4	F2
Chestnut	Resprout	Low	Diagr	F1	F4	F2	F3
Scarlet	Intact	Combined	Htgr	F3	F1	-	-
Scarlet	Intact	Combined	Diagr	F3	-	-	-
Black	Intact	Combined	Htgr	F3	F2	F1	-
Black	Intact	Combined	Diagr	F1	F4	F2	F3

[1]First factor to enter is one with highest correlation with dependent variable; subsequent order of entry depends on degree to which addition of factor improves model. Factors are added until no remaining factor would be significant at $\alpha = .05$.

first or second of the four factors in eight of the twelve models. Factor 2 (root-shoot ratio) never entered first, and entered the model second in only three instances. Factor 1 was again strongly associated with growth of resprout chestnut oak.

Development of Seedling and Sprout Origin Stems beyond Age Two

Age class means for height and diameter growth of chestnut oak (Figures 4 and 5) indicated that the effect of vegetation type, as an index of site quality, was non-significant, with one exception: sprout origin stems in the five-year-old stands were both taller (48 dm) and larger in diameter (61 mm) in the mixed oak type than in the mixed oak-pine type (38 dm in height, 43 mm in diameter). On the other hand, sprout origin stems within an age class and vegetation type were usually significantly larger than the corresponding seedling origin stems. The only exception was for mixed oak-pine sites in the oldest age class, where height and diameter did not differ significantly by stem origin. Sample size in this case was only five pairs, however. Perhaps the most important aspect of Figures 4 and 5 is the magnitude of the difference between seedling and sprout origin stems. Sprout origin stems maintained a height advantage of about 40 dm and a diameter advantage of about 50 mm, which changed little with increasing stand age.

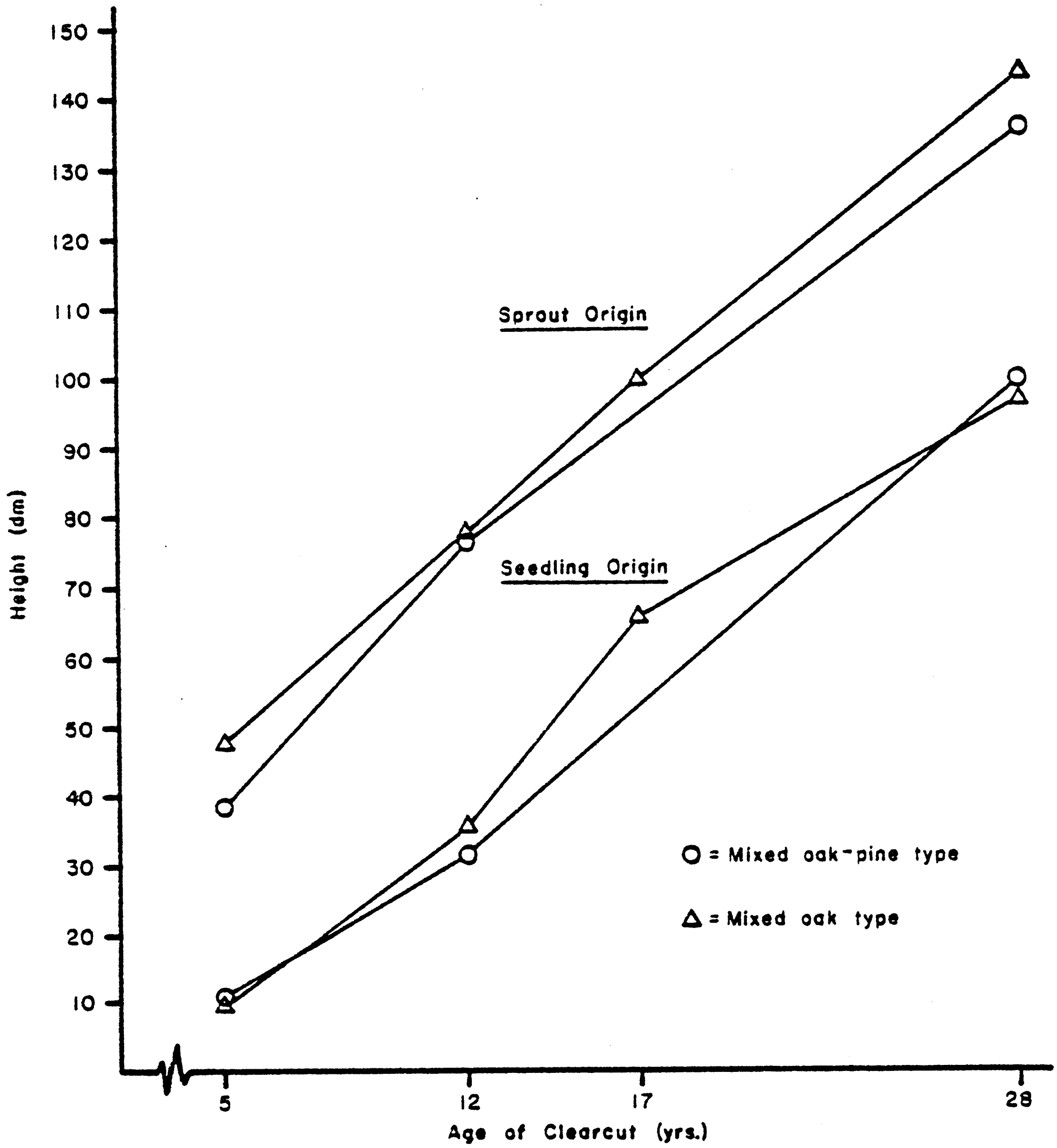

Figure 4: Mean heights for seedling and sprout origin chestnut oak stems in clearcuts of four ages in southwestern Virginia. Means for mixed oak and mixed oak-pine vegetation types are presented separately.

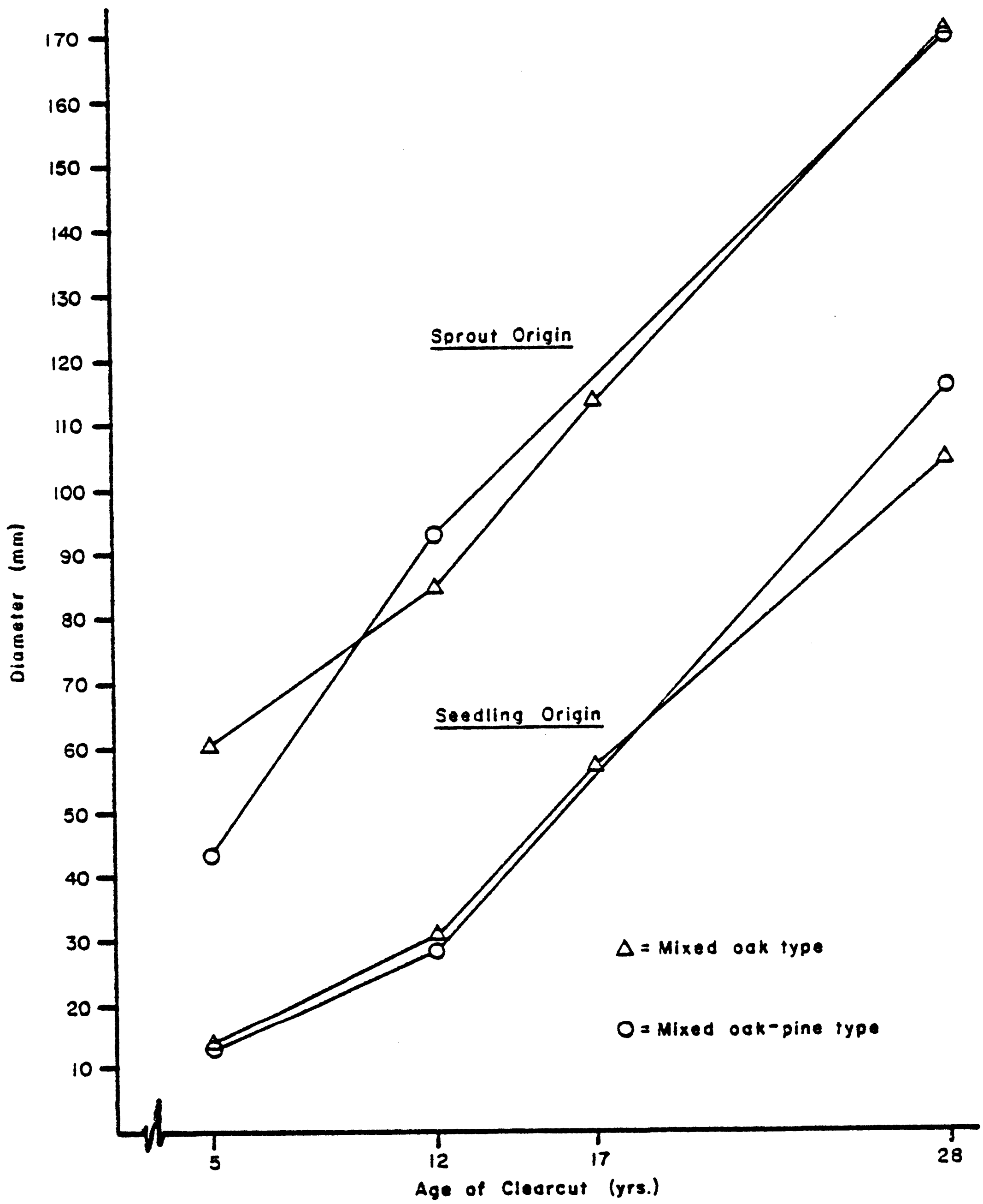

Figure 5: Mean diameter (1.4 m above ground level) for seedling and sprout origin chestnut oak stems in clearcuts of four ages in southwestern Virginia. Means for mixed oak and mixed oak-pine vegetation types are presented separately.

The differences in height attributable to stem origin were also reflected in the relative positions of seedling and sprout origin individuals in the stand canopy. Figure 6 illustrates the subordinate position of seedling origin stems early in stand development, and the gradual ascent of a small proportion to upper canopy strata by age 17. The absence of suppressed sprout origin stems beyond age five is also notable.

The non-parametric correlation coefficients of stump diameter and number of sprouts originating from a stump with sprout size (Table 21) are both cases in which a strong positive relationship becomes weaker with increasing stand age. The correlation between number of sprouts and diameter of tallest sprout is negative, though not statistically significant, in the oldest stand.

Similarly, the strong positive correlations of stem age with stem size (Table 22) which existed in the five-year-old stands for seedling individuals were essentially eliminated by stand age 17. Inspection of the data revealed that few old seedling origin stems are present in the seventeen-year-old stand, and the tallest individuals were about as old as the stand itself.

The data also indicated a possible link between site quality and density of seedling origin chestnut oaks (Table

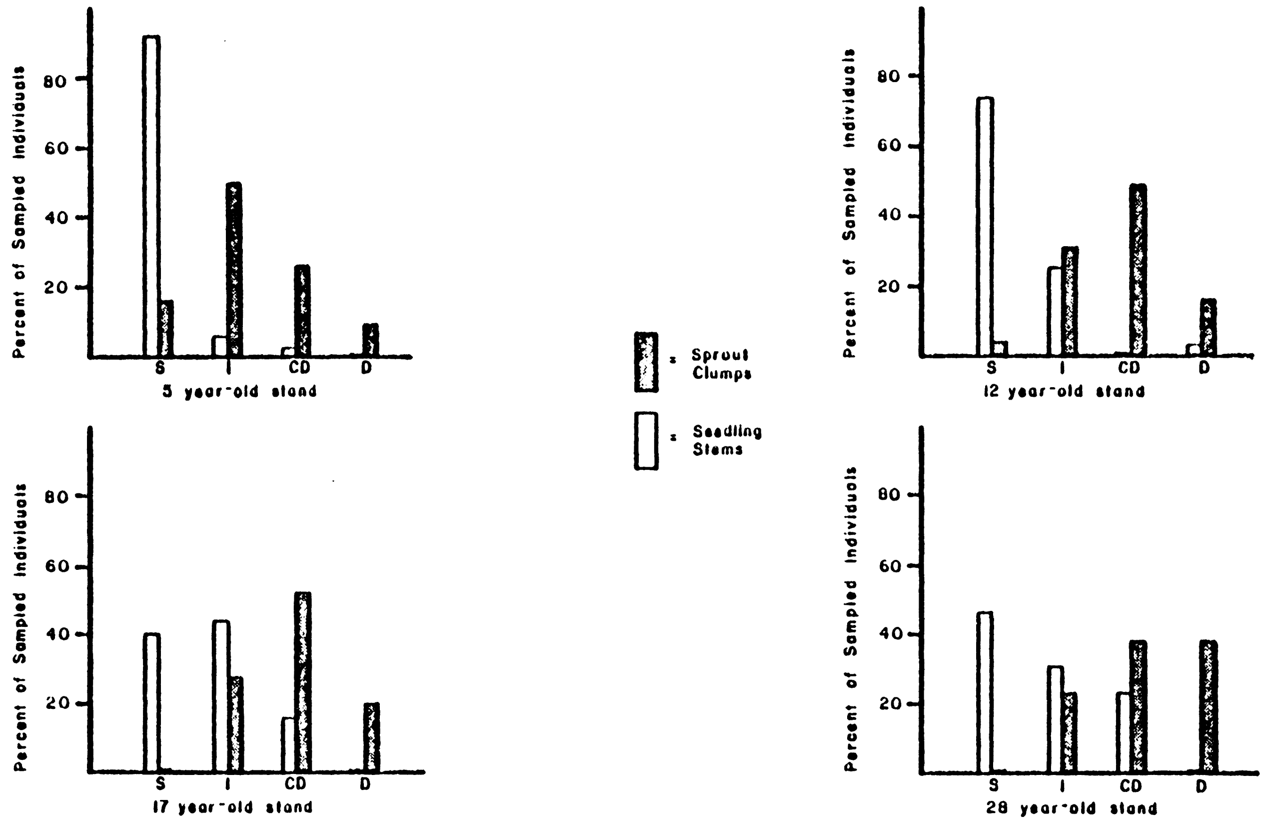

Figure 6: Proportion of seedling and sprout origin chestnut oak individuals in each of four dominance classes in clearcuts of four ages in southwestern Virginia. Abbreviations: S = suppressed; I = intermediate; CD = codominant; D = dominant.

Table 21: Spearman correlation coefficients of stump diameter and number of sprouts originating from a stump with the height and diameter[1] of the tallest sprout from chestnut oak stumps, in 5, 12, and 17-year-old stands in southwestern Virginia. Coefficients followed by * are significant at α=.05 level.

Stand	n	Correlation with Sprout Height	Correlation with Sprout Diameter
		Stump Diameter	
5 year-old (mixed oak)[2]	44	.54*	.58*
5 year-old (mixed oak-pine)	20	.32	.28
12 year-old	72	.27*	.39*
17 year-old	25	.16	.09
		Number of Stems Originating from Stump	
5 year-old (mixed oak)	60	.37*	.36*
5 year-old (mixed oak-pine)	21	.42	.54*
12 year-old	76	.20	.20
17 year-old	25	.17	-.14

[1]1.4 m above ground level.

[2]Five-year-old mixed oak and mixed oak-pine data are analyzed separately because of the significant difference in sprout size between these categories.

Table 22: Spearman correlation coefficients of stem age with stem height and diameter[1] for chestnut oak seedling origin individuals in 5, 12, and 17-year-old stands in southwestern Virginia. Coefficients followed by * are significant at α=.05 level.

Stand	n	Correlation with Stem Height	Correlation with Stem Diameter
5 year-old	85	.52*	.62*
12 year-old	75	.19	.27*
17 year-old	25	-.12	.00

[1]1.4 m above ground level.

Table 23: Density (per hectare) of seedling origin stems and sprout clumps of chestnut oak in two vegetation types within three 5-year-old and three 12-year-old stands in southwestern Virginia.

Stand Age	Stem Origin	Mixed Oak	Mixed Oak-Pine	P-value[1]
5	Seedling	560	130	.005
5	Sprout	400	420	.92
12	Seedling	560	200	.15
17	Sprout	210	120	.97

[1]Probability that distances from sample point to nearest individual (used to determine density) in mixed oak and mixed oak-pine vegetation types are from the same population (Wilcoxon Signed Rank Test).

23). Sample points classified as mixed oak exhibited a higher density of chestnut oak stems of seedling origin than points classified as mixed oak-pine, at least in the five-year-old stands. A response of seedling origin oak density to site quality was to some extent supported by data collected on a quadrat basis two years after harvest in the main study area (Figure 7). However, because of the lower limit on size (1m) for the data set illustrated in Figure 7, the information is not strictly comparable with that extracted from the 5 and 12-year-old stands. Also, each sprout stem greater than 1m tall was tallied, rather than the whole sprout clump singly. Nevertheless, the positive correlation between site productivity ranking and density of seedling origin stems was evident from mixed pine through mixed oak stands. The lack of seedling origin oaks taller than a meter in the mixed hardwood stand deviates from the pattern, however, and requires explanation. No trends in density of sprout origin stems were obvious over the productivity gradient (Table 23).

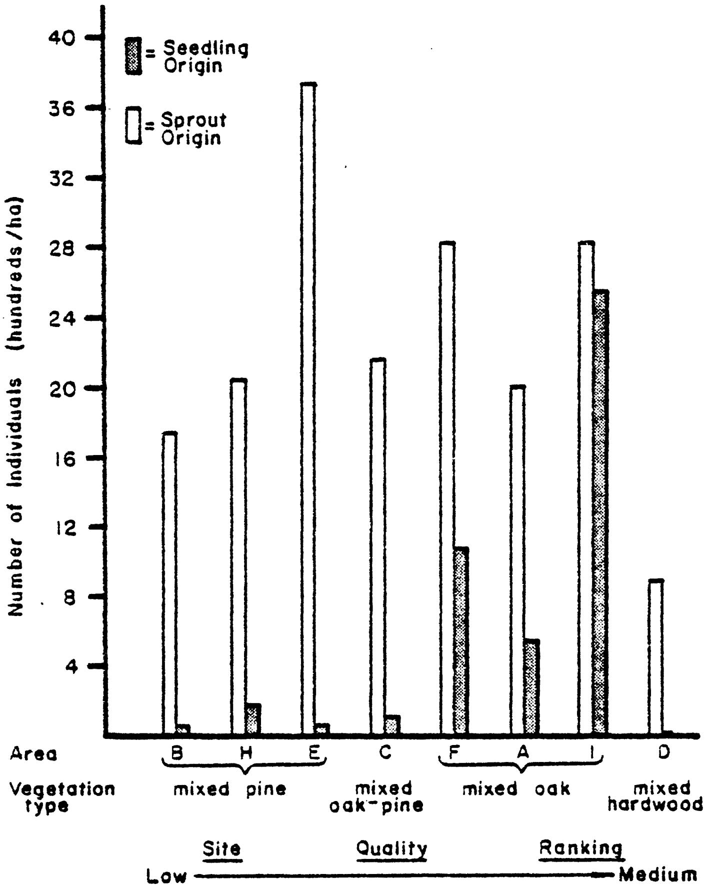

Figure 7: Density of oak individuals (chestnut, scarlet, and black) of sprout and seedling origin which were greater than 1 m in height two growing seasons after harvest in the main study area (Potts Mountain, Craig Co., Va.). Site quality ranking based first on vegetation type, and within types, on Forest Site Quality Index (see Table 2).

DISCUSSION

An ecologist attempting to explain vegetation development might begin with the model

$$V_p = V_o + \sum_{\text{Species}=1}^{n} \sum_{\text{Year}=1}^{p} (\text{Establishment} + \text{Survival} + \text{Production})$$

for an ecosystem with initial vegetation V_o, containing n potential plant species, and reaching vegetation state V_p after p years. In order to accurately model vegetation processes over a broad area, some degree of site-specificity would be required. The task is further complicated by interactions between species and between size or age classes.

The model might be applied to compare the development of three oak species--chestnut oak, scarlet oak, and black oak--after clearcutting in Appalachian oak forests. Because of the early onset of competitive pressures in such stands, and the slow growth of newly established oak seedlings, post-harvest establishment can be disregarded when considering the forest overstory during the initial stages of stand development.

The model then becomes

$$V_p = V_o + \sum_{\text{Species}=1}^{3} \sum_{\text{Years}=1}^{p} (\text{Survival} + \text{Production}),$$

incorporating effective establishment into the term for initial vegetation. V_o thus includes both residual advance regeneration and large trees which were cut during harvesting operations. Such a model provides a framework for understanding the effects of the relationships observed in the current study.

Stump Sprout Development

Sprout Frequency

The proportion of stumps from which at least one living sprout was present two years after clearcutting in the main study area (79, 67, and 56 percent for chestnut, scarlet, and black oak, respectively) (Table 3) was similar to results reported elsewhere for the same species. Sander et al. (1976) compiled results reported in various parts of the Appalachian Oak Forest Region, and estimated that 90 percent of chestnut oak, 85 percent of scarlet oak, and 65 percent of black oak stumps 15-28 cm in diameter produce sprouts. Johnson (1977) reported somewhat lower values---60 and 19 percent---for scarlet and black oaks, respectively, three years after harvest in southern Missouri. Wendel (1975) observed a frequency of 87 percent for chestnut oak ten years after clearcutting in West Virginia. The proportions reported in all studies serve to document the advantage of chestnut oak over the other species with regard to frequency of sprouting.

Other studies which considered the relationship of site quality with sprout frequency reported either no effect (Wendel, 1975) or a positive effect (Johnson, 1977) on the probability of sprouting. On Potts Mountain, however, sprout frequency was highest for each of the three oak species on the least productive, mixed pine sites. Because a maximum of three replicates of each site quality unit were sampled, and because of the confounding effects of such factors as stump size distribution and logging disturbance, no statistical certainty could be attached to the observation that the association between site quality and sprout frequency is negative. Considering the discrepancy between the results reported for Potts Mountain and for Missouri sites, and the lack of statistical validation for either, further research is required to clarify the effect of site quality on sprout frequency. Such a study should focus on stand-to-stand rather than tree-to-tree variation in sprouting behavior. If such research indeed verified the preliminary indications that sprouting percentage is increased on the most stressful sites, one could readily imagine the advantage accrued by species which could maintain already-established genotypes on sites on which initial establishment was difficult.

The results summarized in Table 4 confirm what has been reported elsewhere in the literature (Wendel, 1975;Sander et al., 1976;Johnson, 1977;McGee, 1978)---stumps of larger and older oak trees are less likely to produce sprouts. The inverse relationship between sprout frequency and tree vigor, as measured by recent basal area growth, may be a result of the strong intercorrelations between growth increment and the tree size parameters (r=.6 to .8). On the other hand, rapid wood production might prevent the dormant buds, which ultimately give rise to sprouts, from maintaining themselves close to the wood surface. With the passage of time, the vascular connections to these buds may become ineffective, causing bud death and precluding sprout production. Powers and Wiant (1970) have advanced a similar explanation for sprouting in coastal redwood (Sequoia sempervirens), based on maintenance of vigorous buds near the stem surface. However, they include fire as a possible agent in the death of dormant buds. In the Potts Mountain area, fire intense enough to kill the parent oak trees has been observed to induce abundant basal sprouting. Anatomical investigation would be useful in tracing the origin and maintenance of the dormant buds which eventually become stump sprouts.

There are no reports in the literature of attempts to predict whether an individual stump will or will not produce sprouts. The low predictive power of the discriminant function is indicative of the tremendous variation among stumps of a species in sprouting behavior that is unaccounted for by the size, age and vigor of the stump, and by site quality. In addition to genetic variance, other factors which might contribute to this variation are slope, logging disturbance, orientation of dormant buds above or below the stump, fire history, and season of harvest (Johnson, 1977; Powers and Wiant, 1970;Wendel, 1975), as well as bark thickness, root carbohydrate reserves and hormone levels. Nevertheless, on a management level, one can normally disregard the uncertainty with respect to individual stumps and maximize sprouting within the stand (if that is the objective) by cutting smaller and younger trees.

The life history of almost any tree species can be divided into four arbitrary stages: a period of very slow height growth, called the "seedling" stage, during which a relatively high proportion of photosynthate is diverted into root development; a period of accelerated height growth, called the "juvenile" stage, during which sexual reproduction also begins; a "mature" stage during which height growth is steady and fruit production reaches its maximum; and an "overmature" stage during which height growth essentially ceases. In oak species, the "seedling" stage is protracted in comparison to many of its associates; hence, the difficulty in regenerating oaks, through both artificial or natural means, on sites where fast-growing competitors exist. The production of stump sprouts can be viewed as a means by which the "seedling" stage is circumvented, and rapid height growth associated with the "juvenile" stage of development is attained immediately.

Oak stump sprouts, once considered undesirable by silviculturists because of a reputation for poor form and tendency to decay, are now generally thought of as a supplementary and acceptable form of regeneration (Lamson, 1976). On some Potts Mountain sites oak sprouts are so numerous that they nearly constitute sufficient stocking by themselves. A recent Forest Service guide developed primarily in the Central States (Sander et al., 1976) sets a standard of 546 dominant or codominant oaks/ha for adequate oak stocking at stand age 20-25. However, Oliver (1978) maintains that as few as 110 upper canopy oaks/ha at age 30 is optimal for board foot production in New England. Using the data from Table 3, assuming that 74 percent of the oak stumps which produce sprouts will still support a dominant or codominant stem at stand age 20 (Sander et al, 1976), and including a maximum of one sprout per stump, the projected numbers of upper canopy oak sprouts in the year 2000 on Potts Mountain are 74, 301, 393, and 326 for the mixed hardwood, mixed oak, mixed oak-pine, and mixed pine sites, respectively. Although the large magnitude of the projected oak sprout component is to some extent a result of the small size of the trees in the original stands, it is worth noting that the Potts Mountain stands were typical of vast expanses of Ridge and Valley forests. Whether as an asset or as unwanted weeds, oak stump sprouts will figure prominently in the future of such stands upon clearcutting.

Stem Dimension-Biomass Relationships

The preferred biomass prediction model for oak stump sprouts on Potts Mountain (Biomass component=a(diameter)^{b}) and the amount of variation accounted for by the model (67 to 96 percent for stem weight) (Table 5) are similar to results obtained for understory biomass by other researchers (Martin et al., 1982;Rochow, 1974;Wiant et al., 1979). The lack of improvement in model fit with the inclusion of a term for stem height may be related to the close correlation between diameter and length of these sprout stems. The need for species and site-specific equations is an indication that sprouts differed in growth form among sites and among species. Lower quality sites seemed to have stockier stems with smaller, more numerous leaves than those in more productive areas. Chestnut oak sprouts had a long, thin form, black oak sprouts a squat and sturdy appearance, while scarlet oak was intermediate in form. The differences in appearance of individual stems among the three species could be extended to the sprout clumps as a whole; the tall, upswept chestnut oak clumps were distinguishable at a distance from the bushy scarlet oaks or the sparse clumps arising from black oak stumps.

Where biomass production on an individual stump basis is a primary focus of a research effort, as it was in this study, the necessary accuracy probably requires the individual stem regression approach used here. However, in a broader study in which biomass production per unit area is the variable of concern, greater efficiency may be obtained from measurement of the sprout clump collectively, rather than each sprout stem. Regressions relating total clump biomass to clump diameter and height might be developed to determine if their accuracy was sufficient for the purposes of the particular study.

Sprout Production

Differences among species and among sites were somewhat more clearly defined for sprout production than for sprout frequency. In the case of sprout production the stump rather than the stand is the experimental unit, and the increase in degrees of freedom allows statistical analysis where none was possible for sprout frequency. The analysis of covariance procedure (Table 7) verifies some of the differences apparent in the stump means (Table 6) and reveals others masked by differences in the characteristics of the parent stumps. Thus, there is statistical support for an intrinsic superiority in sprout production for chestnut oak over its two oak competitors, for inherently shorter sprouts in the mixed oak-pine type, and for higher biomass production potential in the mixed pine type than in several more mesic vegetation types.

The few references in the literature concerning relative growth of stump sprouts indicate that chestnut oak is indeed one of the more productive oak species. Height growth for chestnut oak in West Virginia (site index 60-80) was equal to that of northern red oak and superior to white oak throughout the first ten years after clearcutting, while differences in diameter among the species were not obvious (Wendel, 1975). Chestnut oak height growth in the mixed oak plots on Potts Mountain compares favorably with average figures of 0.7 m per year observed for black and white oak on site index 55-70 in Missouri (Johnson, 1979). The significance of the observed interspecific differences would be to give chestnut oak a competitive advantage over scarlet and black oaks if its productive superiority were maintained until the time these sprout units begin intense competition for light and space.

There is a seeming contradiction in the observation that, after adjusting for stump characteristics, the lowest quality sites supported chestnut oak stumps which had the highest potential for biomass production, while exhibiting the next-to-shortest sprouts among the four site classes investigated. However, an hypothesis which considers the competitive interactions taking place on sites of different productivity can be offered to clarify this paradox. The structure of mixed pine sites two years after clearcutting can be described as scattered islands of oak sprouts in a low matrix of huckleberry, blueberry, and bracken fern. The sprout clumps have little competition from the side, and expand laterally to fill the void. The lateral expansion allows more photosynthetic tissue to be exposed, and hence greater biomass production. However, the open conditions on the driest sites might have an inhibiting effect on the upward extension of the chestnut oak sprouts, perhaps because of the diversion of photosynthate into the expansion of roots and lateral branches. Foresters exclude open-grown trees from determination of site index, and plant physiologists often find maximum height growth under less-than-maximum light conditions or some degree of competition (Phares, 1971). Such competition becomes more evident as moisture availability increases. For example, on mixed hardwood and mixed oak sites, oak sprout clumps, while maintaining a dominant position in the developing canopy, are encroached upon much more severely by surrounding vegetation. Two years after harvest these sites averaged 18,920 stems/ha taller than 1 m, while the mixed pine sites averaged only 7630 stems/ha. The increased competition might have had an enhancing effect on sprout height, while inhibiting biomass production per stump.

The hypothesis just advanced does not resolve all conflicts. For example, it does not explain why sprouts in the mixed oak-pine vegetation type, rather than mixed pine, are the shortest, nor does it explain why data from older clearcuts (Figures 4 and 5; Wendel, 1975) show little or no effect of site quality on stump sprout height. Local factors which cause considerable variation in sprout production among plots within the mixed pine and mixed oak-pine types in particular may be responsible for the relative sprout heights in those vegetation types. More extensive sampling would serve to clarify this point. However, despite the contradictions noted, the differences described in sprout production per stump in the present study are at least suggestive of varying levels of competition operating in these young stands.

Regression analysis has been used to predict oak sprouting probabilities from stump characteristics (Johnson, 1977) and individual sprout growth from initial stem size in older clearcuts (Johnson, 1980). However, no attempts to predict sprout production from stump characteristics have been reported, although Johnson (1977) does list correlation coefficients between stump diameter and 5-year sprout height for several oak species. Because of the large amount of variation unaccounted for by the models listed in Table 8, such regression equations will probably be of little utility as a management tool. There are two explanations for the magnitude of the unaccounted variation: (1) Sprout production is largely unrelated to stump resources, and is for the most part controlled by genetic factors and elements of the microenvironment with which stump characteristics have little interaction, or (2) The characteristics of the parent tree measured (diameter, height, age, growth increment) are poor indices of the root resources upon which sprout production depends. It is likely that both of these explanations contribute to the poor performance of the regression models. Some idea of the relative roles of genetics and root resources might be gained by studying sprouting of cut seedling and sapling-size individuals in which family relationships were known, and in which root resources might be sampled more directly. It should be recognized, however, that the factors governing sprout production for small stumps may differ from those controlling sprout production in large stumps. Similarly, species may vary in their sprouting relationships; the better fit of the black oak models (Table 8) is similar to Johnson's (1977) findings , in which the negative correlation between stump diameter and sprout height for black oak was much higher than for scarlet oak.

As was the case with sprout frequency, for which the ability to predict was also weak, there was a significant relationship between sprout production and stump characteristics. However, the relationship between stump sprout production and attributes of the parent tree, illustrated in Table 9, are clouded by the strong correlations between the tree variables. Correlation coefficients between tree height, diameter, and growth increment exceed r=.75, while the correlation coefficients between tree age and the other variables are somewhat lower (r=.3-.6). Nevertheless, a trend of increased sprout production with an increase in tree size and vigor appears to be tempered by decreased production with increased parent tree age, especially in very old trees. Because of the tremendous amount of variation in sprout production unaccounted for by tree variables, analysis of covariance would be of little use in evaluating these two opposing tendencies.

Wendel (1975) found no relationship between stump diameter and tenth-year sprout height for several species, including chestnut, red, and white oaks. Johnson (1977) found a significant negative correlation between stump diameter and fifth-year sprout height for five oak species, including black oak and scarlet oak. The same author later reported that black and white oak sprout height after four years increased with stump diameter up to about 15 cm, and then decreased (Johnson, 1979). The inconsistencies among the three studies and the results reported for Potts Mountain in Table 9 may in part be a function of the age and size distributions of stumps sampled, and of the methods of analysis. Johnson's first study (1977) included many large stumps (up to 75 cm in diameter), and was analyzed by simple correlation. Wendel (1975) also used simple correlation to analyze his data, which covered stumps 13 to 60 cm in diameter. Johnson's 1979 report dealt with stumps 3 to 30 cm in diameter, and utilized curvilinear regression. The approach of the study reported here was to sample sprouting stumps in the proportion of sizes in which they occurred naturally, thus including a relatively small percentage of large stumps. The method of analysis---after having obtained regressions which generally explained only 10-30 percent of the variation in production---was to classify the stump characteristics and use multiple comparisons between the arbitrarily-formed classes.

The general conclusion involving the fewest inconsistencies is that, at least for some oak species, stump sprout production increases up to some intermediate stump size, and then decreases. The initial increase of sprout production with stump size is an extension of the growth advantage of larger or older oak seedlings over smaller seedlings (Table 19; Sander, 1971). An increase in stump size, or seedling size, as the case may be, is associated with an increase in resources which lead to rapid growth. Whereas stump size appeared to be a barrier to the initiation of stump sprouts, its effect on growth of these shoots once initiated appears to be positive, at least up to some critical size. If there is a decrease in sprout production beyond a critical size, the mechanism may be more closely related to advanced age than size (Table 9). Reduced sprout growth from older stumps may be related to some aging process in the dormant buds--presumably initiated many years before--which precludes the production of vigorous sprouts.

It is difficult to compare biomass production per hectare for oak stump sprouts on Potts Mountain to intensively managed, short rotation coppice production reported elsewhere (Cannell and Smith, 1980), usually for *Populus* and *Platanus* species. These coppice systems, which often utilize fertilization on sites inherently far more productive than those found on Potts Mountain, typically produce 7000 to 10,000 kg/ha/yr. In contrast, the annual production of oak sprouts on Potts Mountain was about 250 kg/ha/yr (Table 6). However, commercial energy plantations generally employ densities ranging from several thousand to several hundred thousand stems/ha, whereas the average density of oak stumps in the Potts Mountain study area was only about 400/ha. Cannell and Smith (1980) showed that biomass yield was positively correlated with the natural log of stump density in 83 records reported in the literature. Oak stump densities could be increased if the original stands were cut during earlier stages of development. For example, if a fully stocked oak stand was cut at an average diameter of 8 cm, 3430 stumps/ha would be left (Roach and Gingrich, 1968), of which at least 2400 could be expected to produce sprouts (Table 3). If sprout production per stump were similar to observed production for stumps 5-10 cm in diameter on Potts Mountain (1080 kg per stump after two years), then standing biomass of oak sprouts (stems and leaves) at the end of two years would be 2600 kg/ha. This figure compares favorably with the 1500 kg/ha (excluding leaves) produced over a two-year rotation by quaking aspen (*Populus tremuloides* Michx.) in Minnesota (Perala, 1979). Higher densities of oak stumps might result in reduced per stump production, although per hectare production would probably continue to increase. In assessing the values cited above, it should be kept in mind that the two-year old Potts Mountain stands as a whole---and presumably the oak stump sprout component of these stands---are many years from the culmination of annual biomass increment (Cannell and Smith, 1980). However, site degradation due to nutrient removal is of concern when considering short rotations.

Advance Regeneration Development

Condition at the Time of Harvest

Total densities of oak advance regeneration encountered in the Potts Mountain study area, ranging from 1100 to 9500 stems/ha (Table 10), are within the range of values observed elsewhere in the Eastern Deciduous Forest. Phillips (1963) found densities ranging from 640 to 1470 stems/ha in southern New Jersey, with the highest values occurring on the driest sites. Another study found 3500 to 11,000 oak stems/ha in the understory of several brushy Wisconsin oak stands (Arend and Scholz, 1969). Twenty-eight mixed-oak stands in Pennsylvania sampled by Bowersox and Ward (1972) contained an average of 2000 advance regeneration individuals of the red oak group and 4880 stems of white oak species per hectare. Oak advance regeneration density in 59 stands studied by Carvell and Tryon (1961) in West Virginia ranged from 300 to 137,000 stems/ha and had a median of 6200 individuals/ha. Density was related to site index in a curvilinear fashion, with maximum numbers occurring between site indices 50 to 60, which corresponds roughly with the less productive mixed oak sites in the present study.

Density of small individuals within any plant population is affected to a great extent by the number of propagules produced by the individuals in the population of seed-bearing age or size. This is particularly true for oaks, whose heavy acorns generally remain beneath the tree crown except when removed by rodents or birds, which may act as important dispersal agents. Acorn production is highly variable from tree to tree, from year to year, from site to site, and from species to species (Downs and McQuilken, 1944; Christisen, 1955; Beck and Olson, 1968). The simplifying assumption might be made that acorn production of an individual of a particular species over a number of years is related to tree diameter (Downs and McQuilken, 1944), and consequently that acorn production of a species within a given area is roughly related to the basal area of the species. Beck and Olson (1968) found that, over a twelve year period, scarlet oak produces 14.7 kg of acorns/m^2 of basal area/yr, chestnut oak 11.7 kg/yr, and black oak 7.8 kg/yr. Using Beck and Olson's seed production figures, the estimates of oak overstory basal area for the pre-cut Potts Mountain stands (Sharik, unpublished data), and the mean values of 540, 520, and 220 acorns/kg for scarlet, black, and chestnut oak, respectively (U.S.D.A., 1974), estimates of yearly seed production by species and vegetation type can be made. The ratio of advance regeneration density (from Table 10) to seed production may then be used as an index of success in seedling establishment and survival (Seedling Establishment Index, or SEI) (Table 24). Table 24 clarifies the trends in advance regeneration density noted in Table 10. The higher densities of advance regeneration for chestnut oak compared to its two oak associates are largely a

Table 24: Overstory basal area (m^2/ha), estimated annual acorn production (number/ha)[1], and Seedling Establishment Index (SEI)[2] for three oak species in four vegetation types in pre-harvest stands within the Potts Mountain study area (Craig Co., Va.).

Vegetation Type	Species: Chestnut Oak	Scarlet Oak	Black Oak	Total
Mixed hardwood				
Basal area	8.31	.68	3.44	12.4
# acorns	21,440	5240	14,500	44,180
SEI	.240	.060	.086	.163
Mixed oak				
Basal area	18.0	2.67	1.9	22.6
# acorns	46,440	20,580	8300	75,320
SEI	.178	.037	.054	.126
Mixed oak-pine				
Basal area	12.5	5.89	.28	18.6
# acorns	32,250	45,400	1180	78,830
SEI	.101	.029	.445	.065
Mixed pine				
Basal area	4.63	5.12	.85	10.6
# acorns	11,950	39,460	3580	54,990
SEI	.066	.006	.027	.020

[1]Estimated from oak basal area according to Beck and Olson (1968).

[2]Ratio of advance regeneration density (Table 10) to estimated annual acorn production.

function of its advantage in seedling establishment and survival rather than of higher seed production. The tendency for oak advance regeneration density to be lowest on mixed pine sites also appears to be a result of difficulty in seedling establishment.

Verification of the trends suggested by the SEI values in Table 24 could easily be accomplished by tracing the survival of known densities of acorns on the various sites. If such an experiment confirmed the results discussed above, one could hypothesize that the underlying causes of the differences among sites and species probably involve seedbed characteristics and species adaptations to them. Germination of chestnut oak acorns is favored by the presence of a moist layer of leaf litter at least one inch in depth (Barrett, 1939). Such seedbeds are discontinuous in the mixed pine areas, in which much of the forest floor is covered by pine needles. The apparent advantage of chestnut oak over scarlet and black oaks in seedling-seed ratio may be due to the sturdy taproot produced by the relatively large acorn, which may utilize water resources deeper in the soil than the shallower root systems of the other species. On the other hand, the difference in species behavior may lie in the timing of germination. Acorns of the white oak subgenus, such as chestnut oak, germinate soon after dropping to the forest floor in the fall, while red oak species, including scarlet and black oak, are subject to dessication and predation during the long months before spring germination. Tryon and Carvell (1958) found that white oak (*Quercus alba* L.) seedling establishment was five times that of northern red oak when acorn production was the same for each species.

Based on a twelve year study of the development of several oak species in Illinois, Sander (1972) has asserted that only stems taller than 1.4 m contribute significantly to the main canopy of a stand following clearcutting. It is estimated (Sander et al., 1976) that 1070 such stems/ha are necessary before cutting in order to ensure adequate oak stocking (30 percent of full stocking with oak stems at stand age 20-25 years) in the new stand if there is no contribution from oak stump sprouts. The 213 oak stems/ha taller than breast height in the Potts Mountain study area represent about 20 percent of the established norm for oak regeneration. But how well does this system of evaluating the adequacy of oak advance reproduction apply to Potts Mountain stands? If the 213 stems/ha mentioned above are stratified according to vegetation type, the average density of individuals taller than 1.4 m are 0, 147, 356, and 282 individuals/ha for mixed hardwood, mixed oak, mixed oak-pine, and mixed pine vegetation types, respectively.

Although density of individuals taller than breast height in all vegetation types at the time of harvest was far short of the 1070 stems suggested as a minimum for adequate restocking, the mixed pine and mixed oak-pine types contained more stems of the requisite size than the more productive mixed oak stand. Yet two years later, mixed oak plots contained more than eight times as many oak individuals of advance regeneration origin which were taller than 1 m in height as the mixed pine or mixed oak-pine plots (Figure 7). Stems taller than 1 m were generally part of the subordinate canopy in the two-year-old stands which surrounded the scattered "islands" of stump sprouts, and were considered to have a reasonable chance of survival to maturity.

The contribution of the system proposed by Sander et al. (1976) for evaluating oak reproduction is that it establishes the principle that a minimum number of oaks of some minimum size is required in order to ensure restocking of a stand with oaks after clearcutting. The minimum size and number for a given stand appear to be greatly affected by site quality, composition of competing species, and management objectives. On the midslope positions of Potts Mountain, where fast-growing competitors like yellow-poplar, black locust (<u>Robinia pseudoacacia</u> L.) and maple and birch species are not numerous, a smaller minimum size may be more appropriate than 1.4 meters. The correlation coefficients between the number of oak individuals taller than a meter two years after clearcutting and the number of oak advance regeneration stems taller than six "minimum sizes" at the time of harvest in eight stands in the main study area are: 0 cm, r=.50; 10 cm, r=.72; 20 cm, r=.67; 30 cm, r=.55; 1.0 m, r=.11; 1.4 m, r=-.00. The minimum size which was most closely associated with the relative success of oak regeneration two years later was 10 cm. Small advance regeneration stems thus may make a significant contribution to restocking stands with oak under the competitive conditions prevailing on Potts Mountain.

Survival and Resprouting

Although the capacity of oak seedlings to die back and resprout from dormant buds at the stem base is well known, the occurrence of the phenomenon under various seedling environments has not been studied and the internal mechanisms controlling it are not well understood. Oliver (1978) has suggested that the intolerance of northern red oak as evidenced by the absence of sapling-size oaks in the understory of mature forests, may be caused by the following sequence of events: low light, slow photosynthesis, slow cambial growth, inadequate water conduction, and finally dessication and death. According to Cliver, the problem of slow diameter growth would be most acute for ring-porous trees like oaks, which conduct water predominantly through current-year vessels. The above hypothesis might have been extended to include dieback and resprouting, and the maintenance of a population of oak seedling sprouts on the forest floor.

In the hypothesis proposed by Oliver (1978), the effect of light is indirect and cumulative, while water stress is invoked as the final cause of stem death. In Potts Mountain stands, neither dieback in the mature stands (Table 10) nor in the post-clearcut environments seemed to be related to moisture stress, as connoted by vegetation type and topographic variables. The high incidence of relatively tall and old stems among resprout chestnut oaks (Table 11), along with field observations, suggest that dieback might be related to light indirectly through the form of the oak stem. Many stems which have existed for a relatively long period in the dimly lit forest understory take on a bowed shape, with a wide, flat crown that is presumably effective in intercepting light (Ross et al., 1982). Such a stem form would appear structurally unsuited to supporting rapid upward extension in response to an opening in the forest canopy. Perhaps basal sprouting in understory oaks has evolved as a means of reestablishing a more favorable stem orientation. Research is currently underway to test the effects of light and moisture levels on dieback of northern red oak (Tworkoski, 1981).

Shoot Growth Means

Comparison of shoot growth among intact seedling, seedling sprout, and stump sprout advance regeneration (Table 12) indicated that true seedlings in most cases grew less in height and diameter than the other reproduction types, although the differences were not always statistically significant. These results are in agreement with those of McQuilkin (1975) involving white oak, and are at least in part attributable to the smaller size of seedling oak regeneration at the time of harvest (Figure 2). Differences in average shoot growth among species (Table 12) were small in comparison to the variation among individuals within a species. Differences in shoot growth potential among species during the first few years after clearcutting therefore does not appear to be an important factor in the ultimate survival and dominance of the three oak species studied.

The differences in shoot growth between chestnut oak advance regeneration on medium as opposed to low quality sites (Tables 13 and 14) are best explained with reference to soil and atmospheric water relations on the sites. The low quality sites were located on relatively steep, convex slopes of south or southwest aspect, while the sites of medium quality were on more favorable aspects, were less steep, or occupied a concave slope position. Atmospheric moisture stress is probably higher on the low quality sites due to more intense and prolonged irradiation, and to more rapid air movement and consequently lower humidity. Soil moisture would tend to be lower on the poor sites, as a result of the high evaporative stress and rapid drainage through the coarse-textured soils. Therefore it is not unexpected that the poor sites exhibited less shoot growth and fewer growth flushes among several types of advance regeneration during the two-year period following the clear-cut. Neverthless, it is noteworthy that these differences are observable within such a short time after harvest, that they occur among individuals occupying relatively shallow soil depths and subordinate positions in the developing canopy, and that they occur in resprout as well as intact individuals. Since height growth of competing species was not studied, it is impossible to say whether faster growth of chestnut oak advance regeneration in relatively productive areas indicates a competitive advantage in such habitats. More likely, the rapid growth of oak on the better Potts

Mountain sites is accompanied by faster growth of all species, and hence a hastening of the onset of competition strong enough to affect survival. One effect of a higher level of competition early in stand development is to eliminate the slow-growing genotypes which might survive to maturity in a less competitive environment. The filtering out of slow-growing genetic strains, associated with high levels of density and rapid early growth on more favorable topographic positions, may enhance the productivity advantage of such sites on the basis of water balance alone.

The subordinate position of advance regeneration oak stems two years after clearcutting (Figure 3) does not mean they have no role in the future development of the stand. Density of stump sprout clumps of oak (Table 6) and other species is not sufficient to fully occupy the site at early stages in stand development. Full stocking at a stand age of 20-25 years exceeds 3000 stems/ha (Roach and Gingrich, 1968). Based on the total number of sprouting stumps of all species in the two-year-old Potts Mountain stands, fewer than one thousand will be of stump sprout origin. Early thinnings could favor oaks of advance regeneration origin if they were relatively fast-growing and of good form. Figure 3 also indicates that resprout chestnut oaks were similar in size to intact stems at stand age two. This result is in agreement with McQuilkin's (1975) studies of white oak, and suggests that, because of vigorous resprouting, damage to advance regeneration stems caused by logging is unlikely to have a negative impact on the development of oak advance regeneration.

<u>Prediction Equations for Height and Diameter Growth of Seedling and Seedling Sprout Advance Regeneration</u>

Equations using six measured variables of pre-harvest size, age, and vigor, along with several interaction terms to predict oak advance regeneration growth (Table 15) gave a much better fit than similar equations describing stump sprout production from stump variables (Table 8). This is true not only for intact advance reproduction, but also for resprout stems, which are in a sense very small stump sprouts. If the independent variables used in both stump sprout and advance regeneration growth equations represent resources available within the plant, then the effect of resources on subsequent growth may be asymptotic. That is, an increase in resources from 2 to 3 units may be closely connected with a concomitant increase in growth, while an increase from 99 to 100 resource units may have little effect on growth. The apparent sensitivity of height and diameter growth to plant resources within the range of small sizes represented by advance regeneration stems indicates that projections of post-harvest oak development on the basis of pre-harvest advance reproduction size structure is possible. Such projections would have to be site-specific, although species-specific equations might not be necessary. However, the idea of projecting the oak advance regeneration structure of a stand into the future may have most utility before, rather than after, final harvest. If the present size structure were known, a silviculturist might be able to estimate the amount of time before a minimum number of stems of a minimum size will be present in the understory of a stand under given site conditions and light levels. Further research is needed to determine if advance regeneration growth is as sensitive to original measures of size, age, and vigor under less than full light.

There are strong implications that the stems which grow most rapidly after clearcutting are the stems which have grown rapidly in the recent past (Factor 3) or have attained relatively large size (Factor 1) (Tables 17, 19, and 20). The correlative type of information on which these conclusions are based does not permit determination of whether a cause-effect relationship exists, perhaps through the effect of stored carbohydrates or extensive exploitation of soil or light resources on further shoot growth. An explanation based largely on genetic factors is certainly a viable alternative. Regardless of the mechanism involved, height increment during the immediate pre-harvest period might be incorporated, along with stem size, into a system of evaluating growth potential of the advance regeneration within a stand. The lack of relationship between root-shoot ratio and subsequent growth (Tables 19 and 20) is evidence that the relatively rapid growth of seedling sprouts as compared to true seedlings (Table 12; and McQuilkin, 1975; Sander, 1972; and Liming and Johnston, 1944) is probably not the result of difference in partitioning of resources between root and shoot. A more likely hypothesis is that the larger average stem size of seedling sprouts imparts a growth advantage, as discussed above.

Development of Seedling and Sprout Origin Stems beyond Age Two

Stump sprouts have historically been considered a low quality source of oak reproduction on the basis of poor form and susceptibility to rot, especially associated with high stumps and frequent wildfire (Lamson, 1976). There have also been suggestions from European coppice experience (Daniel et al., 1980) that in the long run sprout origin oak stands are outproduced by seedling origin, or "high", oak forests. The heights and diameters illustrated in Figures 4 and 5 do not represent a comparison between seedling and sprout origin stands, but between stems of different origin within the same stand. Such an intra-stand comparison incorporates the competitive advantage of stump sprouts during the first few years of stand development. Although Figures 4 and 5 give no indication that seedling origin stems begin to approach the size of sprout stems within the 28 year time frame considered, seedling origin oaks do appear to maintain their relative stature despite the early competitive disadvantage. Another drawback of this type of study is that growth is not measured directly on a cohort of individuals, but is simulated from averages for stands of different age. The accuracy of the simulation depends on two assumptions. The first is that height and diameter within the younger stands are similar to height and diameter in the older stands when they were at a comparable age. The second assumption is that there has been no effect of size on survival; if proportionally lower mortality occurred among large individuals, average height and diameter in older stands would be inflated relative tc younger ones. No information was obtained which would reflect on the accuracy of the first assumption, and the second is probably false. Given these complications, firm conclusions regarding the growth patterns of seedling and sprout oaks await the results of long-term studies which follow cohorts of individuals through time. It can certainly be stated, however, that stump sprouts were the most prominent form of oak regeneration in all eight stands sampled, including the 17- and 28-year-old stands. Nevertheless, it is evident from Figure 6 that a small number of seedling origin individuals---perhaps 50 or 100/ha---do attain an upper canopy position.

The lack of effect of site (as expressed by vegetation type) on chestnut oak size in the older clearcuts (Figures 4 and 5)---with the exception of 5-year-old stump sprouts---is somewhat surprising, especially in light of the significant effects found in the two year-old stands (Tables 7, 13, 14, and 18). One possible reason is the effect of competition on seedling origin oaks in the 5-year-old stands, and on oaks of both seedling and stump sprout origin in the 12-year-old stands. Competition may be strong enough to obscure the effect of site potential on suppressed and intermediate stems, yet it has not operated for a long enough period to eliminate these individuals from the stand. The competition factor in 2-year-old stands, and on stump sprouts in 5-year-old stands, is not intense enough to entirely overshadow the effect of site. Site index curves, based on heights of dominants and codominants alone, are usually least effective in assessing site potential in young stands, where curves for different sites tend to converge.

The scarcity of suppressed sprout origin stems (Figure 6) is consistent with reports of the intolerance of this type of individual (Daniel et al.,1980). It was also observed that in particularly dense areas of several stands, chestnut oak stump sprouts appeared low in vigor in response to lateral competition. Further research concerning the response of oak sprouts to competition from above and from the side might have important implications with regard to the use of partial cuts to favor browse production or oak seedling establishment, or the likely effects of initial stand density on the performance of stump sprouts.

The decreasing correlation of stump diameter with sprout size as stand development unfolds (Table 21) may signal an end to the dependence of sprouts on the root system of the parent tree. Turnover among lateral roots is rapid; main laterals a meter or more from the root core are probably not functional for more than a decade or so (Fayle,1968). Although some parts of the parent tree root system undoubtedly remain at stand age 17 years, most of the functioning secondary and higher order roots have probably been initiated since the harvest of the old stand. With the passage of time, subsequent growth would become less influenced by the resources of the original roots. But this does not explain why the early growth advantage of sprouts from large stumps is not maintained or increased, just as large advance regeneration grow more rapidly than small advance regeneration (Table 19). A tenable explanation is that the dominant sprout in each clump in pole-size stands is, more often than not, different from the sprout that was dominant in the 2-year-old clump. Johnson (1979) shows a poor correlation in elongation of individual black and white oak sprout stems from one year to the next. Wendel (1975) reported frequent shifts in dominance within a sprout clump for several oak species, especially during the first five years after harvest. These shifts in dominance would tend to obscure any relationship between stump size and height or diameter of the tallest sprout after the first few years of stand development. However, sprout production variables based on all stems within a clump, such as total biomass production, might continue to show a significant relationship with stump size for a longer period.

The positive correlation between sprout number and size of dominant sprout in stands 5 years old and younger (Table 21) is considered to be a function of their mutual relationship with stump size. Dominant sprout size in these stands is affected by some resource-supplying quality associated with stump size, while sprout number is more likely a product of more dormant buds exposed along a larger circumference (in stumps in which size has not precluded sprouting altogether). But with time passed, dominant sprout size becomes largely independent of stump resources, and sprout number becomes independent of stump circumference. Instead, sprout number represents the number of ways the soil resources available to the common root system must be divided. By comparing different levels of artificial thinning in sprout clumps of northern red oak, Johnson (1980) has shown that such competition can adversely affect height growth of individual stems. The negative, though nonsignificant, correlation observed for dominant sprout diameter in the 17-year-old stand (Table 21) may indicate that different levels of competition are detectable in naturally thinned clumps.

The lack of correlation between age and size among seedling origin stems in the 17-year-old clearcut (Table 22) does not support the notion that successful oak regeneration depends on the continued elongation of large advance reproduction stems. The seventeen-year-old stand's tallest seedling origin stems, which themselves varied only narrowly around a median stem age of 17, could only have been either seedlings which had germinated within a few years of the original clearcut, or stems which had died back and resprouted soon after harvest. Information collected in the main

Potts Mountain study area (Tables 12 and 19) and in studies conducted elsewhere (McGee and Hooper, 1970; Lamson, 1976; Sander, 1971) suggest that seedlings germinating either after or immediately prior to harvest have little chance of survival. On the other hand, a comparison of Tables 13 and 14 shows that chestnut oak advance regeneration individuals which die back and resprout put on about twice as much height growth in the first two years after harvest as stems which continue extension of the original leader. Many of these resprout individuals appeared to have a relatively good chance for survival. Carvell (1979) refers to flat-topped oak advance regeneration which straightens within a few years of harvest. The data presented here indicates that, for chestnut oak, the straightening process involves dieback and resprouting with renewed vigor from the stem base.

Most researchers have found that oak advance regeneration is less abundant on good sites than on poor and fair sites (Arend and Gysel, 1952; Carvell and Tryon, 1961). However, the densities reported here for total oak advance regeneration before clearcutting (Table 10), for oak advance regeneration more than 1 m tall in the same stands two years after harvest (Figure 7), and for seedling origin chestnut oak stems in 5- and 12-year-old clearcuts (Table 23) all indicate that the best oak regeneration occurs on the relatively mesic mixed oak sites. One can best interpret these results by considering the requirements for seedling establishment and survival. Abundant oak establishment depends on the acorn occupying a moist, protected location until, and during, the time that the seed is physiologically ready to germinate. For species such as chestnut oak, which germinate during the fall, the critical period occurs at a season when moisture conditions are most likely to be limiting to germination. Given the droughty conditions typical of fall in southwestern Virginia, mixed oak and mixed hardwood sites might present a more favorable range of seedbeds than mixed pine or mixed oak-pine. Once germination has occurred, survival of drought-tolerant oak species may be influenced more by light conditions than soil moisture. Although overstory cover increases from mixed pine through mixed hardwood vegetation types (McEvoy et al., 1980), light conditions under the uneven canopies of the high-graded mixed oak stands (but not under mixed hardwood) are adequate to support survival and resprouting of oak seedlings. Carvell and Tryon (1961) have shown that disturbance and aspect, through their effect on light reaching the forest floor, are important factors affecting oak advance regeneration in West Virginia. In the Potts Mountain area, where annual precipitation is typically 15-25 cm less than in West Virginia, optimum conditions for oak establishment and survival may have shifted to the relatively mesic sites. The preceding explanation is somewhat simplistic, since it ignores such crucial elements as seed production, dispersal, and predation, and competition from understory vegetation, factors whose relationships with site are not known but may be considerable. It seems likely, though, that light and moisture are the two most important factors influencing understory composition, and hence the makeup of the succeeding generation after clearcutting an Appalachian oak forest.

SUMMARY AND CONCLUSIONS

Using the model for vegetation development introduced earlier,

$$V_p = V_o + \sum_{Species=1}^{3} \sum_{Years=1}^{p} (Survival + Production),$$

an attempt to project the future composition of Potts Mountain stands can be made. The results reported earlier indicate that initial density of chestnut oak was much greater than that of scarlet or black oak in the pre-harvest Potts Mountain stands, although scarlet oak density was slightly higher among tree stratum individuals (>5m in height) in the mixed pine type. Chestnut oak's advantage in initial numbers over scarlet oak was greatest on the mesic sites and less on drier sites. Black oak individuals of various stature were scattered throughout.

Survival of small individuals less than 5m tall was uniformly high (90-95 percent) among the three oak species two years after harvest. Chestnut oak individuals taller than 5 m exhibited somewhat greater survival (i.e., stump sprouting) than the other oaks on all sites. Sprout production of individuals which had been greater than 5 meters was generally highest for chestnut oak, with the differences not wholly attributable to initial stump characteristics. However, for seedling and seedling sprout advance regeneration, no intrinsic differences in production existed between species.

The overwhelming effect of size on subsequent growth has been shown repeatedly in this study. The direct effects of size in obtaining and accumulating resources necessary for growth have been emphasized in the two-year-old clearcuts. However, the indirect effects of maintaining and expanding resources in the face of intensifying competition from adjacent individuals will become increasingly important as the stands mature. Production advantages observed during the first years after harvest should tend to multiply in terms of both growth and survival as canopy closure takes place, and individuals become stratified into suppressed or dominant positions. There is thus some reason to expect tendencies observed early in stand development to persist into later stages.

If the trends exhibited in the first two years of development are maintained, chestnut oak will become more dominant relative to black and scarlet oaks after clearcutting than it is in adjacent mature oak forests of the area. It should increase in dominance on moist sites because of the large cadre of small individuals which exist in the understory of those stands before clearcutting. And it should increase in dominance on dry sites because of the production advantage of chestnut oak stumps over their oak associates. Scarlet oak will probably remain an important species on dry sites after clearcutting because of its dependable production of stump sprouts and the ability of scarlet oak sprout clumps to dominate a wide area through lateral extension. The relatively low frequency of scarlet oak advance regeneration indicates that the species has little ability to successfully invade new territory. Black oak sprouting is uncertain and relatively unproductive, and advance regeneration is sparse. It will probably remain a scattered component of Potts Mountain oak forests after clearcutting. Of the three major oak species on Potts Mountain, then, chestnut oak will probably play the largest role in filling the niche formerly occupied by American chestnut.

Such projections should not be extended beyond midslope Ridge and Valley sites on sandstone parent material, whose vegetation composition is similar to that described previously for the Potts Mountain study area. On lower slope positions of Potts Mountain, on shale-derived soils, scarlet oak and white oak are the dominant oaks in both mature and young stands, and chestnut oak is a minor component. It is not known whether the survival and production relationships differ on these sites from those in the main study area less than a kilometer away. However, it is clear from an examination of the understories of the lower slope stands that initial establishment differs as a reflection of the difference in overstory composition.

One can only speculate about the relative performance of the three species studied under a different harvesting system or under less intensive management. For instance, how did chestnut, scarlet, and black oaks respond to the "silvicultural system" of the 1900-1920 period, in which high-grading---removal of only the largest and best-formed trees of desirable species---was followed by repeated fires? The evidence is contained in the mature oak forests of the southern Ridge and Valley today, such as the stands cut on Potts Mountain. These stands are in general poorly stocked, with an oak component almost totally of coppice origin. Chestnut oak is ubiquitous on all sites, scarlet oak shares dominance with pitch pine on the driest slopes, and black oak is relatively infrequent. It can be reasoned that wildfire, which was frequent in most stands until about 1940 (Ross et al., 1982), favored sprout oak regeneration and the establishment of pine seedlings on the exposed mineral soil while tending to eliminate oaks originating from advance regeneration stems. Consequently, these stands contained more scarlet oak and pitch pine, less of species like black oak which depend on advance regeneration, and more space unoccupied by tree species than would be projected sixty years from today after clearcutting with whole-tree harvesting.

An important objective of the research reported in this dissertation was the development of prediction models for shoot production after clearcutting. This objective was motivated by the desire to isolate several easily measured characteristics of large and small oak stems which could be used in stand management to project the growth potential of these individuals after cutting. But "easily measured" traits are often very indirectly and imperfectly related to growth response. Judging by relative fits of the models, this was more true for sprouts from large individuals (stump sprouts) than for growth of intact or especially resprout oak advance regeneration. The relatively poor fit of the model for stump sprout growth in comparison to the model for resprout growth suggests that resources may cease to be limiting to sprout production beyond some critical size.

It would be most helpful to the silviculturist if, knowing the size distribution for understory and canopy-size oaks within a given stand, and having a reliable estimate of site quality, he could accurately estimate the structure of the oak component of the stand at any point in the future after clearcutting. The information necessary to develop such projections is obviously not forthcoming from a two-year study of oak development. The results of the two-year study do indicate, however, that even long-term studies using regression analysis are not likely to give accurate predictions of aboveground production on an individual stump basis. Unfortunately, regressions predicting second-year sprout production variables from stump characteristics rarely accounted for more than 35 percent of the variation. Forest managers and silviculturists may have to be satisfied with site- and species-specific probabilities for stumps of various diameter classes producing dominant or codominant sprouts at several stand ages. And while the ability to predict growth of advance regeneration stems is much greater, only long-term studies will show whether these relationships are maintained over longer periods of time. In general, it would seem that a rotation length of 70 to 100 years, depending on site, would provide stumps of a size from which sprouting would be relatively dependable and yet vigorous. If final removal were preceded twenty or thirty years earlier by a preparatory cut to stimulate the development of large advance regeneration, this source might contribute significantly to restocking the stand with oaks.

Nearly all major tree species in the Appalachian oak forest utilize some form of sprouting to reoccupy clearcuts. Red maple, sourwood (Oxydendrum arborea (L) DC), blackgum, yellow-poplar, and American chestnut all produce vigorous stump sprouts. Sassafras (Sassafras albidum (Nutt) Nees), and black locust produce fast-growing root suckers. Even pitch pine stumps will sprout. But only the oak species seemingly have the ability to produce generation after generation of sprouts from small individuals in apparently precarious environments---heavily grazed fields, frequently burned areas, and the dimly lit understories of mature forests. The mechanism of sprouting has helped oaks to establish outposts in the prairie vegetation of the Great Plains, to be the primary tree species in the chapparral and savannah ecosystems of California, and to assume prominent positions in the Eastern Deciduous Forest Biome. The ability of large or small oaks to sprout may be due to the multiple buds they produce, to the emphasis in the genus on belowground over aboveground biomass production, or to some less apparent cause. In any case, the strategy allows oaks to build a population with well-established root systems, able to respond with vigor and alacrity to an interruption in the pressure of grazing, fire, or low light.

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APPENDICES

Appendix 1: Equations for predicting stem biomass (dry weight) in the main study area (Potts Mountain, Craig Co., Va.). Range of diameters sampled is 2-40 mm.

Model: Stem biomass (g) = a (stem diameter, mm)^b.

Species	Vegetation Type	n[1]	a	b	R^2
Chestnut oak	Mixed hardwood	41	.069	2.64	.89
Black oak	Mixed hardwood	16	.065	2.56	.67
Chestnut oak	Mixed oak	51	.048	2.71	.96
Scarlet oak	Mixed oak	51	.038	2.72	.92
Black oak	Mixed oak	26	.114	2.35	.90
Chestnut oak	Mixed oak-pine	38	.117	2.46	.96
Scarlet oak	Mixed oak-pine	46	.137	2.34	.95
Black oak	Mixed oak-pine	35	.033	2.82	.78
Chestnut oak	Mixed pine	45	.062	2.62	.77
Scarlet oak	Mixed pine	42	.202	2.16	.87
Black oak	Mixed pine	19	.057	2.54	.83

[1]Number of stems sampled.

Appendix 2: Equations for predicting leaf biomass in the main study area (Potts Mountain, Craig Co., Va.). Range of diameters sampled is 2-20 mm.

Model: Leaf biomass (g) = a (stem diameter, mm)^b.

Species	Vegetation Type	n[1]	a	b	R^2
Chestnut oak	Mixed hardwood	34	.202	2.00	.80
Black oak	Mixed hardwood	16	.372	1.81	.57
Chestnut oak	Mixed oak	40	.244	1.93	.87
Scarlet oak	Mixed oak	40	.235	2.01	.91
Black oak	Mixed oak	18	.086	2.47	.88
Chestnut oak	Mixed oak-pine	32	.364	1.89	.66
Scarlet oak	Mixed oak-pine	37	.392	1.95	.73
Black oak	Mixed oak-pine	32	.291	2.02	.85
Chestnut oak	Mixed pine	37	.255	1.96	.55
Scarlet oak	Mixed pine	34	1.27	1.39	.58
Black oak	Mixed pine	17	.332	1.99	.75

[1]Number of stems sampled.

Appendix 3: Significant differences[1] (α = .05) in stump sprout production between areas within a vegetation type in the main study area (Potts Mountain, Craig Co., Va.).

Species	Vegetation Type	Production Variable	Area with Higher Value	Area with Lower Value
Chestnut oak	Mixed oak	Total biomass	F	A
Chestnut oak	Mixed oak	Height of tallest sprout	F	A
Scarlet oak	Mixed pine	Total biomass	E	H
Scarlet oak	Mixed pine	Height of tallest sprout	E	H
Scarlet oak	Mixed pine	Number of sprouts per clump	E	H

[1]Effect of covariants (stump age, stump diameter, original tree height, 10 year radial growth) accounted for.

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Oak Regeneration After Clearcutting on Steep Slopes in the Ridge and Valley Province of Southwest Virginia

by

Michael Steven Ross

(ABSTRACT)

The development of oak stems of advance regeneration and stump sprout origin was studied during a two-year period following clearcutting and whole-tree removal in eight mid-slope stands in the Ridge and Valley Province of southwestern Virginia. Oak regeneration was also characterized in several older clearcuts. Height and diameter of oaks of stump sprout origin in the two-year-old stands was significantly greater than that of advance regeneration stems, and the difference in size among regeneration types appeared to persist into the oldest (17- and 28-year-old) stands sampled. Chestnut oak, which had been the dominant oak species in most pre-harvest stands, had higher density of advance regeneration stems, higher frequency of stump sprouting, and greater sprout production per stump than scarlet or black oak two years after harvesting. However, shoot growth of advance regeneration during the two-year period did not differ among oak species when initial stem size and vigor were accounted for. Taller stump sprouts in the two-year-old stands were associated with more productive sites (as indi-

cated by site index, topographic variables, and vegetation composition),whereas biomass production per stump was less closely related to site quality. Height and diameter growth of oak advance regeneration during the two-year post-harvest period were significantly greater on sites of medium quality than on sites of low quality. Density of well-established oak stems of advance regeneration origin two years after harvest was greatest in stands of site index 55-65 (base age 50), and fell off on sites of higher and lower quality. Models developed to predict two-year stump sprout production from characteristics of the parent tree generally explained less than 40 percent of the variation among stumps, while models describing growth of advance regeneration individuals from pre-harvest measurements accounted for as much as 82 percent of the variation. Regeneration in most of the two-year-old stands appeared adequate for restocking of oaks to at least their pre-harvest level, although stems will probably be widely spaced and mostly of stump sprout origin on both the poorest and the most productive sites.