

Increased dominance by *Acer rubrum* and the decline of the *Quercus-Carya* climax in the
North Carolina Piedmont

by

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A thesis submitted to the faculty of The
University of North Carolina at Chapel Hill
in partial fulfillment of the requirements for
the Bachelor of Science degree with Honors in
The Department of Biology

Chapel Hill

2000

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Quercus-Carya forests have long been described as the climax community of the North Carolina Piedmont (e.g., Braun 1950). However, *Quercus* and *Carya* species are less shade-tolerant than other species in the area, and it is unclear what factors regulate and maintain this community. Moreover, some authors have suggested that *Quercus-Carya* dominance is declining. The goal of this project was to characterize changes on 14 long-term research plots in Durham and Orange counties, North Carolina. These plots have had relatively little anthropogenic disturbance, and are representative of mature *Quercus-Carya* forests of the North Carolina piedmont. I found that all *Quercus* species have declined in density, with trends in *Carya* less well defined. *Carya* species are increasing in density on most plots, with the exception of *C. tomentosa*, which has consistently decreased in density. Over the same time period, *Acer rubrum* and other shade-tolerant species (e.g., *Fagus* and *Nyssa*) have rapidly increased in density. Analysis of the age structure of *Quercus* populations shows that there is a lack of regeneration at the seedling and sapling levels. Seedling transects located within several of the long-term sampling plots contain high densities of *Acer rubrum*, and the canopy layer of the forest is becoming progressively more similar to the seedling layer of the forest.

Forest simulation models provide one way to extrapolate compositional changes into the future. However, parameterization of a forest gap model, ZELIG, to Piedmont forests proved problematic, as the model consistently predicted a *Fagus grandiflora* climax forest. This may be because, barring disturbance, the model simply predicts that the most shade-tolerant species wins. Trial scenarios with the model suggested that extensive thinning of the understory of *Quercus-Carya* forests, such as would result from a low-intensity groundfire, would allow *Quercus-Carya* seedlings to survive to maturity. The model failed to simulate the recent rise in dominance of *Acer rubrum*, except when the seed rain of this species was increased dramatically. The sensitivity of the ZELIG model to the species composition of the seed rain suggests the need for further work to more accurately simulate this component of forest dynamics.

Introduction

Forests of the North Carolina Piedmont typically have been described as a *Quercus-Carya* climax community (e.g., Braun 1950). Support for this assertion comes from various sources: observations of extant mature hardwood forests (Oosting and Blomquist 1944), written descriptions of the early vegetation (Davis 1996), witness trees found in old surveying records (Orwig and Abrams 1994), pollen counts from cores taken from various lake bottoms and bogs (Clark and Royall 1996), and logging records (Healy 1985). There is at least general agreement that *Quercus-Carya* communities were predominant when Europeans arrived in North Carolina, and that these communities were relatively stable, at least over appropriate spatial (i.e., bigger than a gap and smaller than the Piedmont) and temporal (i.e., longer than a successional sequence but shorter than cycles of glaciation) scales. The species involved in the climax depend primarily upon on the moisture and nutrient regime of the site, but members of the two genera are dominant in mature stands across both gradients (Coile 1933, Oosting and Blomquist 1944, Keever 1950, Peet and Christensen 1980a, Peet and Christensen 1980b).

Oosting (1942) was one of the first authors to designate the *Quercus-Carya* community as the regional climax, and suggested that the community is a true climax in the Clementsian sense, meaning that it would maintain itself without significant natural or anthropogenic disturbances. However, species of *Quercus* and *Carya* are generally less shade-tolerant than many other species in the area, such as *Acer rubrum* and *Fagus grandifolia* (Burns and Honkala 1990), and many authors have recognized the *Quercus-Carya* community as a proclimax in the Clementsian sense, meaning that it needs significant disturbances to maintain itself (e.g., Abrams and Seischab 1997).

There are two major models in the literature that have been proposed to explain the nature of this disturbance. One model proposes that the disturbance operates in the understory of Piedmont forests, and preferentially favors *Quercus-Carya* seedlings and saplings. This understory disturbance could occur in several ways. First, low-intensity understory fires occurred occasionally in the forests of the Piedmont, and it appears that such fires caused less damage to *Quercus-Carya* populations than to those of other species (e.g., Oosting and Blomquist 1944). *Quercus* and *Carya* seedlings and saplings are more resistant to fires than most other species, perhaps due to the larger investment in roots possible for stems developing from large seeds. Furthermore, mature *Quercus* and *Carya* stems have the ability to re-sprout from their roots, which may allow them to regenerate faster than other species (Burns and Honkala 1990). After a low-intensity fire, reduced competition from seedlings and saplings of other species may have allowed *Quercus-Carya* stems to survive in greater numbers to maturity. Second, herbivores may preferentially browse from species that are competitive with *Quercus* or *Carya* species in the understory. *Quercus* and *Carya* species may simply be less palatable than other species because of the high tannin content of oaks and low nutrient value of hickory leaves (Burns and Honkala 1990). Reduced competition from other species' seedlings and saplings would allow *Quercus-Carya* stems to survive in greater numbers to maturity. Both of these processes could have played important roles in the maintenance of *Quercus-Carya* communities in different historical periods. Fire was probably common before the arrival of Europeans, and persisted as a forest management tool until the early 20th century. However, forest fires have been infrequent for most of this century (Frost 1998). In contrast, grazing probably had a negligible impact before the arrival of

Europeans, but may have increased dramatically in importance after European livestock became established, allowing continuing maintenance of *Quercus-Carya* communities, even after fires began to be suppressed by European settlers (Peet, *personal communication*).

The second model proposes that the disturbance operates in the canopy of Piedmont forests, and that this disturbance increases light levels on the forest floor, allowing *Quercus* and *Carya* seedlings and saplings to survive to maturity. Such canopy disturbances could occur in several ways. First, hurricanes and other catastrophic storms have hit Piedmont forests two or three times a century, and often cause significant damage to the canopy layer of the forest. This damage would open small gaps that might have ideal light-levels for *Quercus* and *Carya* seedlings and saplings, which would then be released from their previous state of suppression in the understory of the forest and would be more likely to survive to maturity (Lorimer 1984). Second, logging of occasional trees may open up the canopy and allow light to reach the forest floor in greater amounts, releasing *Quercus* and *Carya* seedlings and saplings from suppression and allowing them to survive to maturity. As above, both of these processes could have played important roles in different historical periods. Levels of windthrow probably have remained relatively constant over time, but high-grading of the forests after European settlement may have allowed *Quercus* and *Carya* species to become even more dominant in Piedmont forests in the past several centuries. Note that the size of the gap involved here is critical, as large gaps allow for colonization and eventual dominance by *Pinus* species, in effect resetting the forest to an early part of the successional sequence (Peet, *personal communication*).

Many have observed in recent years that *Quercus-Carya* communities appear not to be regenerating (e.g., Abrams et al. 1995). Few if any *Quercus* or *Carya* seedlings or saplings appear in the understory. Furthermore, a conspicuous cohort of more shade-tolerant species such as *Acer rubrum* have entered the understory and appear to be drastically increased in abundance (Lorimer 1984; but see Muth 1996 for a discussion of difficulties with shade-tolerance measurements). This trend is disturbing, as historical records suggest that these species played only minor roles in the pre-European forests (Davis 1996). Several authors have discussed this trend and found empirical support for its existence in other areas (e.g., Abrams et al. 1995, Clark and Royall 1996, Lorimer 1984, Reich 1993). This study examines data for several long-term study plots in the Duke Forest to document the occurrence and extent of this trend on the North Carolina Piedmont.

The conceptual models above also suggest hypotheses to explain this trend. On the one hand, if the disturbance operates at the understory level, then reduction in this disturbance regime could be increasing the mortality of *Quercus* and *Carya* seedlings and saplings. Grazing pressure is less than it was a century ago when livestock were allowed to roam wild on forested land. Fires also are becoming increasingly rare in the Duke Forest, as suburban development has increased the pressure to suppress natural fires. Either (or both) of these changes could be driving the current trend away from a *Quercus-Carya* dominance. On the other hand, if the disturbance regime operates at a canopy level, then some reduction in this disturbance regime could decrease the light allowed into the understory. Recent windthrow events (excluding Hurricane Fran, which has so far had indeterminate effects on Piedmont forest regeneration) may simply not have been

severe enough to let into the understory the levels of light required by *Quercus* and *Carya* seedlings and saplings. Large-scale clear-cutting may also have allowed excessive amounts of light into the forest floor, encouraging the formation of a dense, even-aged hardwood stand that does not allow sufficient light in to the understory to allow *Quercus* and *Carya* regeneration. Finally, as a null hypothesis, we may consider that this trend is not really occurring to any significant degree in the Duke Forest. This study attempts to clarify the relative importance of the mechanisms invoked by these hypotheses to the extent possible with available demographic data.

Computer simulation of forest dynamics has become an increasingly important tool for understanding relationships in forest communities. Individual-based “gap” models in particular have become increasingly important for integrating complex successional processes. As part of this study, a gap-based computer model, ZELIG (Urban 1991), was parameterized so that trends in North Carolina Piedmont forests could be projected into the future. In addition, it was hoped the model would allow a more critical evaluation of the hypotheses discussed above. ZELIG is derived from the FORET model of Shugart and West (1977). However, in ZELIG each cell in the model can interact with other cells, as trees shade other trees in adjacent cells. In addition, moisture, nitrogen, and fire processes are modeled in a spatially explicit manner in ZELIG, which enhances its usefulness. Numerous detailed descriptions of the dynamics of ZELIG have been published separately (e.g., Urban 1990, Urban et al. 1991, Randolph 1996, Miller and Urban 1999a, Miller and Urban 1999b, Miller and Urban 1999c).

Methods

Study Sites

This study was conducted using 14 permanent research plots located in Durham and Orange Counties, North Carolina. Eleven of these plots are located in the Duke Forest of Duke University, two are located in the Hill Forest of North Carolina State University, and one is located in the Mason Farm Biological Reserve of the North Carolina Botanical Gardens. Mean monthly temperatures in the area range from 4.4°C in January to 25.8°C in July, with temperatures commonly exceeding 38°C during brief periods in the summer. Mean annual precipitation is 105.2 cm, with slightly more precipitation falling in summer than in winter (NC Climate Office 1999). Soil parent material varies widely from Triassic Basin sediments to Carolina slate to diabase intrusions (Sutter 1987). More information on the physical environment of the area can be found in Billings (1938), Oosting (1942), and Peet & Christensen (1980).

All plots are located in hardwood stands that are among the least-disturbed hardwood forests available in this area. Nevertheless, many of these stands have had some form of disturbance prior to the establishment of the plots (e.g., low-intensity grazing by livestock and selective cutting). The plots cover a range of forest types, land-use histories, and environmental conditions, and are typical of mature forests in the Piedmont of North Carolina (Table 1). Fairly comprehensive soil and site data are available for many of the study sites (Table 2). Note that soil characteristics can vary substantially over small spatial scales in the Piedmont (Palmer 1991, Reed et al. 1993), and only average values are displayed here.

Generally, the size and species of all stems greater than 1 cm in diameter at breast height (DBH) were recorded each time the plot was sampled. However, on the Duke Forest plots, new stems that reached the minimum size were not systematically recorded after the first sampling date until 1978, and the minimum size stem recorded was 0.5" (~1.27 cm) until 1978, not 1 cm. For this study, the years in which ingrowth were not recorded have been removed from the data set, and the difference between the various minimum sizes is ignored. Note that on Oosting Plot only stems greater than 2 cm were recorded, which may decrease the accuracy with which understory plants are surveyed on this one plot. Big Oak Woods Plot only had stems greater than 2 cm recorded in the first year it was sampled, and for consistency data from all later years was truncated at 2 cm as well. Plots were sampled every three to five years, with the exception of a period from 1961 to 1978, when Duke University stopped sampling their plots.

The size of several plots was increased between 1978 and 1988. The distribution of all species in all plots was examined using Arcview. Species were relatively homogeneously distributed within each plot. Changes in plot size could, therefore, be ignored, given that summary statistics for these stands were calculated on a per unit area basis. A small sampling effect may occur, as new trees are included in each plot as it is widened. However, preliminary analyses with and without areas of later plot expansion were essentially identical, and the total plot area in any given year is used in this study. The one exception is Rocky Plot, where there is a north-south gradient in cation concentration and soil clay mineralogy. The northern half of the plot has shrink-swell clays, high levels of magnesium, and has a diabase intrusion that causes considerable environmental heterogeneity. The southern half of the plot is more homogeneous in

character, with lower clay content and lower levels of magnesium in the soil. Only data from the southern half of the plot was considered, both to minimize any sampling effects (northern areas increased more in size with each plot expansion than did southern areas) and to make the Rocky Plot more homogeneous in its environmental characteristics.

Taxonomic Considerations

Species are abbreviated in graphics in this paper by a four-letter code, with the first two letters of the code being the first two letters of the genus involved and the next two letters of the code being the first two letters of the species involved. A list of the abbreviations used is located in Appendix 1. Abbreviations are also introduced in the text, where appropriate. Species names in this study follow Kartesz (1994). Obsolete species names in the dataset were changed to current species names as needed. However, the genus *Carya* (CASP) presented some taxonomic difficulties. At the beginning of the study period many *Carya* stems were recorded as *Carya ovalis*, but as time went by these were more often considered as *Carya glabra* (CAGL). Furthermore, the existence of *Carya ovalis* as a distinct species is problematic, as it is specifically excluded in the *Flora of North America* (1993), but retained by Kartesz (1994). All stems recorded as *Carya ovalis* were changed to *Carya glabra*, following *Carya glabra sensu* Sarg. Furthermore, occasionally, a *Carya* stem could not be identified to species, and was simply recorded as a member of the genus *Carya*. Where possible, these stems were fully identified later, and the current dataset was updated to reflect this information. In most plots, the few remaining unidentified stems were insignificant in the analysis of the plot, and were ignored. However, in the Bormann plot there were numerous trees identified only to the

genus *Carya*, and on this plot all *Carya* species were simply analyzed as a genus. Important *Carya* species in the study area are *C. glabra*, *C. ovata* (CAOV), and *C. tomentosa* (CATO), whereas *C. carolinae-septentrionalis* (CACA) and *C. cordiformis* (CACO) are only locally abundant. Important oak species in the uplands of the study area are *Q. alba* (QUAL), *Q. coccinea* (QUCO), *Q. rubra* (QURU), *Q. stellata* (QUST), and *Q. velutina* (QUVE), whereas *Q. phellos* (QUPH), *Q. michauxii* (QUMI), *Q. shumardii* (QUSH), and *Q. lyrata* (QULY) are locally abundant in alluvial sites.

Analysis of plot data

Summary statistics were calculated for each plot for every sampling year using SAS software. The principal summary statistics used were basal area (BA), expressed as m²/ha at breast height, and density, expressed as stems/ha. Either of these statistics can be expressed as a relative measurement, simply by dividing by the total BA or density for all species in a plot (and multiplying by 100, to express the result as a percent). Trends in BA and density for important species in each plot were graphed using Microsoft Excel 2000.

This dataset presented an interesting challenge for statistical analysis, as the plots cannot be regarded as replicates. First, the plots differ in environmental conditions, topography, and successional age, and cannot be expected to react similarly to possible forces affecting oak-hickory populations. Second, plots varied in size and sampling duration and intensity, leading to greater certainty for summary statistics for some plots than others. Third, plots with the same size and sampling regime would have different uncertainties in their summary statistics if environmental differences influenced the

number of species or individuals involved in the calculations. Finally, because plots were not all sampled in the same years, the year sampled cannot be treated as an independent variable, since there might be, for example, significant variation in weather or the abilities of the various field crews from one year to the next.

In light of these difficulties, a Wilcoxon's signed-ranks test was performed to test the null hypothesis that there is no trend away from *Quercus* and *Carya* dominance. The average change in relative density per year was tested, under the assumption that if there were no effect, then as many rank changes would be positive as negative. In this case, a one-tailed test is used because the null hypothesis is only that *Quercus-Carya* dominance is not decreasing. Wilcoxon's signed-rank test is useful in this case because it is non-parametric and conservative, considering only rank order of changes. However, its use here is problematic for several reasons. First, each plot is weighted equally, despite large differences in plot size. Second, considering changes in relative density per year weighs all plots equally, despite differences in duration of the various plots. Finally, Wilcoxon's signed-ranks test assumes that the population of relative density values that each plot is drawn from all has the same general distribution. As we have no replication, this is difficult to ascertain. In order to estimate the population of relative density values that each plot is drawn from, a bootstrapped distribution of possible relative density values was created using the Jackboot macro for SAS software (SAS Institute 2000). For several plots, 1500 samples were drawn with replacement from the most current years data, and summary statistics generated for each species in each of these samples. The distribution of relative density values generated from bootstrapping was approximately

normal for all species with greater ~25 stems on a given plot, and thus different species on different plots appear to be drawn from the same general distribution.

The size distribution of each *Quercus* and *Carya* species with more than 50 members in a single plot was examined for each plot using univariate kernel density estimation. Kernel density estimation is a non-parametric technique where a known density function, the kernel, is averaged across the observed data points to create a smooth approximation of the actual density function of the data (Silverman 1986). The kernel used was a Gaussian curve, and kernels were equally spaced throughout from the smallest observed DBH to the largest observed DBH for a particular species on a particular plot. Kernel bandwidth was calculated using the Sheather and Jones plug-in method. Calculations were done using the KDE procedure in SAS software.

Finally, seedling data from transects located within several of the study plots were examined. All available seedling transects located within hardwood stands were used, with the exception of seedling transects from Big Oak Woods, which presented some technical problems with data analysis in that the data were stored in a slightly different format than with other seedling transects. To see trends in dissimilarity between canopy and seedling strata, both the seedling and tree map data were ordinated by relative density using non-metric multidimensional scaling (NMS). NMS is an iterative search for the arrangement of ranked scores on a lower dimensional surface that has the least stress with the original dissimilarity matrix. Sorensen distance was used as the measure of dissimilarity between plots. Species that were not surveyed consistently in all plots were excluded. *Viburnum* species, for example, have been counted more consistently recently than in the past, and were dropped from the data set. Occasionally a stem has

only been identified to the genus level, and its species is unknown. Such stems were excluded from the analysis as well. Calculations were done with the “thorough” setting on the autopilot mode of PC-ORD (McCune and Mefford 1999). The autopilot routine in PC-ORD selects the number of dimensions that minimizes the final stress associated with the ordination, as long as this number of dimensions is at least 5 less than the next lowest dimension in standardized stress values rescaled from 0-100, and the final stress associated with this number of dimensions is lower than at least 95% of the Monte Carlo tests.

Parameterization of ZELIG

A version of the ZELIG model (Facet Model 97.5) was obtained from Dr. Dean Urban of Duke University. Most parameters needed to simulate Piedmont forests were taken from Randolph (1996). His procedure is briefly described below. There are two general classes of parameters in ZELIG: species parameters and site parameters. Species parameters used in this study are very similar to those used in the Randolph study. Species tolerance classes for shade and nutrient stress were interpreted from *The Silvics of North America* (Burns and Honkala 1990). The taper equations used are general equations for types of trees, such as evergreen versus deciduous. Species-specific allometries relate DBH to biomass in various tree components (stem, bark, live branch, dead branch, and coarse roots) and represent a synthesis of several papers (Peet et al. 1980, Clark et al. 1985, Clark et al. 1986a, Clark et al. 1986b, Clark et al. 1986c, Busing et al. 1993, Phillips et al. 1981). Regeneration parameters, which affect establishment of new stems, were estimated as accurately as possible from data from Duke forest seedling

transects and Burns and Honkala (1990). For example, the fecundity of each species is expressed in ZELIG on a relative scale from 1 to 9. This relative fecundity scale was estimated using abundance data from Duke Forest seedling transects and descriptions in Burns and Honkala (1990). Randolph calculated the values of G, a multiplier that modifies the diameter increment versus DBH curve, through trial-and-error fitting with Duke Forest plot data. Once the other species parameters were parameterized, the value of G was varied until each tree species had a realistic growth curve over time.

I made two changes to Randolph's species parameters. First, DBH versus height allometries were recalibrated from Duke Forest data where possible, avoiding Randolph's use of data from the Cowetta Hydrologic lab. All regressions were fitted using Kalidograph for Macs, which essentially uses the algorithms for fitting complex regressions developed in *Numerical Recipes for Fortran*. Second, maximum height, DBH, and age parameters for particular species were taken from North Carolina record trees, rather than from North American record trees, in order to take into account regional variation. Species parameters are listed in Appendix 2.

Site parameters for the model were taken largely from the Randolph study. The various parameters pertaining to soil series were taken from data in the USGS soil survey manuals for Durham and Orange counties, using the method of Cosby et al (1984). Most of the parameters changed in the current study were involved in the calculation of the weather regimes. I recalculated weather summary statistics (average precipitation per month, etc.) from a 90-year mean for Durham, North Carolina (NC Climate Office 1999), as well as the gamma parameters that govern the distribution of rain events within a month. In addition, I changed the free-flow fraction (the proportion of precipitation that

hits the soil and percolates through quickly, without having a chance to be absorbed) to reflect some changes in the soil water balance model since the Randolph study. Site parameters are listed in Appendix 3.

Model Verification

The model was used to simulate succession from bare ground. Generally, successional trends were as expected for the Piedmont region (Figure 1). *Pinus* species quickly colonize bare ground, along with some *Liriodendron tulipifera* stems. A cohort of *Quercus*, along with other hardwoods, takes the place of *Pinus* stems after they die. Two aspects of the model output were unexpected. First, *Acer rubrum* (ACRU) levels were underestimated by a factor of 3 or 4. It is unclear why this occurred. Second, there was a trend towards high levels of dominance of *Fagus grandifolia* over time, which did not appear in the Randolph study. For example, when the model simulates an upland stand the stand is composed almost entirely of *Fagus grandifolia* five hundred years after establishment, with *Fagus grandifolia* having a BA of over 20m²/ha. Most plots in our study have a BA of *Fagus grandifolia* of much less than 5 m²/ha, and only on moist, sheltered slopes does *Fagus grandifolia* approach a BA of 15 m²/ha, so the model is seriously overestimating the abundance of this species. Of our study plots only Duke 43 and Duke 44 have a larger BA of *Fagus grandifolia* than this, which makes sense as these plots have rich alluvial soils.

The model's overestimation of *Fagus* dominance appears to be a consequence of recent changes in the soil water balance model. Drought days were typically overestimated in previous versions of the model, and it appears that Randolph

parameterized G to correct for this problem. The current version of the model more explicitly calculates the speed of flow of water through the different soil layers, and thus in theory should fix this problem. However, the model now underestimates drought days, allowing species that prefer mesic habitats (e.g., *Fagus*) to dominate what should be dry upland sites. In addition, the values of G for many species may now be incorrect, since the other parameters on which G's parameterization was based have changed. In addition, part of the "error" in calculating the number of drought days the soil experiences may be because the current soil water balance model in ZELIG cannot accurately model the complexities of the thick clay layers present in Piedmont soils (Dean Urban, *personal communication*). For example, ZELIG assumes that water infiltrates through each soil layer at the same speed, which clearly would not be a realistic assumption in a soil that has a hard fragipan (e.g., Duke 35).

Experiments with the ZELIG model

Due to the serious concerns with the soil water balance portion of the model, the accuracy of any predictions would be suspect. Consequently, few tests were conducted. Nevertheless, two specific scenarios were tested to assess whether trends over time from these scenarios would shed light on the hypotheses discussed in the introduction. In the first scenario, succession was simulated from bare ground with different thinning regimes occurring in each run. The thinning events cut all stems below a certain threshold size to simulate a low-intensity disturbance (e.g., fire) in the understory. Each simulated run had only one thinning event, which had a certain time of occurrence and intensity. Thinning events could occur at three different times: 50 years after stand initiation, 100 years after

stand initiation, and 250 years after stand initiation. Thinning events would either remove all stems below 5cm, all stems below 30cm, or all stems below 100cm (i.e., all stems on the plot). All of these combinations were simulated, plus a control scenario in which no thinning occurred (i.e., Figure 1), for a total of 10 different simulated runs.

In the second scenario, the SEED parameter in ZELIG was varied for different species. The SEED parameter is a relative parameter that controls the number of seedlings established from each species. In this scenario, all species were set to have SEED parameters of 1, while one or more test species were set to have a SEED parameter of 9. Essentially, the test species have nine times the fecundity of all the other species. This scenario was examined to assess the sensitivity of the model to inaccuracies in at least this one regeneration parameter. There were three simulated runs, one for each of the three groups of test species. In the first run, *Acer rubrum* (ACRU) had fecundity 9 times greater than that of every other species. In the second run, all *Carya* species (CASP) had fecundity 9 times greater than that of every other species. In the third run, all *Quercus* species had fecundity 9 times greater than that of every other species

Results

Compositional Change

Total density is increasing over time in almost every plot. Only plots Duke 10, Duke 44, and Bormann have decreased in total density over their sampling periods. The decrease in density on Duke 44 is particularly striking, where the total density has declined 46% over 62 years. Duke 43, a site located very close to Duke 44 and in many ways very similar, increased in total density by 52% over the same time period. Construction near Duke 43 may have increased the light available to trees in that plot, and may explain the discrepancy between density trends in Duke #43 and Duke #44. Plots that increased in total density varied widely in the magnitude of the change, with Duke 37 increasing in density quite rapidly, while nearby Duke 36 decreased less (Table 3). Hurricane Hazel and Hurricane Fran have had different effects on each plot, and may explain some of the variation in changes in total density levels. The plots with shorter sampling durations may also be showing short-term random trends.

Total basal area is also increasing over time for almost every plot. The sole exception is Rocky plot, which decreased in basal area by 48% over 19 years. This is not due to changes in plot size on Rocky; limiting the Rocky dataset to only those trees originally within the plot does not change the trends in basal area significantly. Rocky Plot was damaged by severe drought in the summer of 1985 that killed a substantial number of canopy *Quercus*, which may explain the decrease in basal area. Plots that increase in total basal area varied widely in the magnitude of the change, with

Woodenbridge increasing quite rapidly in basal area (Table 4). The plots with shorter sampling durations (e.g., Oosting) may be showing short-term random trends.

Trends in density of individual species within each plot were highly idiosyncratic for each plot (Table 5a). Generally, shade-tolerant species seem to be increasing in density in the understory of all the plots. *Acer rubrum* (ACRU), *Nyssa sylvatica* (NYSY), *Ostrya virginiana* (OSVI), and *Fagus grandifolia* (FAGR) seem to be doing especially well. On Rocky Plot, *Cercis canadensis* (CECA) and *Morus rubra* (MORU) are also greatly increasing in abundance. These two species, and *Cercis canadensis* in particular, are often described as liking fertile, calcium-rich sites (e.g., Weakley 1999), which makes their abundance on Rocky Plot understandable. However, it is unclear why these two species are not increasing on other fertile plots (e.g., Oosting). All *Quercus* species are decreasing in density, with the exception of *Quercus alba* in Duke 44. However, trends in *Carya* seem to be less defined, with some *Carya* species increasing in density in drier plots. *Carya tomentosa* is increasing in density on the Bormann plot, for example, and *Carya glabra* is increasing on Duke 35.

Trends in basal area of individual species within each plot were similarly idiosyncratic for each plot (Table 5b). As with the density trends above, *Acer rubrum* appears to be increasing in basal area on several plots. However, on many plots *Quercus* and *Carya* species appear to be increasing in basal area. *Quercus alba* in particular appears to be increasing in basal area on many of the plots. Changes in basal area lag behind changes in density by several decades, and it is not unusual to have a plot on which a particular oak species is decreasing in density and increasing in basal area, due to the growth of a few big canopy trees. Because of this, only trends in density were tested

with the Wilcoxon's signed ranks test (Table 6). For all *Quercus* species tested, I rejected the null hypothesis that relative density values were not changing over time at the $P < 0.05$ level. *Carya* species showed no consistent trends, as only *Carya tomentosa* was significantly decreasing at the $P < 0.05$ level. The other two *Carya* species tested, *C. glabra* and *C. ovata* appear, on average, to be increasing (i.e., they have more positive signed-ranks than negative-signed ranks).

Analysis of the size structure of *Quercus* species shows a reduction in density in the smaller size classes of all *Quercus* species. Typical data are shown in Figure 2, which displays trends over time in the size structure of *Quercus alba* on the Bormann plot. Note that the curve's mode shifts right over time, and that the entire curve shifts down over time. This implies that the mean size (and thus the age) of *Q. alba* is increasing over time, but that the density of *Q. alba* is decreasing in all size classes over time. Note that the overall density of *Q. alba* in smaller size classes has dropped particularly dramatically. Few new stems are being established to fill the smaller size classes, as other *Q. alba* stems vacate these size classes. This demographic shift is robust, occurring on all plots for all *Quercus* species tested (i.e., those species with more than 50 stems on a plot). *Carya* trends are less clear, and vary among plots. *Carya tomentosa* seems to show the same demographic shift as *Quercus*, whereas *C. glabra* and *C. ovata* do not. Unexpectedly, *Cornus florida* (COFL) shows the same demographic shift as well. The arrival of *Discula dostractiva* (dogwood anthracnose) in North Carolina may have contributed to this decline, as may have the severe drought of the summer of 1985 (Peet, *personal communication*). Comparing the changes in size distribution for *Acer rubrum* (Figure 3) with those for *Quercus alba* reveals that the size distribution for *A. rubrum* has

a concave shape, as is common for plants, and the curve shifts upwards over time in all size classes, but particularly in smaller size classes. *Acer rubrum* populations thus have considerable demographic momentum, in that there are large numbers of small, established stems that we can expect to gradually age and become larger.

The optimum ordination in NMS, as determined by PC-ORD's Autopilot routine, has 3 dimensions. A 3-dimensional ordination makes the results harder to visualize and their interpretation more difficult, but some clear trends are present (Figure 4). Axis 1 correlates directly with *Acer rubrum* and inversely with *Fraxinus* (FRAX) species and *Morus rubra* (MORU). Axis 2 correlates directly with *Acer rubrum*, *Prunus serotina*, and *Quercus alba*, and inversely with *Fraxinus*, *Liriodendron tulipifera* (LITU), *Liquidambar styraciflua* (LIST), *Carpinus caroliniana* (CACR), and *Ulnus rubra* (ULRU). Axis 3 correlates directly with *Cornus florida* and inversely with *C. ovata*, *Pinus echinata* (PIEC), *Pinus taeda* (PITA), and *Q. stellata*. This axis is difficult to interpret, but appears related to the differing clay mineralogy of the sites, with 2:1 soils at the bottom and 1:1 soils at the top of Figure 4. There also appears to be two environmental gradients in Figure 4a. One can be interpreted as a calcium gradient (viz. Peet and Christensen 1980), with higher calcium sites (e.g., Rocky) in the lower left hand corner of the plot and lower calcium sites in the upper right hand corner of the plot (e.g., Duke 36). The second can be interpreted as a moisture gradient, with drier sites (e.g., Rocky) in the upper left hand corner of the plot and wetter sites in the lower right hand corner of the plot (e.g., Duke 44).

Ordination results support the conclusion that the seedling layers in these plots have changed less over time than the canopy layers of these plots. Most seedling data

moves randomly over time in ordination space, while tree maps show a clear movement towards the seedling data (as one would expect). The canopy layer is becoming more similar to the seedling layer over time, as the distance between the two groups in ordination space for each plot decreases. Seedling data scores higher on Axis 1 than tree map data, implying that this movement of the tree layer of forests towards seedlings is also a movement towards increased *Acer rubrum* dominance.

The seedling layers of Duke 43 and Duke 44 are very similar to one another, and appear close to each other on all three axes. The seedling layers for Duke 43 and 44 appear to vary more from year to year than other plot's seedlings, wandering over a larger portion of ordination space over time. This could be due to chance flooding events that introduce more variation in the seedling stratum. Seedling layers for each plot seem to be more spread out than tree layers, which often clump together into three groups: Those with shrink-swell clays (Duke 35), wetland sites (Duke 43 and Duke 44), and upland hardwoods (everything else, with Rocky Plot being a slight outlier due perhaps to its high calcium levels). The shrink-swell clays on Duke 35 may explain why Duke 35 is different from the other upland hardwood plots' tree layers, which move as a unit over time. Most upland hardwood plots' tree layers are increasing on Axis 1 and Axis 2, and decreasing on Axis 3, which implies that *Acer rubrum* (directly related to Axis 1 and 2) is increasing in importance on all plots while *Cornus florida* (directly related to Axis 3) is decreasing.

Output from the model

Low-intensity thinning events that removed only stems less than 5 cm had very little effect on the trajectory of forest succession, regardless of when the thinning events

occurred. *Fagus grandifolia* tended to decrease more in BA after these low intensity thinning events, probably because the model allows high densities of small *Fagus grandifolia* stems in the understory, and these are removed with logging. This is functionally similar to what one would expect from a low-intensity fire, which would preferentially hurt *Fagus* species, which have very thin bark. However, because of the nature of regeneration in the model, which is independent of forest composition, *Fagus* saplings soon return to pre-thinning levels.

Removing all stems less than 30 cm from a site causes, understandably, more severe changes in forest succession. When this thinning event takes place 50 years after establishment of the stand, the period of pine dominance is lengthened, as large deciduous understory trees (e.g., *Liriodendron tulipifera* and *Quercus alba*) are removed. If, however, this thinning event takes place 100 years after establishment, the transition to a *Quercus-Carya* community is sped up, perhaps because increased light levels release the *Quercus* understory from suppression. Most interestingly, if this thinning event takes place 250 years after establishment, the dominance of *Quercus-Carya* communities are greatly lengthened and increased (Figure 5). This appears to be because, as above, *Fagus* saplings, being particularly numerous, are hit very hard by the thinning event. Increased light available to the forest floor also releases those oaks and hickories suppressed in the understory.

When all stems less than 100 cm were removed from a plot (essentially clear cutting the stand), the successional sequence was reset and begun anew. Regardless of when the thinning event took place, *Pinus* species rapidly increased in dominance, mimicking typical patterns of old field regeneration in the Piedmont. A few trees larger

than the 100 cm cutoff did exist, and these rapidly increased in BA, as these few remaining trees took advantage of the available light.

The manipulations of the seed parameters are more difficult to interpret, but reveal a severe dependence on this one parameter. In the simulation where *Acer rubrum* was nine times more fecund than other species, it functionally replaces *Pinus* species as an early colonizer, but remained dominant over the whole 500-year simulation. Interestingly, the increase in *A. rubrum* fecundity corresponded with an increase of *Carya* in the understory, for unknown reasons. In the simulation where *Quercus alba* was nine times more fecund than other species, there were moderate increases in the BA of *Quercus* communities, as well as with *Carya* species and *A. rubrum*. *Liriodendron tulipifera* also does much better under this scenario, competing with *Pinus* early in the successional trace. Finally, if *Carya* species are made 9 times more fecund than other species, *Quercus*, *A. rubrum*, and *Liriodendron tulipifera* again also increase in BA significantly (Figure 6). It is unclear why increases in *Quercus* or *Carya* fecundity increase the presence of *A. rubrum* and *Liriodendron tulipifera* so consistently. The model appears highly sensitive to these parameters, which suggests that a careful sensitivity analysis will be required before we can have confidence in the model's output.

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Discussion

Trends in density and basal area on our plots show an increase in total basal area and total density over time. A large cohort of shade-tolerant species is growing in the understory, led by *Acer rubrum* and *Nyssa sylvatica*. The understory of the forest is growing less open and "park-like" and becoming denser, perhaps because the plots are recovering from some sort of suppression or disturbance event. This result is similar to that recorded by Abrams et al. (1995) and Orwig and Abrams (1994), who studied dry upland sites in West Virginia and Virginia, respectively, and found a similar increase in density in the understory over time. Both studies reported a similar compositional shift towards *A. rubrum* and away from *Quercus* species. They also found an increase in *Fagus grandifolia*, which was not as apparent on our sites. *Fagus grandifolia* increased in density and basal area on some of the wetter plots, such as Duke 43, Duke 44 and Big Oak Woods. *Fagus grandifolia* also increased on some north-facing plots, like Woodenbridge Plot. Overall, however, *F. grandifolia* is a minor component of most of our sites. This suggests that *Fagus grandifolia* is unable to withstand the dry soil conditions common on most upland sites, and is only competitive with *A. rubrum* on more mesic sites.

Trends over time in the size distribution of *Quercus* populations show that much of the decline in *Quercus* density occurs in the understory. *Quercus* stems that are established appear to survive fairly well, and thus the basal area of many *Quercus* species that have members in the canopy of the forest is increasing while their density is

decreasing. Data from seedling transects on several of our plots support this conclusion, with little to no *Quercus* seedlings present. At the same time, *Acer rubrum* has become extremely abundant in the understory and seedling layers. It is likely that increased competition with shade-tolerant seedlings is at least partially responsible for the decline in *Quercus* regeneration. These results are similar to those of Geiger (1952) and Bordeau (1954), who studied some of the same soil types in the Duke Forest and found high levels of mortality for *Quercus* seedlings in deep shade. *Quercus* seedling levels also appear to have periodicities in our data set, with many more seedlings being recorded the year after a mast year. However, most of these seedlings die by the next year. Carvell and Tryon (1961) and Ferrel (1949) had similar results, reporting particularly high levels of seedling mortality after mast years for forests with a thick understory.

Ordination results show that the tree layer of the forest is becoming more similar over time to its seedling layer. This provides further proof that the current forest is not in equilibrium, but is changing significantly over time. It is interesting to note that despite the decline of all *Quercus* species present in our sample sites and the rapid increase in *Acer rubrum* density, plots appear to be diverging over time. The seedling layers of each plot are further separated from each other in ordination space than the tree maps are, with the exception of the tree maps for Duke 43 and Duke 44, which occupy their own region in the ordination space. The tree layers of each plots trend towards their seedling layers, and diverge from the other plots' tree layers over time. This is similar to the results of Christensen and Peet (1984), who found that community differentiation increased over time for plots in the Duke Forest.

It remains unclear why more shade-tolerant seedlings are increasing in abundance and *Quercus* is decreasing in abundance. The current data are unable to adequately resolve which, if any, of the particular hypotheses posed in the Introduction are correct. The fire-suppression hypothesis is popular in the literature, and the current lack of wildfires in Durham and Orange counties may explain some of the increase in shade-tolerant species in the understory. Certainly, low-intensity fires are possible here. There is considerable debate on what the likely fire return time was before the arrival of Europeans, with estimates ranging from 4-6 years (Frost 1998) to 30 or more years for hardwood stands in the North Carolina Piedmont (e.g., Oosting and Blomquist 1944). One would expect that wet sites had a longer fire return and would be less dependent on fire to destroy other, more shade-tolerant, seedlings. However, the trend away from *Quercus* species is just as evident in wet alluvial plots (e.g., Big Oak Woods) as in dry upland plots. Furthermore, it is puzzling that *Carya tomentosa* is the only species of *Carya* found to be significantly decreasing in density over time, as *C. tomentosa* is, if anything, more sensitive to fires than other hickories (Burns and Honkala 1990). Perhaps this species of hickory is simply less shade-tolerant, and is able to survive in fire-prone ecosystems because of its prolific sprout-stumping abilities.

The effects of European livestock on Piedmont forests are not examined in this study, but almost certainly grazing thinned forest understories somewhat during the 19th century (Oosting and Blomquist 1942, Peet, *personal communication*). It is not known how intensely swine and other free-roaming animals exploited the plots used in this study. It is possible that the plots in this study are simply recovering from grazing, and the current change in the forest represents a return to the pre-European climax. This

would seem unlikely, since *Acer rubrum* does not appear to have been an important component of pre-European forests (Orwig and Abrams 1994). However, it would explain the increases in density we found in *Carya* species, which presumably would be more palatable to herbivore species than the tannin-rich *Quercus* species (Burns and Honkala 1990). If this is the case however, it is still unclear why *C. tomentosa* is decreasing in abundance over time. Note that, contrary to what is hypothesized above, it is also possible that herbivory has an overall negative effect on *Quercus* seedlings, as deer and other animals consume acorns (Abrams 1998).

The effects of hurricanes and other catastrophic windstorms were not examined specifically in this study. However, Hurricane Fran, which passed through the Piedmont in 1996, clearly impacted many of our study sites, causing decreases in basal area. While a detailed analysis of the effects of Hurricane Fran is beyond the scope of this study, it is clear that any small increase in *Quercus* species populations after Fran is obscured by the larger trend away from these species. Moreover, other research suggests that stems suppressed in the understory benefit most from the increased light levels after a severe storm damages the forest canopy (Foster 1988). Therefore, for our sites one would, if anything, expect severe windstorms to hasten the increase in *Acer rubrum* dominance. Further study of the plots in this study several decades down the road might shed more light on the importance of windstorms in maintaining *Quercus-Carya* communities.

It is also unclear what impact prior thinning and selective cutting have had on these forests. One could argue that the forest is simply recovering from its logging history. However, this appears unlikely for two reasons. First, logging events appear to have been of low-intensity, and the plots have been free of human disturbance for at least

40 years, and in the case of Big Oak Woods close to 100 years. Realistically, few sites that have been less disturbed remain in this region of the North Carolina Piedmont (Sutter 1987). Second, any logging would have been likely to include *Quercus* species, and thus one would expect *Quercus* populations to increase after logging ceased. It is possible that forests that were clear-cut at some distant time in the past have an even-aged cohort of canopy species that is more dense than the usual uneven-aged forest would be (Peet, *personal communication*). This might inhibit *Quercus* regeneration by decreasing light levels at the forest floor. However, many of our plots show no evidence of being clear-cut or even substantially thinned by logging, and thus are unlikely to have an abnormally dense even-aged cohort.

This study shows a large increase in the dominance of *Acer rubrum* in the understory. This same increase has been discussed in numerous papers (e.g., Lorimer 1984, Abrams 1992). This study cannot determine the causes of this increase, but suggests that it is related to the higher shade tolerance of *Acer rubrum* than *Quercus* species and the lack of some disturbance mechanism to restrict the growth of red maple seedlings. Abrams (1998) attributes the cause of this increase to increased fire suppression and the ability of *A. rubrum* to be a "super-generalist," surviving in many different habitats. It is also possible that human disturbance has increased the populations of *A. rubrum* somewhat (through ornamental plantings, edge effects on forest, etc.), and that the increase in *A. rubrum* on our relatively protected plots may be do to an increase in *A. rubrum* seed dispersal from human-disturbed areas (Urban, *personal communication*). Regardless of the causes of increased *A. rubrum* dominance

and decline of the *Quercus-Carya* climax, the large cohort of shade-tolerant species in the understory of these plots suggests this trend will continue to impact forests in the future.

Conclusion

Quercus-Carya communities are in decline in the North Carolina Piedmont. All *Quercus* species are decreasing in density over time. Trends in *Carya* species are less clear, but *C. tomentosa* appears to be decreasing in abundance as well. *Acer rubrum* and other shade-tolerant species are dramatically increasing in density. Kernel density estimation shows that *Quercus* species are not regenerating at the seedling level, but that *Quercus* stems currently in the canopy are surviving and maturing. The species composition of trees on each plot is becoming more similar to the species composition of the seedling layer of each plot. Simulations with ZELIF suggest that a properly timed thinning event (or perhaps a low-intensity fire) could help maintain *Quercus-Carya* communities. However, ZELIG proved very sensitive to the fecundity parameters for each species, and simulations with altered fecundity yielded results that are often difficult to interpret. In order to use ZELIG more accurately, more work needs to be done to adequately parameterize this component of the model.

Table 1. Characteristics of Study Sites

Name	Location	Size (ha)	Established	Disturbance history	Notes
Big Oak Woods	wet lowland	2.36	1986	no cutting since before 1900	Beavers flooded some areas
Bormann	dry upland	1.96	1952	selective cutting prior to 1930	Low calcium
Bryan Center	mesic upland	1.30	1986	old field, abandoned circa 1780	Near ornamental plantings at Duke
Hill #23	dry-mesic upland	0.40	1946	selective cutting prior to 1930	Thinned 1947
Hill #24	dry-mesic upland	0.40	1947	selective cutting prior to 1930	Thinned 1947
Oosting	dry-mesic upland	6.55	1990	cutting circa late 1800s	Only stems >2cm are recorded
Duke #10	dry-mesic upland	0.10	1933	selective cutting prior to 1930	
Duke #35	dry-mesic upland	0.10	1934	selective cutting prior to 1930	Shrink-swell soils
Duke #36	dry-mesic upland	0.10	1934	selective cutting prior to 1930	
Duke #37	dry-mesic upland	0.10	1934	selective cutting prior to 1930	Severe damage by Hurricanes Hazel and Fran
Duke #43	wet lowland	0.10	1935	selective cutting prior to 1930	Construction near plot in 1950s
Duke #44	wet lowland	0.10	1935	selective cutting prior to 1930	
Rocky	dry upland	2.04	1978	selective cutting prior to 1950	Very rocky, high calcium
Woodbridge	dry-mesic upland	0.53	1984	selective cutting prior to 1950	

Table 2. Soil Characteristics of Study Sites

Name	Soil Type	Slope	Aspect	pH	Ca ppm	Mg ppm	K ppm	Soil water (1-l
Big Oak Woods	Chewacla loam	0%	flat	4.76	341	120	71	
Bormann	Herndon silt loam	1%	90	4.42	512	53	60	
Bryan Center	White Store clay loam	0%	flat					
Hill #23	Georgeville silt loam	3%	135					
Hill #24	Georgeville silt loam	6%	90					
Oosting	Georgeville silt loam	varies	varies	6.00	1395	220	134	
Duke #10	Georgeville silt loam	8%	110	4.54	28	42	66	
Duke #35	Enon loam	2%	225	4.30	316	29	26	
Duke #36	Enon loam	2%	220	4.34	98	51	66	
Duke #37	Enon loam	3%	220	4.48	102	44	72	
Duke #43	Cartecay silt loam	0%	flat	4.72	1263	261	58	
Duke #44	Cartecay silt loam	0%	flat	5.26	1825	263	98	
Rocky	Herndon silt loam	7%	135	5.40	1221	213	89	
Woodbridge	Appling sandy loam	5%	270					

Table 3. Percentage change per year of total density (stems/ha).

Plot	Percentage change per year (%)
Duke #37	4.7
Duke #36	2.7
Hill #24	2.6
Woodbridge	2.2
Hill #23	1.8
Duke #35	1.8
Big Oak Woods	1.7
Rocky	1.6
Duke #43	0.8
Oosting	0.8
Bryan Center	0.5
Bormann	-0.1
Duke #10	-0.3
Duke #44	-0.7

Table 4. Percentage change per year of total basal area (m²/ha)

Plot	Percentage change per year (%)
Woodbridge	4.3
Oosting	3.1
Hill #24	1.6
Hill #23	1.6
Duke #10	1.3
Duke #35	1.3
Duke #44	1.2
Big Oak Woods	1.1
Bryan Center	1.1
Duke #36	0.4
Duke #37	0.4
Duke #43	0.4
Bormann	0.3
Rocky	-2.5

Table 5. The five species with the largest percentage increase in density (a) or basal area (b) over the sampling period and the five species with the largest percentage decrease in density (a) or basal area (b). If there were not five species more than 20% different from the change in total density, fewer species are displayed.

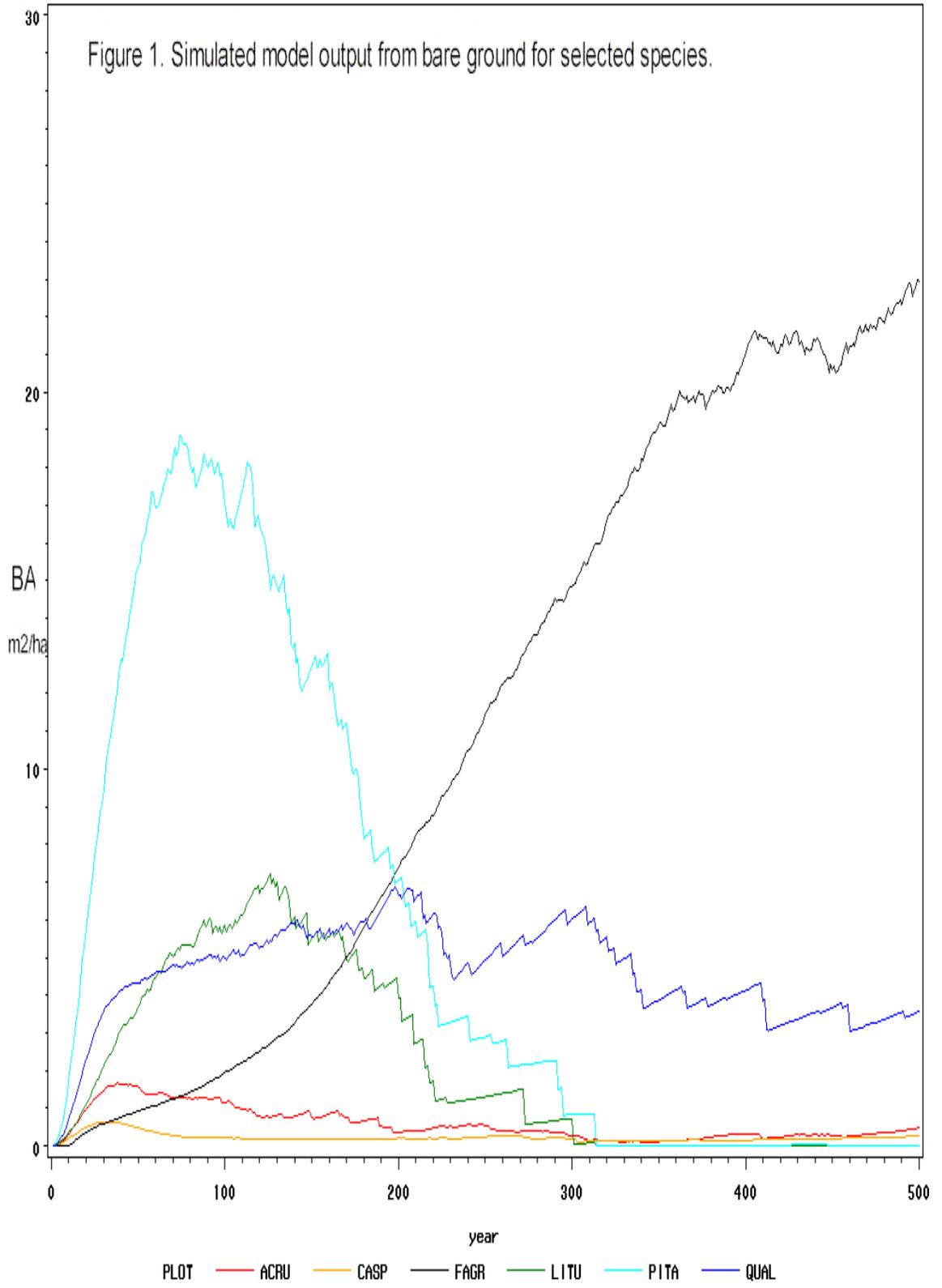
(A.) Density	Plot													
	Big Oak Woods	Bormann	Bryan Center	Duke #10	Duke #35	Duke #36	Duke #37	Duke #43	Duke #44	Hill #23	Hill #24	Oosting	Rocky	Woodbridge
Top increasing	ASTR	PRSE	LIJA	ACRU	FRAX	ACRU	ACRU	AESY	FAGR	OXAR	OSVI	ACSA	MORU	FAGR
species	PRAM	ACRU	OSVI	FRAX	CAGL	NYSY	QUVE	NYSY	COFL	NYSY	ACRU	PRSE	ACRU	NYSY
	FRAX	CATO	MAGR	NYSY			OXAR	FAGR	QUAL	ACRU	NYSY	ILOP	PRSE	ACRU
	CELA	LITU	PRSE	JUVI					OSVI		OXAR	ULAL	CECA	
			HAVI									FAGR	ACSA	
Top decreasing	JUVI	QUAL	CHVI	COFL	PIVI	JUVI	COFL	CAGL	ACRU	QURU	QUAL	PIEC	ILDE	CATO
species	QUFP	MORU	QUCO	CATO	PIEC	CACA	CACA	FRAX	LIST	CAOV	CAGL	SAAL	CATO	QUVE
	QUPH	QUST	CELA	CAGL	QUST	QUCO	QUAL	LIST	CACR	CATO	PIEC	QUST	QUVE	QUAL
	QULY		PITA	QUVE				BENI	FRAX	QUCO	FRAX	COAM	QUST	CAGL
	MORU		PRSP	CACA				ACRU	QURU	QUVE	QUVE	JUNI	LITU	QUCO

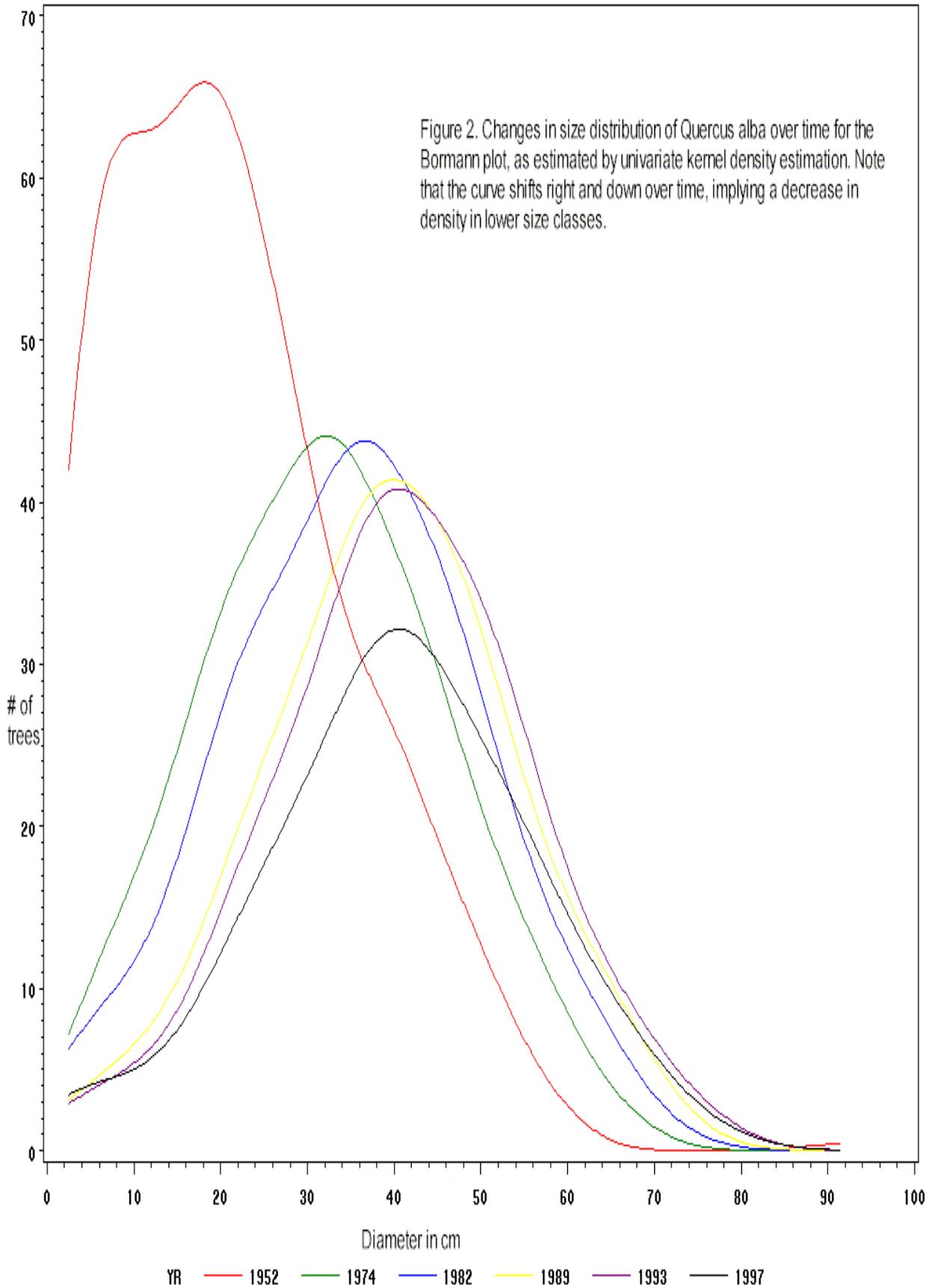
(B.) Basal Area	Plot													
	Big Oak Woods	Bormann	Bryan Center	Duke #10	Duke #35	Duke #36	Duke #37	Duke #43	Duke #44	Hill #23	Hill #24	Oosting	Rocky	Woodbridge
Top increasing	ASTR	ACRU	OSVI	QUCO	PITA	ACRU	ACRU	FAGR	MORU	OXAR	MORU	JUVI	ULAM	CRAT
species	PRSE	LIST	QUVE	QURU	QUAL	LITU	JUVI	AESY	ACSA	QUFA	OSVI	PRSE	ACSA	QURU
	VIPR	OXAR	LIJA	QUAL		CACA	CAGL	NYSY	FAGR	FRAX	ACRU	CECA	ULAL	OXAR
	CELA	CAGL	QURU	CAPA		JUVI	OXAR	LITU	OSVI	LITU	QUAL	CHVI	CELA	FAGR
		CAOV	COAM	ACRU		QUAL			COFL	QUAL		ILOP	FRAX	QUAL
Top decreasing	QULY	FRAX	COFL	CACA	QUPH	CATO	COFL	BENI	ACRU	CAOV	CAGL	CAOV	COFL	CAGL
species	ULRU	QUST	ULAL	CAGL	CAGL	QUCO	CACA	QUAL	VIPR	CATO	PIEC	PIEC	CHVI	COFL
	JUVI	COFL	PITA	CATO	COFL	COFL	CATO	ACRU	FRAX	JUNI	JUVI	SAAL	QUST	QUVE
	QUSH	MORU	PRSE	NYSY	PIVI	QUVE	QUVE	FRAX	QURU	PIVI	COFL	COAM	AMAR	LIST
	CAGL		DIVI	JUVI				QURU	CAGL	CACR	JUVI	FRAX	JUNI	QUVE

Table 6. Results of Wilcoxon's signed-ranks test on the average change in relative density (%) per year.

Species	# of positive ranks	# of negative ranks	Probability
CAGL	60	45	Not significant
CAOV	53	25	Not significant
CATO	23	82	P<0.05
QUAL	99	6	P<0.005
QUCO	3	25	P<0.05
QURU	21	84	P<0.05
QUVE	9	9	P<0.01
QUST	0	36	P<0.005

Figure 1. Simulated model output from bare ground for selected species.





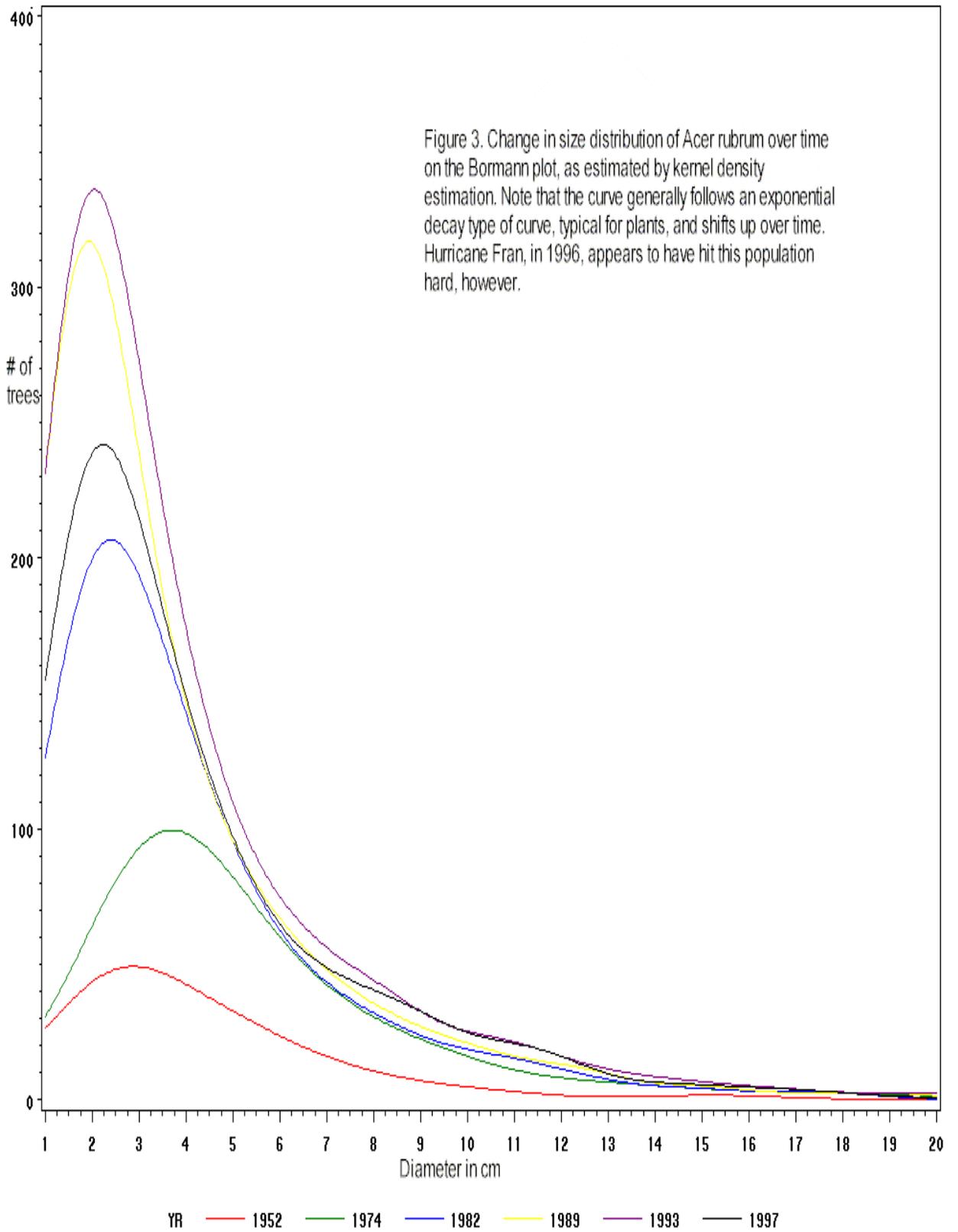


Figure 4a NMS ordination of hardwood plots' trees and seedlings

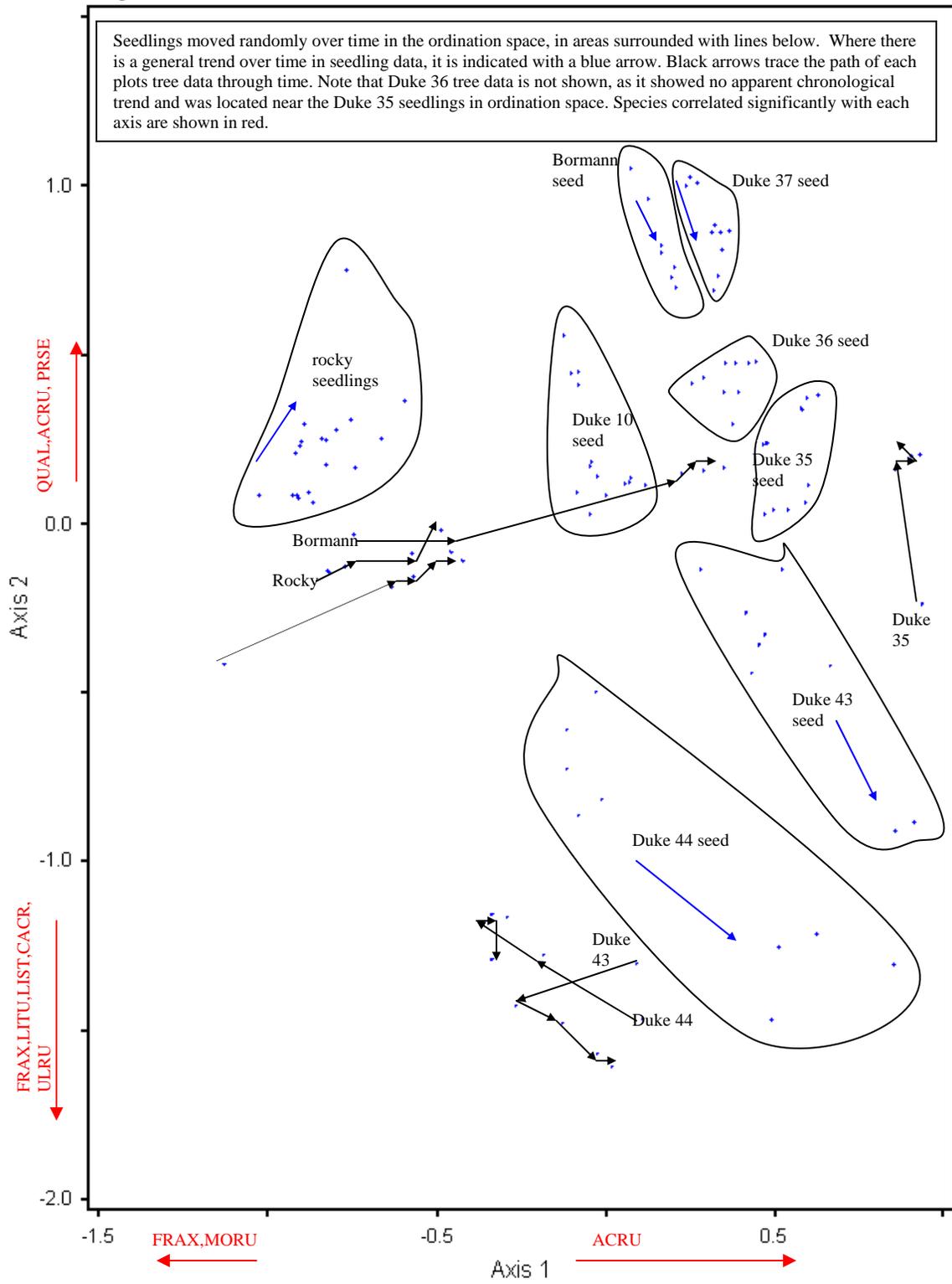


Figure 4b NMS ordination of hardwood plots' trees and seedlings

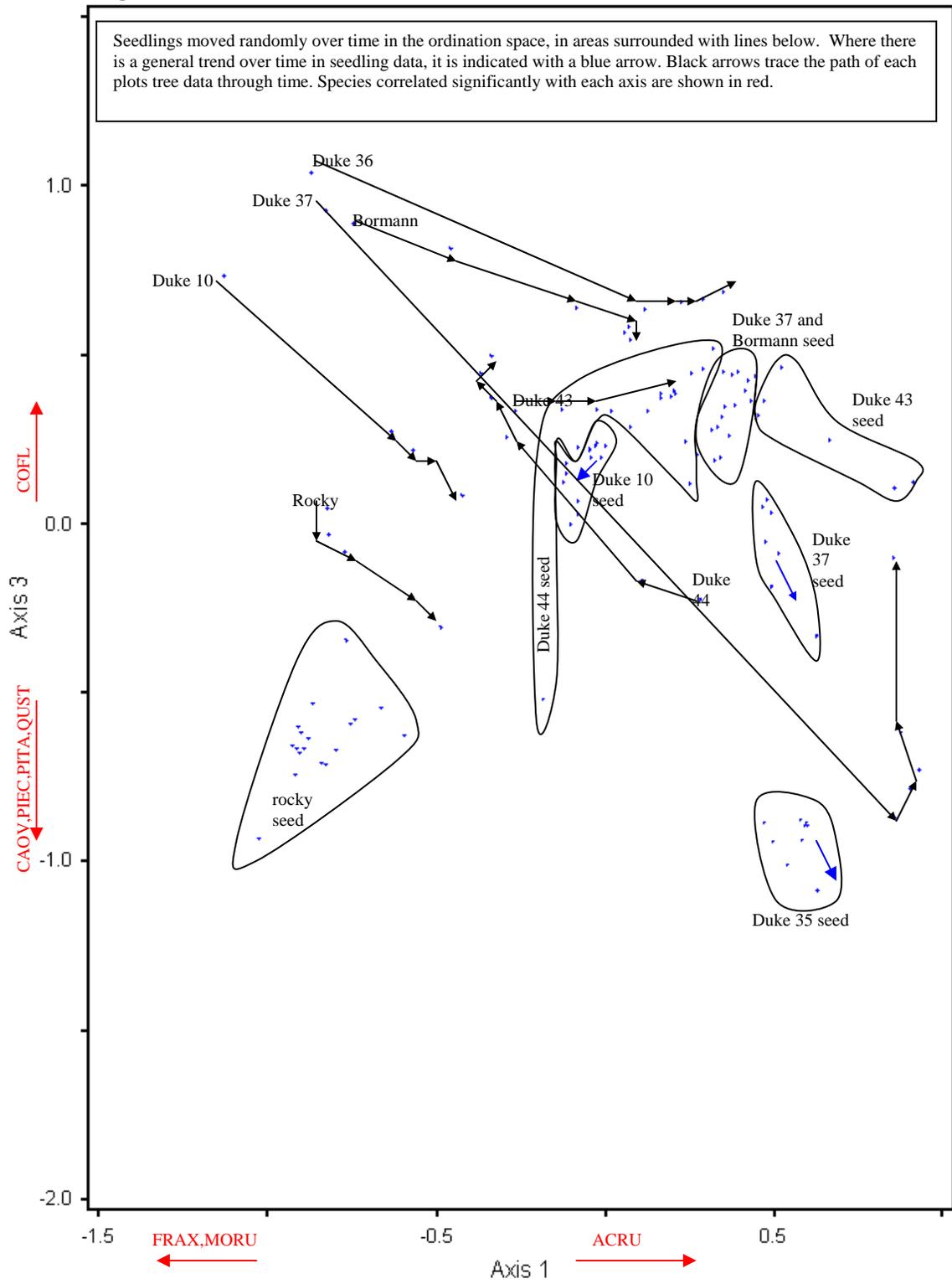
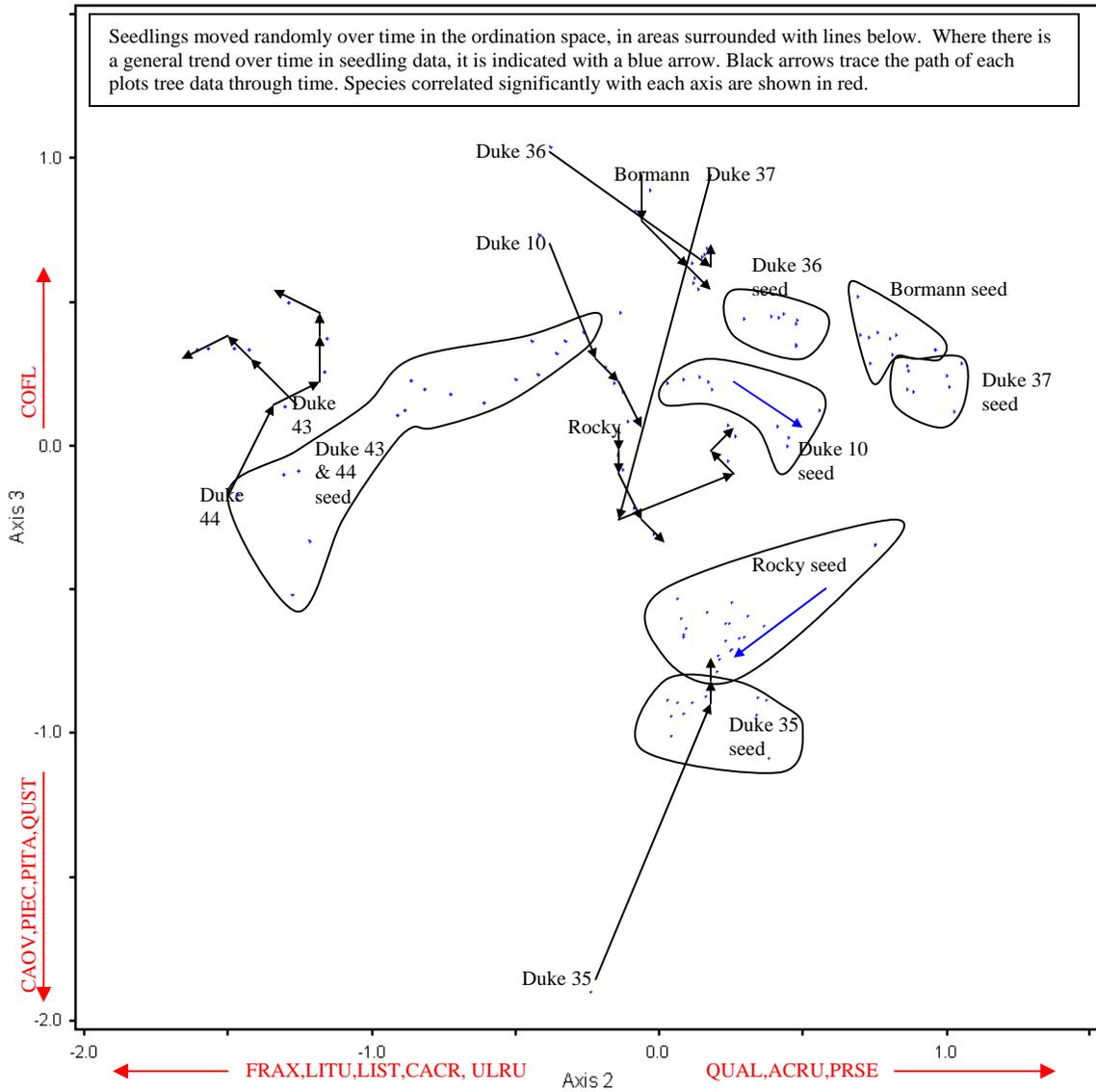
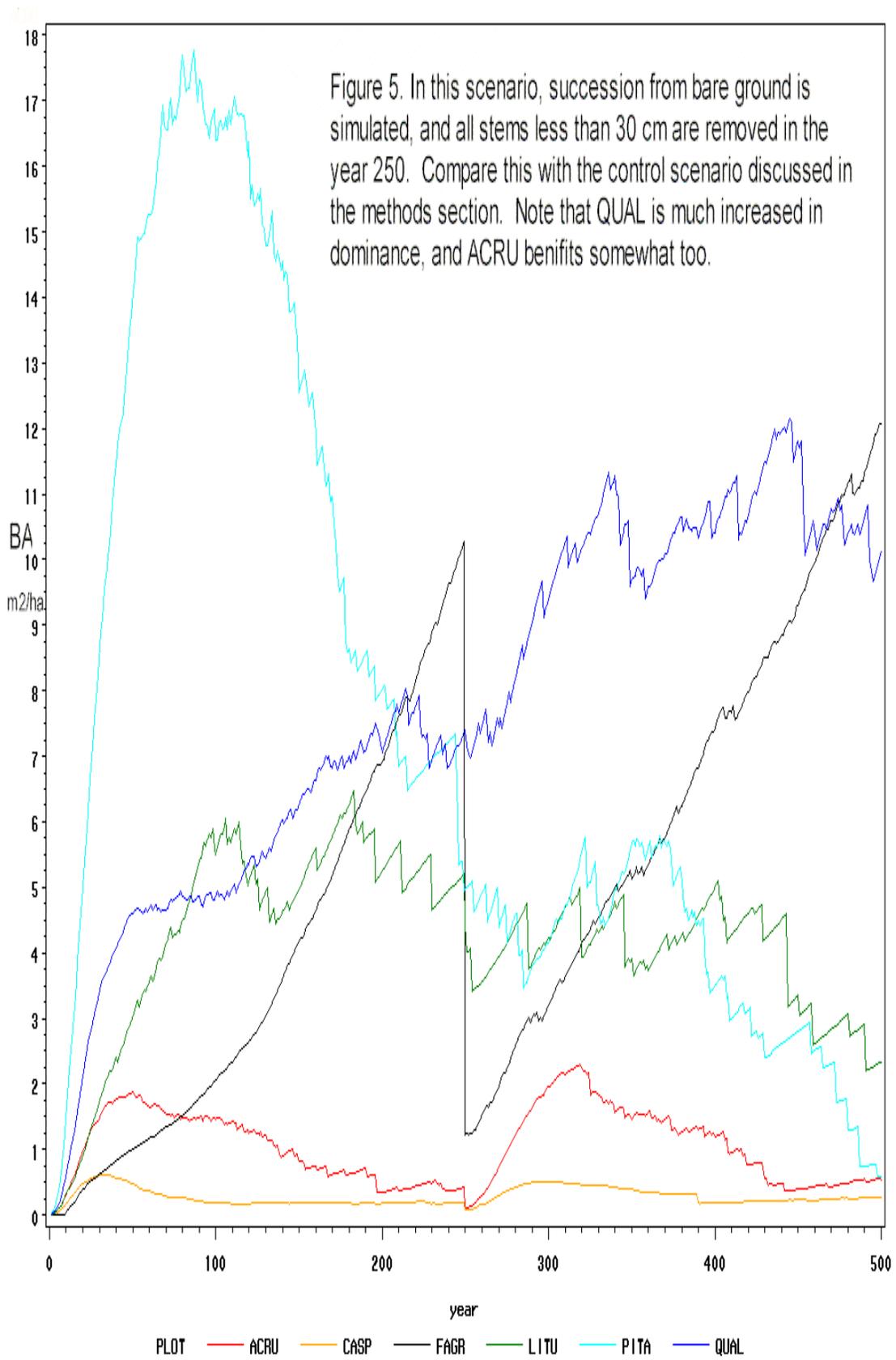
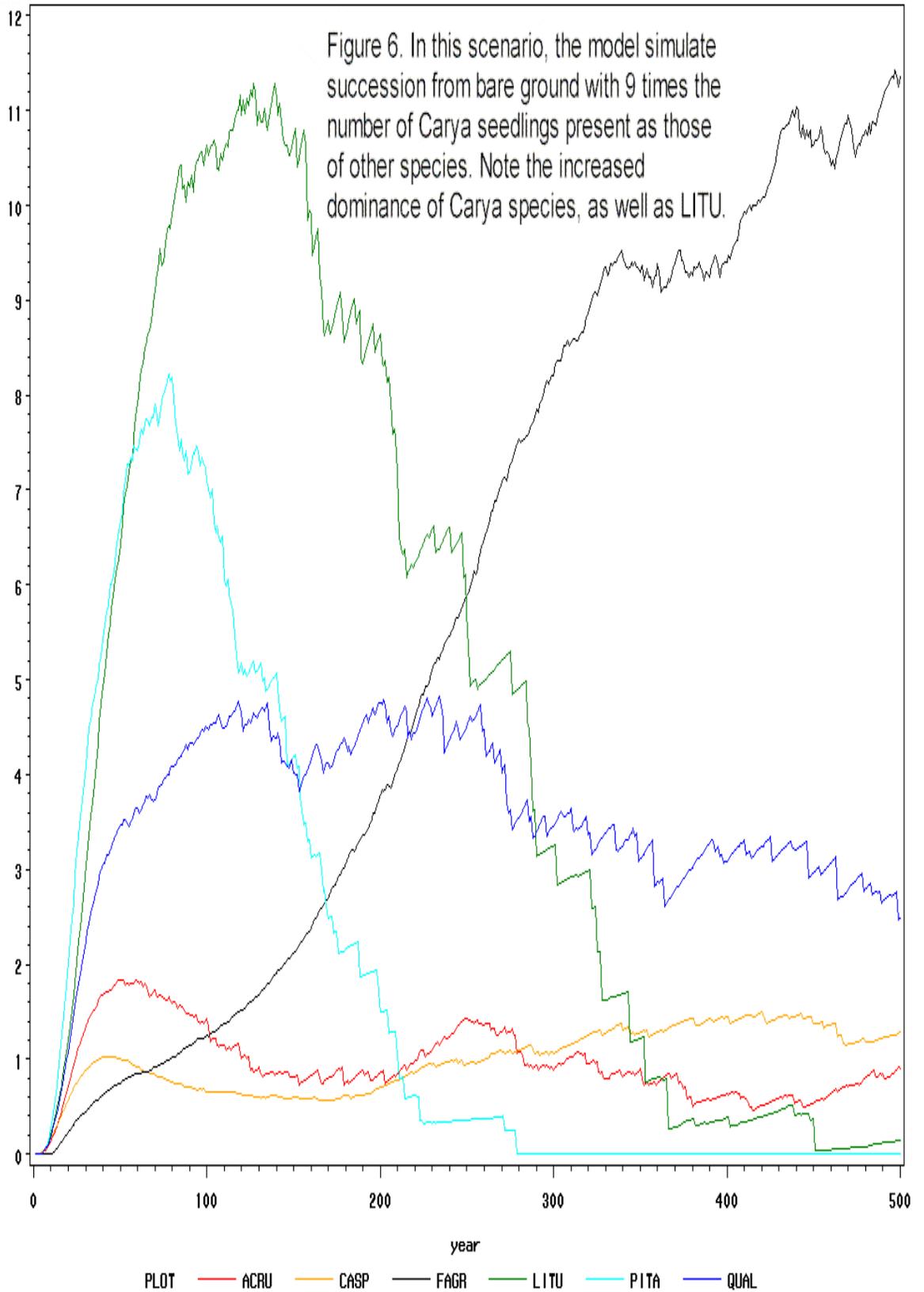


Figure 4c

NMS ordination of hardwood plots' trees and seedlings







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Acknowledgements

This project would not have been possible without the kind support and encouragement of many people. I am greatly indebted to Robert K. Peet, who has been an advisor, employer, and friend for the past two years. His support and advice during this study made it possible, and played an invaluable role in my development as an ecologist. I am also deeply indebted to Dean Urban, who provided the ZELIG model used in this study. His frequent meetings with me crystallized my goals for this project, and his knowledge of Fortran and the mechanics of ZELIG helped immensely in adapting ZELIG to the UNC mainframe. Becky Brown was always willing to discuss the details of writing a thesis with me, and provided much needed moral support. Jason Fridley helped spur my thinking on the statistical aspects of this paper. Weimin Xi tirelessly performed many of the tedious tasks necessary for the maintenance of the large amount of data from the Duke Forest permanent sample plots. Tom Phillipi answered all my annoying SAS questions, and many of his SAS codes form the basis of the SAS codes I developed for this project. Finally, I thank the extended family of the Peet/White "Progress in Ecology" lab group for their friendship and encouragement, and all the field crews over the years that have toiled in the summer sun to make this dataset a reality.

Data on seedling, sapling, and tree demography was collected as part of a long-term study by R.K. Peet and N.L. Christensen and was supported by NSF grants DEB-9707551, DEB-7708743, DEB-7804043, DEB-8102775, BSR-B314655, BSR-8905926, and BSR-9107357.

Appendix 1. Species Abbreviations used in graphics in this study.

Common Name	Species Name	Abbreviation
Red Maple	<i>Acer rubrum</i>	ACRU
Sugar Maple	<i>Acer barbatum</i>	ACBA
Painted Buckeye	<i>Aesculus sylvatica</i>	AESY
Serviceberry	<i>Amelanchier arborea</i>	AMAR
Pawpaw	<i>Asimina triloba</i>	ASTR
River Birch	<i>Betula nigra</i>	BENI
Carolina Shagbark Hickory	<i>Carya carolinae-septentrionalis</i>	CACA
Bitternut Hickory	<i>Carya cordiformis</i>	CACO
Pignut Hickory	<i>Carya glabra</i>	CAGL
Common Shagbark Hickory	<i>Carya ovata</i>	CAOV
Sand Hickory	<i>Carya pallida</i>	CAPA
Mockernut Hickory	<i>Carya tomentosa</i>	CATO
Hickory spp.	<i>Carya spp.</i>	CASP
Sugarberry	<i>Celtis laevigata</i>	CELA
Northern Hackberry	<i>Celtis occidentalis</i>	CEOC
Redbud	<i>Cercis canadensis</i>	CECA
Fringe-Tree	<i>Chionanthus virginicus</i>	CHVI
Hazel-Nut	<i>Corylus americana</i>	COAL
Dogwood	<i>Cornus florida</i>	COFL
Hazel-nut	<i>Corylus americana</i>	COAM
Hawthorn	<i>Crataegus spp.</i>	CRAT
Persimmon	<i>Diospyros virginiana</i>	DIVI
Heart's-a-bustin'	<i>Euonymus americanus</i>	EUAM
American beech	<i>Fagus grandifolia</i>	FAGR
Ash spp.	<i>Fraxinus spp.</i>	FRAX
Witch Hazel	<i>Hamamelis virginiana</i>	HAVI
Carolina Holly	<i>Ilex ambigua</i>	ILAM
Possum Haw	<i>Ilex decidua</i>	ILDE
American Holly	<i>Ilex opaca</i>	ILOP
Black Walnut	<i>Juglans nigra</i>	JUNI
Eastern Red Cedar	<i>Juniperus virginiana</i>	JUVI
Japanese Privet	<i>Ligustrum japonicum</i>	LIJA
Chinese Privet	<i>Ligustrum sinense</i>	LISI
Sweet Gum	<i>Liquidambar styraciflua</i>	LIST
Tulip Poplar	<i>Liriodendron tulipifera</i>	LITU
Bull Bay	<i>Magnolia grandiflora</i>	MAGR
Umbrella Tree	<i>Magnolia tripetala</i>	MATR
Red Mulberry	<i>Morus rubra</i>	MORU
Black Gum	<i>Nyssa sylvatica</i>	NYSY
Hop Hornbeam	<i>Ostrya virginiana</i>	OSVI
Sourwood	<i>Oxydendrum arboreum</i>	OXAR
Short-Leaf Pine	<i>Pinus echinata</i>	PIEC

Loblolly Pine	<i>Pinus taeda</i>	PITA
Scrub Pine	<i>Pinus virginiana</i>	PIVI
Eastern Sycamore	<i>Platanus occidentalis</i>	PLOC
Cherry spp.	<i>Prunus serotina</i>	PRSE
White Oak	<i>Quercus alba</i>	QUAL
Scarlet Oak	<i>Quercus coccinea</i>	QUCO
Spanish Oak	<i>Quercus falcata</i>	QUFA
Black Jack Oak	<i>Quercus marilandica</i>	QUMA
Willow Oak	<i>Quercus phellos</i>	QUPH
Chestnut Oak	<i>Quercus prinus</i>	QUPR
Red Oak	<i>Quercus rubra</i>	QURU
Post Oak	<i>Quercus stellata</i>	QUST
Black Oak	<i>Quercus velutina</i>	QUVE
Overcup Oak	<i>Quercus lyrata</i>	QULY
Sassafras	<i>Sassafras albidum</i>	SAAL
Winged Elm	<i>Ulmus alata</i>	ULAL
White Elm	<i>Ulmus americana</i>	ULAM
Slippery Elm	<i>Ulmus rubra</i>	ULRU
Black Haw	<i>Viburnum prunifolium</i>	VIPR
Downy Arrow-wood	<i>Viburnum rafinesquianum</i>	VIRA

Appendix 2. Species Parameters for This Study

28	Species parameters for Duke Forest (FINAL)														
100	35	*	Canopy area, expected canopy height for these species												
ACru	Acer rubrum						Red maple								
	150	157	27.4	-0.0521	0.8969	1650	1260	6601	4	155	3	4	2	2	48
99.9	30														
	0.95997	-1.46336	0.50339	15.1	-0.0314	0.95	0.21								
	4.7104	2.2797	3.2553	2.0898	2.6462	2.5968	4.7840	1.1660							
	-1.8268	2.3035	-1.3359	2.2148											
	0.435	0.670	0.083	15.7	22.3	25.3	13.1	1							
CAca	Carpinus caroliniana						American Hornbeam								
	150	36	24.4	-0.1532	1.1456	550	1344	6011	5	180	3	1	4	1	3
99.9	20														
	0.95997	-1.46336	0.50339	15.1	-0.0314	0.95	0.21								
	4.1166	2.4758	2.8734	2.1695	2.7354	2.7038	4.8090	1.2195							
	-2.1774	2.4547	-1.7254	2.3706											
	0.983	0.670	0.083	15.7	22.3	25.3	13.1	1							
CAsp	Carya species						Pignut Hickory								
	500	104	41.8	-0.0540	1.0298	550	1853	5524	3	190	2	4	4	2	50
99.9	50														
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40								
	3.9354	2.5841	4.2574	1.9745	1.5236	3.0581	-0.8887	3.3599							
	-2.6106	2.6576	-2.1393	2.5675											
	0.624	0.670	0.083	15.7	22.3	25.3	13.1	1							
COfl	Cornus florida						Flowering dogwood								
	125	66	11.0	-0.0674	0.7992	600	1900	6011	5	165	2	2	4	1	20
99.9	10														
	0.95997	-1.46336	0.50339	15.1	-0.0314	0.95	0.21								
	4.7891	2.1511	3.6746	1.8157	4.5254	1.7713	5.6298	0.7936							
	-1.1426	1.9458	-0.7252	1.8811											
	0.655	0.670	0.083	15.7	22.3	25.3	13.1	1							
DIvi	Diospyros virginiana						Common Persimmon								
	150	98	25.3	-0.0907	1.5164	475	2678	6700	4	125	3	3	8	1	18
99.9	20														
	0.90895	-1.46990	0.56095	15.1	-0.0314	0.90	0.25								
	3.8882	2.5341	2.7042	2.3013	0.9295	3.0044	-1.7265	3.3476							
	-2.8096	2.5814	-2.1545	2.4406											
	0.665	0.083	0.670	22.3	25.3	22.3	7.0	1							
FAgr	Fagus grandifolia						American Beech								
	400	142	35.1	-0.0764	1.1300	400	1327	5556	5	95	2	7	5	1	20
99.9	20														
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40								
	4.4170	2.4093	3.2923	2.0784	3.4124	2.3765	5.1260	1.0676							
	-1.7994	2.3242	-1.3597	2.2502											
	0.665	0.083	0.670	22.3	25.3	22.3	12.6	1							
FRsp	Fraxinus species						Ash species								
	225	130	35.5	-0.0598	1.0482	900	1144	5756	2	185	1	3	2	1	10
99.9	30														
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40								
	4.8208	2.3478	3.7639	2.0732	0.6851	3.0826	3.8996	1.3852							
	-1.9094	2.3957	-1.3367	2.2885											
	0.776	0.083	0.670	22.3	25.3	22.3	12.6	1							
JUvi	Juniperus virginiana						Red Cedar								
	300	132	15.2	-0.0223	0.7543	850	1739	5556	3	240	3	4	4	0	00
99.9	40														
	0.90895	-1.46990	0.56095	15.1	-0.0314	0.90	0.25								

-2.8405 2.6036 -2.2899 2.5046
 0.388 0.083 0.670 22.3 25.3 22.3 7.0 2
 PLoc Platanus occidentalis American Sycamore
 500 183 36.0 -0.0268 1.0072 1800 1944 5500 3 80 2 4 3 1 30
 99.9 20
 0.90895 -1.46990 0.56095 15.1 -0.0314 0.90 0.25
 4.2529 2.4674 1.9440 2.2719 2.4965 2.4499 4.7124 1.1011
 -2.2735 2.4243 -1.7725 2.3427
 0.665 0.083 0.670 22.3 25.3 22.3 7.0 1
 PRsp Prunus species Cherry
 248 126 32.0 -0.0148 0.5042 1200 1500 6011 2 185 1 5 4 1 15
 99.9 10
 0.95997 -1.46336 0.50339 15.1 -0.0314 0.95 0.21
 4.7296 2.2919 3.2923 2.0784 2.4717 2.5370 4.7214 1.1341
 -1.7132 2.2450 -1.1565 2.1427
 0.983 0.670 0.083 15.7 22.3 25.3 13.1 1
 QUal Quercus alba White oak
 407 222 37.8 -0.0263 0.8209 925 1600 5556 3 175 2 6 2 2 20
 99.9 50
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 4.5454 2.4219 3.7344 2.0695 1.5089 3.0432 -2.9897 3.9448
 -2.7944 2.7337 -2.1690 2.6030
 0.736 0.083 0.670 22.3 25.3 22.3 12.6 1
 QUco Quercus coccinea Scarlet oak
 400 146 29.9 -0.0259 0.5322 900 2056 4000 2 180 3 2 2 2 50
 99.9 40
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 5.9130 1.9541 3.6344 2.2835 1.5627 3.0461 -0.9665 3.3787
 -1.5591 2.3543 -0.9287 2.2178
 0.665 0.083 0.670 22.3 25.3 22.3 12.6 1
 QUfa Quercus falcata Southern Red Oak
 150 225 30.8 -0.0493 1.0730 950 2678 6011 2 215 2 3 2 1 25
 99.9 20
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 4.3154 2.4566 3.3599 2.3059 1.4599 2.9869 -1.1404 3.3307
 -2.4602 2.5780 -1.9130 2.4700
 0.604 0.083 0.670 22.3 25.3 22.3 12.6 1
 QUma Quercus marilandica Blackjack Oak
 400 102 18.6 -0.0487 0.9328 425 2511 5556 3 250 3 3 3 1 20
 99.9 40
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 4.8478 2.3597 3.7883 2.1518 1.2442 3.0752 -1.3424 3.4174
 -1.9284 2.4543 -1.2866 2.3165
 0.703 0.083 0.670 22.3 25.3 22.3 12.6 1
 QUph Quercus phellos Willow Oak
 400 250 27.4 -0.0493 1.1241 1600 3400 5333 2 110 2 1 2 1 20
 99.9 30
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 4.5454 2.4219 3.7344 2.0695 1.5089 3.0432 -2.9897 3.9448
 -2.7944 2.7337 -2.1690 2.6030
 0.669 0.083 0.670 22.3 25.3 22.3 12.6 1
 QUpr Quercus prinus Chestnut Oak
 300 193 19.5 -0.0797 1.4926 520 1600 4500 3 180 3 3 2 1 50
 99.9 40
 0.97576 -1.22922 0.25347 15.1 -0.0314 0.95 0.40
 3.6622 2.6635 3.1687 2.3843 -1.1500 3.6320 -4.0462 4.0483
 -2.6346 2.6832 -2.0827 2.5131

	0.665	0.083	0.670	22.3	25.3	22.3	12.6	1											
QUru	Quercus rubra			Northern red oak															
	400	188	42.1	-0.1429	3.0000	1000	1500	4589	3	150	2	2	2	1	30				
99.9	40																		
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40												
	4.8478	2.3597	3.7883	2.1518	1.2442	3.0752	-1.3424	3.4174											
	-2.0826	2.5131	-1.4941	2.3958															
	0.572	0.083	0.670	22.3	25.3	22.3	12.6	1											
QUst	Quercus stellata			Post Oak															
	373	142	27.4	-0.0714	1.3821	550	2678	6011	3	275	3	2	2	2	25				
99.9	30																		
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40												
	5.1096	2.1525	3.4092	2.1467	3.1839	2.4845	0.8150	2.7606											
	-1.6018	2.2607	-1.0348	2.1441															
	0.677	0.083	0.670	22.3	25.3	22.3	12.6	1											
QUve	Quercus velutina			Black oak															
	200	158	32.3	-0.0989	1.8827	650	1800	5200	3	190	3	1	1	1	25				
99.9	20																		
	0.97576	-1.22922	0.25347	15.1	-0.0314	0.95	0.40												
	4.8313	2.2993	3.5138	2.2341	-0.9425	3.6171	-3.7677	4.0183											
	-2.4780	2.5869	-1.8409	2.4546															
	0.593	0.083	0.670	22.3	25.3	22.3	12.6	1											
ULsp	Ulmus species			Elm															
	275	141	19.7	-0.0753	0.9412	1450	2302	6106	4	130	2	9	4	1	25				
99.9	30																		
	0.95997	-1.46336	0.50339	15.1	-0.0314	0.95	0.21												
	4.1166	2.4758	2.8734	2.1695	2.7354	2.7038	4.8090	1.2195											
	-2.1774	2.4547	-1.7254	2.3706															
	0.983	0.670	0.083	15.7	22.3	25.3	13.1	1											

Parameters are:

MSP, sci-name, common name;
 Amax, Dmax, Hmax, H2, H3; G; DDmin,max; L,M,N; seed, seedling lag
 time,
 NSprt, SDmax, DLR (max litter depth for regen), seedling-rooting
 depth;
 T0, T1, T2; S1, S2; BT; SLR;
 Bo0, Bo1; Bk0, Bk1; BL0, BL1; BD0, BD1;
 AW0, AW1; TW0, TW1;
 TNC(leaf,wood,froot), TLC(leaf,wood,froot); SLA; FRT
 Allometric data from FSDB, Oregon State, via Steve Garman.

Notes:

PIvi used for unavailable tolerances and parameters for conifers.

Species equivalents from Peet 1980 used to determine appropriate substitute tree in the case of missing hardwood biomass parameters

Height regressions produced from N.C. Piedmont field data.

Max age and dbh values were taken from North Carolina Record trees.
 Species calibrated at 50 drought days/3806 degree days two-sided using
 Silvics of North America.

Seed parameter being subjectively estimated as relative # of seedlings of species typically visible in understory with 9 high and 1 low.

Lag-time currently being used to slow down or increase establishment rate of species based on descriptions from literature.

Upper-bound of degree days for PIVI seemed in error since species was being excluded from representation within known association groups; new upper bound taken from average of upper bounds for associates (PIec, PIta, JUvi, FRspp, QUma) from typical Piedmont locale until literature source/value can be located.

No dbh/ht growth data avail. for Divi. Estimated by using suggested species equiv from Peet 1980 (nysy), discussion from Silvics of N.A., and Grow program from ZELIG to create hypothetical data set for poor, intermed., and good sites. SAS used to regress resulting data with height vs. dbh.

Appendix 3. Site Parameters in this Study

Duke Forest, Durham NC			* Locale					
35.5	79.0		* Latitude, Longitude					
9			* Number of soil types NSOILS					
1	10	0.10	Congaree Fine Sandy Loam (1.42 m) * name, # of layers,					
fff								
10.00	2.86	1.24	* depth of soil layer, field capacity, wilting point					
10.00	2.86	1.24						
10.00	2.86	1.24						
10.00	2.86	1.24						
10.00	2.86	1.24						
13.50	3.86	1.68						
33.00	12.27	7.27						
25.40	7.26	3.15						
10.20	5.84	2.54						
10.20	5.84	2.54						
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0	
0.1	0.5	1.2	1.8	6.1				
2	9	0.10	Chewacla Loam (1.52 m)					
10.00	2.88	1.49						
10.00	2.88	1.49						
18.00	5.18	2.68						
10.00	3.72	2.20						
15.00	5.58	3.31						
13.00	4.84	2.87						
20.00	6.63	4.20						
36.00	13.24	7.85						
20.00	5.80	2.52						
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0	
0.1	0.5	1.2	1.8	6.1				
3	5	0.10	Mayodan, Cecil, Wedowee Sandy Loam (1.09 m)					
10.00	2.90	1.26						
10.00	2.90	1.26						
15.20	5.65	3.35						
45.80	18.57	12.51						
27.90	11.31	7.62						
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0	
0.1	0.5	1.2	1.8	6.1				
4	6	0.10	Herndon Silt Loam (1.48 m)					
10.00	1.95	0.90						
10.00	1.95	0.90						
21.00	5.53	3.39						
28.00	7.70	4.86						
33.00	12.33	9.01						
45.70	12.57	7.93						
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0	
0.1	0.5	1.2	1.8	6.1				
5	7	0.10	Tatum, Goldston, Wilkes Silt Loam (0.86 m)					
10.00	1.95	0.90						
10.00	2.32	1.30						
10.00	2.75	1.73						
10.00	3.08	2.12						
10.00	3.08	2.13						
21.10	6.50	4.50						
15.20	4.18	2.64						
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0	

0.1	0.5	1.2	1.8	6.1						
6	9	0.10	Georgeville, Appling, Herndon, Cecil Silt Loam (1.52 m)							
10.00	1.95	0.90								
10.00	2.49	1.49								
10.00	3.08	2.13								
10.00	3.08	2.13								
10.00	3.08	2.13								
16.00	4.93	3.41								
20.30	6.26	4.33								
25.40	6.99	4.41								
40.60	7.90	3.64								
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0			
0.1	0.5	1.2	1.8	6.1						
7	10	0.10	White Store Loam (1.83 m)							
10.00	2.83	1.36								
10.00	3.04	1.60								
10.00	3.35	1.98								
10.00	3.83	1.58								
10.00	3.84	1.58								
63.00	25.78	19.34								
9.00	3.54	2.19								
16.00	5.92	3.29								
30.00	10.64	5.74								
15.00	3.95	1.66								
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0			
0.1	0.5	1.2	1.8	6.1						
8	6	0.10	Iredell Gravelly Loam (1 m)							
10.00	2.88	1.49								
10.00	2.88	1.49								
10.00	3.74	2.73								
10.00	3.74	2.73								
10.00	3.74	2.73								
50.00	18.68	13.65								
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0			
0.1	0.5	1.2	1.8	6.1						
9	5	0.10	Orange Stony Loam (0.5 m)							
10.00	2.74	1.48								
10.00	2.77	1.52								
10.00	3.74	2.74								
10.00	3.74	2.74								
10.00	3.74	2.74								
2.1	13.0	0.3	0.9	1.3	61.9	50.0	5.0			
0.1	0.5	1.2	1.8	6.1						
3.30										
1.00	0.100									
0.70										
165										
-0.8	-0.4	3.8	7.9	13.8	17.9	19.7	19.3	16.3	9.2	3.6
0.1										
11.2	11.7	17.1	22.1	27.0	30.8	32.3	32.0	28.9	22.8	17.0
11.9										
9.4	10.2	10.9	9.7	10.4	10.9	12.4	13.0	9.4	7.6	6.6
9.4										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00										
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00										

* Annual input of N AIN

* Turnover rates for fine roots and wood

* adjustment factor for bulk density

* Elevation for the following weather data

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0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
0.00
2.660 -0.075      * intercept and slope for V(T) from T
0.000 0.534      * intercept and slope for V(R) from R
16.000 -0.12586   * coefficients to predict raindays from PPT
7 5 5 5 3 4 4 3 3 3 7 4      ! order parameters for GAMMA
1115555566666999 *optional soil map for use with simulations.  Each
number
9996666655555111 *is the soil type in a grid cell.  Note that for this
study
1569561569561569 * only white store soil was used, but this grid must
remain
9651669651669651 * in driver file for technical reasons.
5619561956195656
1965661965196555
6655111666555999
1659615951696556
5619561956195656
1965661965196555
6655111666555999
1659615951696556
1115555566666999
9996666655555111
1569561569561569
9651669651669651

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Temperature data means are from 90-year records from Durham.
Precipitation data means are from 90-year records from Durham.

Coefficients for VT and VR are from pooled long-term data from
station 1, highlands, and raleigh-durham airport.
Climate data updated August 14, 1995.