VEGETATIONAL CHANGES RESULTING FROM FOREST CONVERSION IN THE CENTRAL PIEDMONT OF VIRGINIA AND THEIR IMPLICATIONS FOR WILDLIFE

by

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Chapter I

INTRODUCTION

In 1976, 399,053 acres (161,495 ha) of commercial forest land in the Piedmont region of Virginia were classified as in the loblolly pine (Pinus taeda) forest type (Sheffield 1976a,b). This accounted for 24 percent of the area designated as softwood and 6 percent of the total combined softwood-hardwood area. Since the 1976 forest survey, loblolly pine area on both forest and non-forest industry lands has continued to expand at the expense of native pines (Virginia pine, Pinus virginiana, and shortleaf pine, P. echinata) and hardwoods. Loblolly is preferred over Virginia and shortleaf pines due to its greater innate growth capacity.

In Virginia, the natural range of loblolly pine includes the Coastal Plain and the eastern fringe of the Piedmont (Boyce 1974, Boyce and McClure 1975); however, it has been successfully introduced to the central Piedmont. Although incapable of propagating naturally, yield studies of hand- and machine-planted loblolly by the Virginia Division of Forestry have shown it to be the most productive pine species for the central region (T.A. Dierauf, pers. comm.).

The introduction of loblolly pine to the central Piedmont occurred in the 1930's when the Civilian Conservation Corps provided the manpower to plant it on abandoned agricultural land. The establishment of loblolly on old-field sites was most common up to the mid-1950's. At this time, the Virginia Division of Forestry and the timber industry in general, began converting forested areas to loblolly pine plantations. Most, if not all of these forested areas, were the product of natural successional processes following the abandonment of crop-lands near the turn of the century. Incentives for conversion were the lack of agricultural land for sale and its subsequent high cost. Boyce (1974) and Boyce and McClure (1975) noted that the stabilization of agricultural land throughout the South could have substantially reduced the production of Southern pine timber. Conversion of natural forest to pine was one way of offsetting this potential loss.

Presently, according to individuals within the Virginia Division of Forestry, the amount of loblolly pine acreage in old-field versus second-growth forest sites is approximately equal, due to the extensive plantings of loblolly pine on idle crop-land in the 1930's to the mid-1950's. Currently, 95 percent of the acreage being planted to loblolly is on second-growth forest sites. In the central Piedmont, the high economic profit associated with loblolly pine serves as an impetus to the conversion of even more natural forest.

Although there is an extensive amount of acreage presently classified as loblolly pine forest in the Piedmont of Virginia, relatively little consideration has been given to what effect these pine plantations have on the wildlife of the region. The shift from idle crop-land to natural forest as a new source for the establishment of loblolly pine plantations has prompted the Virginia Division of Forestry to request that a study be conducted to evaluate conditions for wildlife in converted stands. Conflicting opinions exist as to the value of such stands to wildlife; however, there is no data base to support any opinions. If a multiple-use program is to be implemented on public lands and recommendations are to be made to private landowners, forest managers will need information on post-conversion successional history relative to wildlife habitat.

Little quantitative research has been conducted in post-logging developmental stages. Qualitatively, pine succession in converted stands has been generalized by Johnson et al. (1974) as follows. A denuded site persists until the first growing season. An early forb stage develops in the first growing season and is displaced by perennial grasses the third year after conversion; grass coverage is gradually reduced in response to the formation of a canopy by developing pines and hardwoods. From crown-closure (which may occur in six or seven years depending on pine spacing and site conditions) to mid-rotation, a period of approximately 15 years, ground-story vegetation is severely suppressed due to heavy shading and a mat of pine needles. Young stands up to crown-closure are inhabited by a wide variety of birds and mammals--a progression of species as the habitat changes, while older stands support little or no wildlife since they lack adequate food and cover (Johnson et al. 1974). From mid-rotation to the final sawtimber harvest, the value of the plantation to wildlife will depend on the types of silvicultural treatments applied (Johnson et al. 1974).

In converted stands at the Virginia state forests, the shading problem created by crown-closure is compounded by the development of a hardwood midstory. Hardwood growth on such sites is prolific due to sprouting. Because of intense shading by the pine overstory-hardwood midstory, the herb and shrub strata are quite devoid of vegetation. Having been planted to loblolly in the mid-1950's, and being on a sawtimber rotation of 40 to 45 years, these stands are just now coming of age for their first thinning. If the hardwoods are not removed during the pine thinning operations, the additional light reaching the midstory will stimulate vigorous growth of the suppressed hardwoods. Such rapid restoration of a closed canopy by hardwoods will in turn restore the current understory conditions.

At the present time, it is necessary to quantify vegetative succession within converted stands to gain some insight as to how habitat conditions for wildlife vary over time.

The specific objectives of this study were:

1. To quantify changes in the composition and structure of vegetation in loblolly pine stands converted from natural forest as a function of time since establishment.

2. To compare the vegetative structure and composition of converted stands with that of the pre-conversion natural stands.

3. To appraise habitat conditions for selected wildlife species in the natural forest and various aged loblolly pine stands.

4. To establish a data base for subsequent studies of wildlife-habitat relationships in the central Piedmont of Virginia.

Chapter II

LITERATURE REVIEW

The first significant study dealing with the utilization of coniferous plantations by wildlife was conducted by Edminster (1935, cited by Smith 1958) in eastern New York. Stands examined were even-aged, 12 to 20 years old, and 100 acres (40 ha) or more in size. Edminster found that few rabbits (Sylvilagus floridanus) and no grouse (Bonasa umbellus) penetrated more than 300 ft (91 m) into the plantations. Penetration for white-tailed deer (Odocoileus virginianus) and gray squirrels (Sciurus carolinensis) did not exceed 200 ft (61 m). From these distance measurements, he recommended that plantations of a similar nature should not be greater than 600 ft (183 m) in diameter, preferrably 400 ft (122 m), and should "be separated by hardwoods and food-bearing shrubs and by open land in narrow concentric strips."

In the ensuing years, relatively little research was undertaken dealing with conifer plantations and wildlife (Smith 1958). With the large-scale planting of conifers on abandoned farm land in the 1930's through the 1950's, conservationists became concerned about the value of such land to wildlife (Smith 1958). This prompted a study by

Smith (1958) on two reforested areas in southern New York. The intent of this study was to determine the effect of conifer reforestation on wildlife distribution and to recommend management practices which could make these plantations more attractive to wildlife. The 62 stands selected were quite diverse--10 species of conifers in mixed and pure plantings, different age classes and acreages, and a variety of edge conditions. As part of his analysis, Smith characterized wildlife succession as a function of increasing tree height and dominant plant life form. It is a generalized depiction of wildlife succession since the use of a plantation by wildlife is influenced by many secondary factors such as the species of conifer, the area, and the nature of the surrounding cover and openings (Smith 1958).

Reforestation of agricultural lands continued at a rapid rate until the 1960's (Boyce 1974). The amount of crop-land had been rapidly decreasing until 1962, at which point it stabilized and brought a halt to the 40 year trend of increasing forest acreage in the U.S. and the Southeast in particular (Boyce 1974). The timber industry responded by accelerating the conversion of natural forest to pine plantations. In 1970, Wheeler reported that the wood-using industry owned 40 million acres (16,187,778 ha) of forest land in the South. Another 17 million acres (6,879,806 ha) were in public ownership and 141 million acres (57,061,917 ha) were owned by private individuals. According to Arner (1972), most of the forest industry and public ownership land was under an even-aged management program. Data he obtained from 43 timber companies in the Southeast and 30 national forests in the Southern Region revealed that their annual conversion of forest to pines was 605,500 acres (245,042 ha) and 112,150 acres (45,386 ha), respectively.

Johnson et al. (1974) echoed the sentiments of wildlife biologists, environmentalists, sportsmen, and others, when they remarked that a point of great concern is the extensive conversion of hardwoods to pine. In their discussion of management planning, they noted that little baseline data existed on wildlife and understory vegetation in pine plantations of different ages and treatments. As part of a program of management, they suggested that the forest "manager should consider the important species of lesser vegetation associated with each stage in the development of a stand, their value to wildlife, and their ecological requirements."

To date, most studies of the value of pine plantations to wildlife have dealt with those of old-field origin as opposed to those converted from native forest. There have been no studies on sites converted from natural forest which have traced pine succession from the initial planting up to mid-rotation or later. Quantitative vegetational studies of pine succession on converted sites have focused on opposite ends of the successional spectrum, and have been somewhat limited in scope.

As compared to the pre-conversion forest sites, early pine seral stages are quite productive. Within the loblolly-shortleaf pine-hardwood forest type, studies by McKee (1973) and Perkins (1973) in the Mississippi flatwoods and Stransky and Halls (1978) in east Texas, have examined the effects of various site preparation methods on vegetation and wildlife for several years following conversion. Stransky and Halls noted substantial increases in total forage yield--browse and herbage--in loblolly pine stands one and three growing seasons after establishment. McKee found that winter deer food production was 5 to 20 times greater on converted sites (one- to four-year-old plantations) than on pre-converted sites; rabbit utilization was also significantly greater in the plantations. According to Perkins, studying the same areas, the interior of the natural forest proved to be relatively poor habitat for songbirds and ground-dwelling small mammals. He reported that the young pine stands were characterized by a higher abundance and variety of animals. For some species, favorable habitat conditions were short-lived, e.g., it took only three years for quail (<u>Colinus virginianus</u>) feeding conditions to deteriorate.

In the central Piedmont of Virginia, Chamberlain and Crandall (1964) compared plant and small mammal communities of one- to six-year-old converted loblolly stands with mature native forest stands. Although vegetation structure and composition differed among converted and natural stands, there was no appreciable difference in the composition of small mammal populations. Both the Chamberlain and Crandall (1964) and Perkins (1973) studies noted that the drastic change in the vegetational community caused by the conversion process reduced or eliminated species specially adapted to live in mature forest stands.

According to Johnson et al. (1974), the patterns of small mammal succession and quail populations described by Perkins (1973) resembled those found in their studies on loblolly pine plantations in the Georgia Piedmont. Brunswig and Johnson (1973) sampled loblolly pine stands in the Georgia Piedmont for bobwhite quail food plants. These converted stands, ranging from one to seven years of age, were established on areas previously supporting loblolly pine forest type. Vegetative data were coupled with data obtained on the relative abundance of quail, the distribution of coveys, and their food habits. Ranking of age classes based on bird density and least hunting effort matched the ranking based on total quail foods by frequency and of annual quail food plants by occupancy and frequency. From their analyses, Brunswig and Johnson concluded that quail hunting was optimal in two-year-old stands and deteriorated rapidly in stands older than three years. Structural and compositional changes in vegetation with time adversely affected other animals as well as quail. Within the same general area, Atkeson and Johnson (1979), working in converted loblolly pine plantations aged 1 to 15 years, reported that small mammal populations were most abundant in stands aged one to four years, and declined thereafter. Fifteen-year-old plantations supported few animals. They believed that the density and composition of small mammals were associated with the density of ground-layer vegetation.

In the flatwoods of Mississippi, Perkins (1973) noted that rapid successional changes were due to the favorable growing conditions of the region. The successional rate in the Georgia Piedmont also seemed to be accelerated; pine canopy closure occurred at the age of seven (Atkeson and Johnson 1979). In comparison, Umber and Harris (1975) found succession to proceed at a relatively slow rate owing to the poor growth and survival of slash pine (*Pinus elliottii*) on the central Florida sandhills. Data spanning a 13 year period were obtained on land converted from longleaf pine (Pinus palustris) - turkey oak (Quercus laevis) to slash pine. As with other studies, they observed that the conversion process resulted in an increase in the understory vegetative biomass (relative to the native forest); this change was concomitant with greater numbers of rodents and arthropods. The marked expansion of rodent population levels following site preparation and planting quickly subsided after the third year. Bird numbers remained higher in the forest areas due to a dependence upon vertical as well as horizontal heterogeneity in the habitat. Noble and Hamilton (1976) also found bird density and species diversity to be lower in plantations as compared to the natural forest; as the number of vegetative strata increased in a stand, density and the number of birds increased. Their conclusions were based on a census in southeastern Louisiana of wintering and breeding bird populations inhabiting loblolly stands aged 6, 20, and 46 years, and a mature pine-hardwood forest stand.

Unlike Umber and Harris (1975), who monitored biomass changes for all forbs, grasses, and woody plants within the understory, Hebb (1971) only inventoried (frequency and density) food plants used by game species in the sandhills.

Successional changes of game food plants were studied by Hebb over a duration of 13 years on slash pine plantations in northwest Florida which had been established on sites originally classified as longleaf pine-turkey oak forest type. Game food plant production was favorable for seed-eating species such as bobwhite quail and mourning doves (Zenaidura macroura) for several years following conversion owing to the profusion of forbs. By the fourth or fifth year, forbs were displaced by grasses which were of little use to game. Comparing converted and natural areas, it was found that conversion decreased game foods by eliminating scrub oak (primarily Quercus laevis) acorn and browse production, and except for the first few years there was no compensation for this loss.

In a loblolly pine plantation established on a cutover longleaf pine site in central Louisiana, Blair (1960), Blair (1967), Blair and Enghardt (1976), and Blair and Feduccia (1977) studied changes in the composition and growth of deer forage as a function of pine thinning and the development of a hardwood midstory. Data were compiled over a 17 year period, having been initiated when the plantation was 30 years old. According to these studies, repeated pine thinnings during a sawtimber rotation stimulated the development of a shrub-tree midstory which grew beyond the deer feeding zone and intensified the shading of the herbaceous and low woody forage. Hardwood density and basal area increased directly with the intensity of pine removal, and by stand age 35, five growing seasons after a third thinning, hardwoods had become the primary factor inhibiting the growth of forage. The presence of this hardwood component offset the benefit of managing pine at a lower level of basal area to enhance forage yields (Blair and Feduccia 1977). Based on the cumulative results of these studies, Blair and Feduccia (1977) stated that "the invasion and uncontrolled growth of hardwoods in loblolly pine plantations can substantially limit the carrying capacity of millions of acres of habitat for white-tailed deer in the South."

Chapter III

STUDY AREAS

Situated in the central Piedmont of Virginia (Fig. 1), the Buckingham-Appomattox and Cumberland State Forests encompass an area of approximately 40,000 acres (16,188 ha). Of this amount, about 30,000 acres (12,141 ha) have been zoned for commercial timber production (VDF 1973, 1974). Forty percent of the commercial forest land is covered by second-growth oak-hickory-pine forest, while the remainder is in pine (mostly loblolly) plantations (S.F. Warner, pers. comm.). Pine plantations are managed on a 40 to 45 year rotation for sawtimber; the first thinning is made at about 20 years, and one, sometimes two additional thinnings are executed prior to clear-cutting (T.A. Dierauf, pers. comm).

Principal drainage systems of the state forests are the Willis, Appomattox, and Slate River systems, all of which are contained in the James River Basin (VDF 1973, 1974). The topography is moderately rolling; average elevation above sea level is approximately 650 ft (198 m) and 350 ft (107 m) for the Buckingham-Appomattox and Cumberland State Forests, respectively (VDF 1973, 1974).

The central Piedmont region is underlaid by metamorphic and igneous rocks (Calver 1964). Soils are classified as

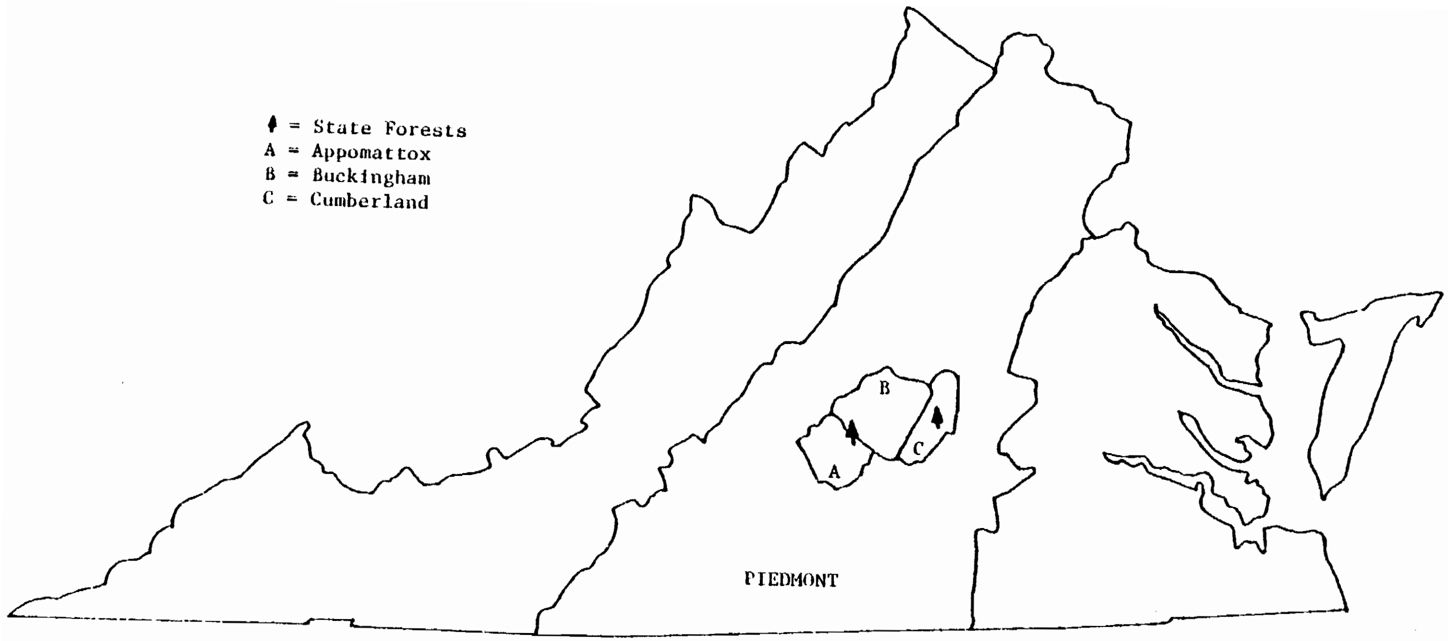


Fig. 1. The location of the Buckingham-Appomattox and Cumberland State Forests within the Piedmont region of Virginia. Piedmont boundaries are defined according to the 1976 Forest Survey's designation by counties (Sheffield 1976 a,b). As a consequence they do not strictly conform to the actual boundaries of the physiographic province.

hapludults (formerly red-yellow podzolic and some gray-brown podzolic soils) (Nelson and Zillgitt 1969). In the study plantations, soils were primarily of the Cecil, Tatum, and Appling series (red-yellow podzolic soils). Surface and subsoil texture varies from sandy loams to clays (Robinson et al. 1961). Due to past agricultural practices, erosion has removed more topsoil in this region than from any other part of Virginia (Culbertson 1948). According to Culbertson (1948), the extensive erosion was the result of intensive crop farming (intertilled crops of tobacco and corn).

Climatically, the state forest areas are characterized by warm summers, relatively mild winters, and normally adequate rainfall (VDF 1973, 1974). Mean annual temperature ranges from 55 to 60 F (12.8 to 15.6 C), with a frost-free growing period of 200 days (VDF 1973, 1974). Mean annual precipitation is approximately 40 in (102 cm) (VDF 1973, 1974).

Chapter IV

METHODS

4.1 SELECTION OF STANDS

During the summer of 1978, 21 loblolly pine plantations within the Buckingham-Appomattox and Cumberland State Forests were selected for study (Table 1). The 21 stands represented three replications of seven developmental stages which ranged in age from 1 to 22 years following planting. In general, clear-cutting and site preparation preceded the planting of loblolly pine by seven to nine months (Table 1). Each of four stages (1, 3, 9, and 22 yrs) consisted of three stands which had been planted the same year; the remaining three stages each contained one stand whose age differed by one year (Table 1). The 22-year-old stands, the oldest stands available, were approaching their first thinning. In addition to these pine plantations, three hardwood and three natural pine-hardwood stands, typical of sites presently being converted, were selected for comparison (Table 2).

An effort was made to select stands situated on upland sites of moderate site quality with fairly level terrain because these conditions are preferred for both on-going and

Table 1. Loblolly pine plantation summary.

State Forest[a]	Management Unit (no.)	Stand No.[b]	Year Planted	Site Prep[c]	Site Origin[d]	Mean Height (m)[e]	Site Index[f]	Site Prep & Planting Dates
C	Headquarters (19)	1	1956	B(P)	H	16.2	56	-------
C	Winston (25)	20	1956	B(P)	H	14.9	50	-------
BA	Loth (5)	4	1956-57	B(P)	H	15.4	53	-------
C	Arrowhead (18)	5	1959	B(P)	H	15.1	56	-------
C	Oak Hill (26)	31	1960	B(P)	H	14.1	55	-------
BA	Woolridge (13)	41	1960	B(P)	H	15.4	60	-------
C	Nettles (15)	1	1962	B(P)	H	13.2	56	-------
BA	Loth (5)	14	1963	B(P)	H	12.7	58	-------
C	Oak Hill (26)	61	1963	B(P)	H	13.1	59	-------
C	Booker (20)	21	1969	B	H	8.5	63	B summer 1968; planted spring 1969.
BA	Jamison (7)	38	1969	B	PH	6.2	47	B summer 1968; planted 1969
C	Faulkner (7)	13	1969	DC&B	PH	7.2	53	DC&B 1968; planted spring 1969
BA	Jenkin's Creek (16)	9&6	1972	B(RR)	PH	4.5	--	B(RR) 2 March 1972; planted 23 March 1972 (some Virginia pine planted)
BA	Woolridge (13)	4	1973	DC&B	H	5.1	--	DC&B 1972; planted 1973
C	Mt. Airy (6)	3	1973	DC&B	PH	4.3	--	DC&B summer 1972; planted 1973 (some Virginia pine planted)
BA	Ferguson (27)	59	1975	DC&B	H	2.4	--	DC May-June 1974; B June 1974; planted December 1974 and January and March 1975.
BA	Ferguson (27)	61	1975	DC&B	PH	2.3	--	DC May-June 1974; B June 1974; planted December 1974 and January and March 1975
C	Booker (20)	38	1975	DC&B	PH	2.3	--	DC August-September 1974; B September 1974; planted April 1975
C	Oak Hill (26)	68	1977	DC&B	PH	0.9	--	DC 10 May 1976; B 28 June 1976; planted February-March 1977
C	Booker (20)	38	1977	DC&B	PH	0.6	--	DC 5 May 1976; B 28 June 1976; planted March 1977
C	Faulkner (7)	10	1977	DC&B	H	0.9	--	DC 12-19 July 1976; B 4 August 1976; planted November 1976, but had to replant May 1977 due to freeze kill of winter 1977.

[a] C=Cumberland; BA=Buckingham-Appomattox
[b] Stand size ranged from 1.6 to 19.4 ha; pine spacing varied from 2.1 x 2.4 to 2.4 x 2.7 m.
[c] B(P)=bulldoze (piled); B=burn; DC&B=drum-chop and burn; B(RR)=bulldoze (root-rake)
[d] H=hardwood forest; PH=pine-hardwood forest
[e] Measurements were made 17 to 20 March 1979 of 10 dominants/codominants evenly distributed throughout the sample area.
[f] From site index curves (base age 25) for loblolly pine plantations (Burkhart *et al.* 1972)

Table 2. Natural forest stand summary.

State Forest[a]	Management Unit (no.)	Stand No.[b]	Forest Class	Mean Age (yrs)	Mean Height (m)[d]	Site Index[e]	Stand History
C	Oak Hill (26)	86	PH	58	20.4	63	Pine component salvage thinned.
BA	4H (18)	42	PH	62	21.0	63	Pine component salvage thinned.
C	Arrowhead (18)	3	H	74	25.1	71	Pine component salvage thinned.
C	Nettles (15)	2	H	77	22.4	63	Appears to have undergone some thinning.
C	Headquarters (19)	2	H	80	21.2	58	Hy-grade logged; Virginia pine salvage thinned.
BA	Talbert (6)	29	PH	83	20.4	56	Pine component salvage thinned.

[a] C = Cumberland; BA = Buckingham-Appomattox

[b] Stand size ranged from 4.9 to 32.0 ha.

[c] PH = Pine-hardwood forest; H = hardwood forest

[d] Measurements were made from 17 to 20 March 1979 of 10 dominants/codominants (oaks, primarily *Quercus alba*) evenly distributed throughout the sample area. Age was determined by taking an increment core at breast height and averaging the ring counts made by two individuals.

[e] From site index curves (base age 50) for upland oak in the Southeast (Olson 1959)

future plantings of loblolly. The relative abundance of certain plant species which are indicative of site quality was used as an additional guide to stand selection. Over the years, silvicultural treatment of converted sites on the state forests has been quite varied. Such inconsistency has resulted in clear-cutting being followed by: bull-dozing of residual debris into piles; drum-chopping and burning; burning; herbicidal spraying and burning; herbicidal spraying; root-raking by bulldozer; or no site preparation. Site preparation at the state forests was followed by hand- or machine-planting of loblolly pine seedlings. If after two or three years, or as late as five to eight years, the hardwood growth became too competitive with the planted pines, some stands were "released" by aerial spraying with a hardwood selective herbicide or chopping with brush hooks. Research conducted by the Virginia Division of Forestry has shown virtually no difference in either the survival or growth of machine- and hand-planted loblolly pine seedlings (Garner and Dierauf 1973). The use of herbicides for either site preparation or release has been discontinued; in fact, release work of any kind is no longer performed. Since no consistent method of site treatment was employed at the state forests, selected stands were only required to have undergone some type of preparation to expose mineral soil prior to planting with loblolly pine. Also, to reflect current management practices, stands selected for this study had never been subjected to chemical treatment or mechanical release.

An attempt to relate soil type with site indicator vegetation in stands was unsuccessful. Soils of the region have been highly modified through intensive and varied land-use in the past (Culbertson 1948). As a consequence, the delineation of basic soil types may not be reflective of the actual soil conditions which exist.

4.2 VEGETATION SAMPLING

A sampling scheme was devised for quantifying the composition and structure of vegetation in each stand in a manner which allowed for statistical comparisons among developmental stages. Vegetation measures were also selected for their possible utility in evaluating habitat conditions for white-tailed deer (*Odocoileus virginianus*), bobwhite quail (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), small mammals, and songbirds. The sampling scheme was designed under the assumption of a 4000 m^2 sample area in each stand, and to accommodate nested quadrats which varied in size and number according to the vegetative stratum being sampled. Quadrat dimensions by strata were

5x5 m for the overstory, 4x4 m for the transgressive layer, and 1x1 m for the ground layer. The strata were defined as follows: the overstory was comprised of woody stems having a dbh greater than 2.54 cm; the transgressive layer contained woody stems which were greater than or equal to one meter in total height and less than or equal to 2.54 cm dbh; and the ground layer was occupied by all woody stems less than one meter in total height and all herbaceous stems. Quadrat sizes chosen are typical of those used by plant ecologists while the delineation of strata is in accordance with a methodology proposed by the Biological Services Program of the U.S. Fish and Wildlife Service (States et al. 1978). Forty quadrats were used per 4000 m^2 sample area, which translates to 25, 16, and 1 percent of the sample area for the overstory, transgressive, and ground strata, respectively. For basal area measurements in natural forest stands, it was necessary to sample 50 percent (80 quadrats) of the 4000 m^2; sampling intensity for the same variable in pine plantations remained at 25 percent of the area. The use of one large plot in preference to a number of smaller non-contiguous plots was precluded by the extremely dense vegetation in stands five and nine years of age.

Sampling of the various vegetative strata was conducted in a systematic manner. Over the years, stands of pine have been planted with a spacing that has ranged from 6x6 ft (1.8x1.8 m) to 8x9 ft (2.4x2.7 m) (trees 8 ft apart, rows 9 ft apart) (S.F. Warner, pers. comm.). Such uniformity in the planting of pines will in turn have a non-random influence on the distribution of natural vegetation. To avoid the possibility of consistently sampling along rows, sampling lines were situated so as to cut diagonally across pine rows (Daubenmire 1959, 1968:85). This method of distributing plots was checked during the sampling process by noting the placement of quadrats relative to rows. Besides providing a more representative sample of the area, this procedure made it easier to relocate flagged sample points in dense vegetation and to detect any errors in the initial layout of such points.

Stands were quite irregular in size and shape, and differed greatly with respect to accessibility along their perimeter. Thus, a reference line was established within the largest portion of a stand rather than attempting to set up a baseline along its perimeter. Reference lines were initiated well beyond the edge of a stand, and were flagged at 10 m intervals to create a grid for sampling the overstory stratum. Sample lines were placed perpendicular to the reference line at each 10 m mark (Fig. 2). Sample points chosen on adjacent sample lines were offset by five

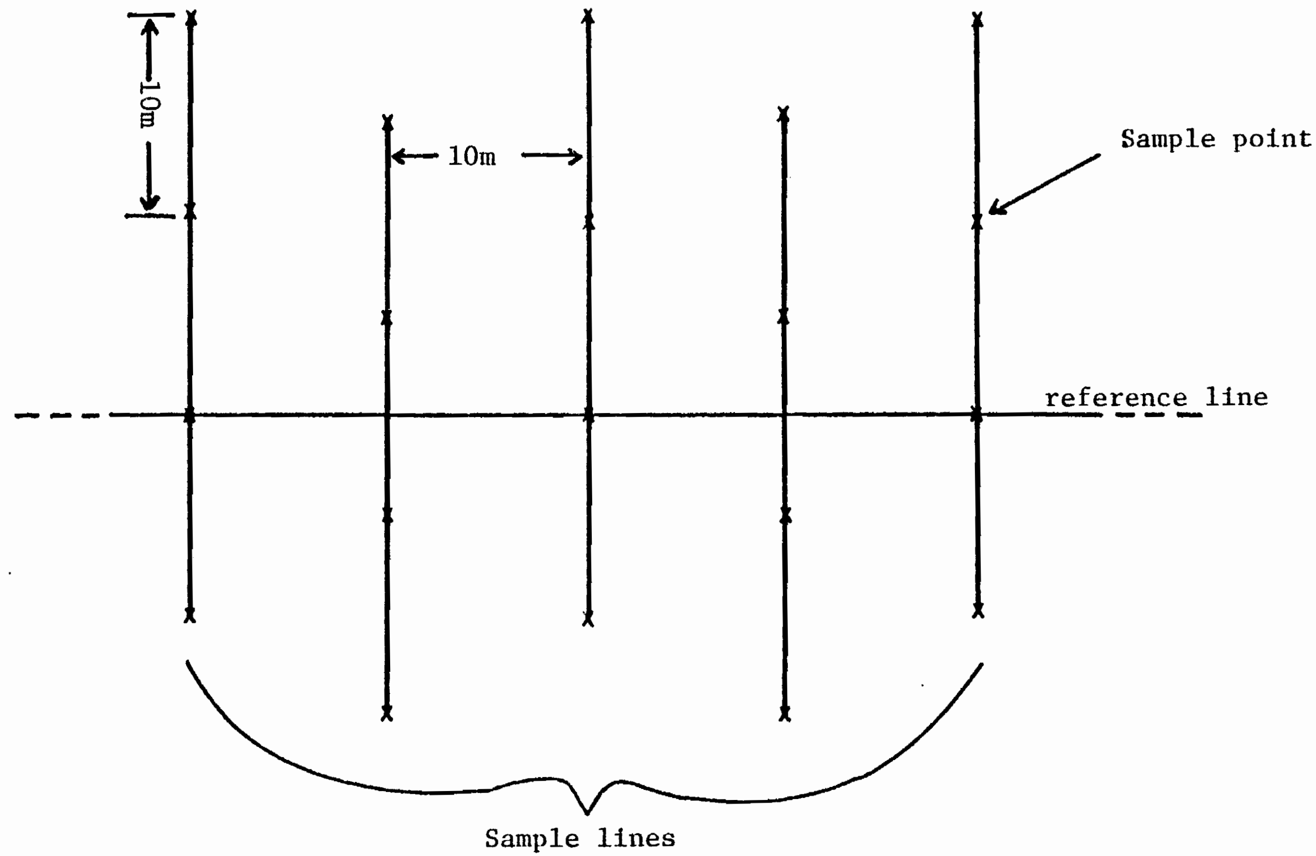


Fig. 2. Stand sampling design.

meters to provide a more even distribution of samples in the stand.

In an effort to maximally disperse the sample points, sample lines were limited to a length of 30 m, while reference lines were restricted to 100 m. If stand boundaries were such that a sample line fell short of 30 m, the remaining sample points were accommodated by extending subsequent sample lines beyond 30 m. Where it was necessary to provide even more sample points a second reference line was set up within a portion of the stand which could not be adequately covered by a continuation of the original sample lines. When a sample point fell on a trail or some atypical discontinuity, e.g., a large girdled hardwood that was not removed during the original clear-cut, an alternate sample point was chosen along the sample line by extending it the necessary amount beyond 30 m. Sample points were sufficiently removed from the stand perimeter to avoid edge effects.

For each stand, running variances of vegetative measures were computed on a cumulative basis to determine the minimum number of quadrats to obtain an adequate sample. For each vegetative variable measured, the data were examined in the aforementioned manner, and if the sampling intensity was subjectively determined to be insufficient, the stand was revisited and additional samples were taken. The running variance was recomputed on the basis of the increased sample size. This procedure was repeated until the variance became relatively stable--a saturation level for precision. Time being critical, this approach minimized over-sampling. The number of species encountered on a cumulative plot to plot basis was also recorded as another way of testing the adequacy of the sample size.

4.2.1 Overstory stratum

At each overstory sampling point a 10x10 m area was partitioned into four equal quadrats, one of which was randomly selected for the actual vegetation sampling. For basal area measurements in natural forest stands, two 5x5 m quadrats were randomly chosen. Time limitations and high vegetative densities in younger stands dictated the use of a 5x5 m quadrat in lieu of the traditional 10x10 m quadrat. Basal area and density for trees having a dbh greater than 2.54 cm were determined on a species basis. A stem was considered an individual if it originated less than 15 cm above the ground. Canopy closure at the center of each 10x10 m area was estimated by using a spherical densiometer (Lemmon 1956) in the manner suggested by Strickler (1959). Calculation of percent canopy closure differed slightly from

Strickler in that the total number of occluded points from the four readings was divided by 68--the highest possible total--and then multiplied by 100. Closure measurements were made 9 July to 6 August 1978, and just prior to the spring eruption of hardwood foliage, i.e., 15 to 20 March 1979, in order to determine pine cover.

4.2.2 Transgressive stratum

Density for woody species which were greater than or equal to one meter in total height and less than or equal to 2.54 cm dbh was determined by counting all stems within a 4x4 m quadrat centered in each 10x10 m area. Due to the dense sprout growth in converted stands, density counts and total coverage estimates were made for each separate 2x2 m subsection and then averaged. Total percent coverage for transgressives provided insight to understory development over time. Within the transgressive stratum, a notation was made as to which woody stems had 50 percent or more of their foliage below 1.5 m, i.e., the upper limit of the white-tailed deer feeding zone according to various researchers (Halls 1974, Blair and Feduccia 1977). This is a somewhat qualitative method, but on a relative basis over time it should permit the monitoring of browse and cover which undergoes mortality or gradually grows above the reach of deer. Transgressive stems were further categorized as palatable or unpalatable. Palatable species were those that either had been found in rumen samples of Piedmont deer by Harlow and Hooper (1972) (Appendix Table III), or had been foraged by deer at the Buckingham-Appomattox and Cumberland state forests (Appendix Table IV). The transgressive stratum was sampled from 9 July to 6 August 1978.

4.2.3 Ground stratum

Percent ground coverage for woody species less than one meter in total height and all herbaceous species was estimated using a 1x1 m quadrat centered in each 10x10 m area. Density was computed from stem counts for tree species within the ground stratum. Other measurements made within the 1x1 m quadrat included the following attributes: percent coverage of total vascular plants, total grasses, fungi, mosses, lichens, rock (includes lichens), litter, woody debris (diameter >1 cm), and bare soil; litter depth was recorded down to mineral soil. For the ground stratum as well as the other strata, species frequency was determined as the proportion of quadrats in which the species occurred. Sampling of the ground stratum was conducted from 2 to 22 September 1978.

Coverages for the ground and transgressive strata were estimated by the cover classes proposed by Daubenmire (1959, 1968:43) as modified by Bailey and Poulton (1968), where 0= 0-1%, 1= 1-5%, 2= 5-25%, 3= 25-50%, 4= 50-75%, 5= 75-95%, and 6= 95-100%. Class midpoints, 0.5, 3.0, 15.0, 37.5, 62.5, 85.0, and 97.5, were used in the subsequent calculations of average coverage for individual species and attributes.

4.2.4 Vegetative density profile

A 20 cm high, 50 cm wide board (McEvoy 1978) was used to measure vegetative density in five successive strata centered at 0.1, 0.5, 1.0, 1.5, and 2.0 m above the ground. Intervals of 10 percent, i.e., 0 to 10, 10 to 20, etc.,were used to designate what portion of the gridded board was covered by living vegetation. The midpoint values of these intervals were used in subsequent computations of average density for each stratum. Measurements of the vegetative profile were taken at 20 evenly distributed locations within a stand. An estimation of vegetative density at a particular level above the ground was made by viewing the board at a standard distance from a randomly chosen direction. A standard distance at which to estimate the amount of vegetation covering the board was arrived at through a preliminary sample of a range of distances to determine the point of maximum discrimination among strata and stands. As a result of these trials, a standard distance of four meters was used for all stands. This entire procedure for quantifying the vegetative structure within stands is a modification of a method proposed by Nudds (1977). Measurements of summer vegetative density were made from 15 to 21 August 1978, while winter estimates were made from 15 to 20 March 1979.

4.3 ANALYSES

4.3.1 Ordination

The degree of similarity of loblolly pine stands both within and among age classes was examined through the use of polar ordination, a geometric technique in which forest stands may be graphically displayed according to their compositional-structural similarity. By integrating composition and structure on a species basis, the method provided insight to vegetational changes over time in converted stands. The Bray-Curtis model (Bray and Curtis 1957) was chosen in lieu of other methods. With all ordination techniques, the ability to make meaningful ecological interpretations is hampered by stands differing greatly in species composition (Beals 1973, Gauch 1977). The wider the range encompassed by a group of stands along an environmental gradient, the less effective are ordination models in depicting stand-environment relationships (Beals 1973, Gauch 1977).

Stand ordination was accomplished by utilizing the Cornell University ecology program CEP-25A, ORDIFLEX (Gauch 1977). An ordination of converted stands based on ground stratum data seemed to most clearly exemplify the successional process. Frequency and coverage values for each species had been transformed to an importance value (IV= relative frequency + relative coverage) (Mueller-Dombois and Ellenberg 1974:118-120). IVs were then used in the computation of a similarity index for each pairing of stands. To accommodate the program's maximum input limitation, species occurring in less than 3 of the 21 stands were deleted from the data set. Their removal had virtually no effect on ordination results since their IVs were quite small. Because of the manner in which the similarity index was computed, the deletion of rarely occurring species necessitated the relativization of stand IV totals to 100 percent. The exclusion of these "rare" species resulted in the use of 138 species for the ground stratum ordination of converted stands.

4.3.2 Statistical Analysis

Data collected were analyzed by the use of a nested analysis of variance design (Sokal and Rohlf 1969:253-269), i.e., samples nested within stands, stands nested within age classes/developmental stages. The 21 converted stands represented 3 replications of 7 age classes which varied in age from 1 to 22 years since planting. The number of samples per stand ranged from 20 to 80 depending on the particular variable. For each habitat variable, the nested ANOVA was used to test if the variation among age classes was significantly greater than the variation among stands within age classes. Where differences among age classes were significant (0.05 level), a Waller-Duncan k-ratio t-test (Waller and Duncan 1969, Duncan 1975) was used to compare means. This test is an improved and more exact version than the more commonly used Duncan's multiple range test (Waller and Duncan 1969). A k-ratio value of 100 was selected which is analogous to a significance level of 0.05 in testing a single difference (Waller and Duncan 1969). Based on their evaluation of ten multiple comparison procedures, the Waller-Duncan method was one of two procedures recommended by Carmer and Swanson (1973). Habitat variables which were determined to be significantly different among age classes were graphed as a function of time since planting to depict successional trends.

The nested ANOVA design was classified as a mixed model (Sokal and Rohlf 1969:254-256). Age classes were fixed while subordinate levels of stands and samples were considered random. Criteria used in the selection process for stands represented the current and future approaches to the establishment and treatment of converted stands. The limited number of stands which came closest to fulfilling these criteria left little option for selection. As a consequence, the choice of stands within each age class could be considered randomly imposed. With regard to sample distribution, time and manpower constraints necessitated the systematic placement of quadrats relative to a reference line; the origin of the line was arbitrary.

A nested ANOVA design was also used to compare the natural forest hardwood and pine-hardwood stand classes. All statistical tests were performed using SAS-76 (Barr et al. 1976).

4.3.3 Richness, evenness, and diversity

For each vegetative stratum of each natural and converted stand, richness, evenness, and diversity measures were computed. The total number of species in a sample, richness (S), was determined as well as areal species richness (ASR), the average number of species per quadrat or unit area (Squiers and Wistendahl 1977). Species richness should be expressed on an area basis since the greater the area sampled the more rare species are encountered. Despite the dubious value of diversity (Eberhardt 1969, Hurlbert 1971, Peet 1974, Poole 1974:396-397) and equitability indices (Sheldon 1969, Peet 1974, 1975), the Shannon-Wiener information theory index (H') (Pielou 1966a,b) and species evenness (J') (Pielou 1966b) were used to permit comparisons with other studies. The equations for these measures are:

$$H' = -\sum_{i=1}^{S} Pi \ln Pi \qquad (1)$$

where Pi= the proportion of abundance of the ith species, and S= the number of species in the sample.

$$J' = H'/H'max \qquad (2)$$

where H'max= ln S= the maximum possible H' for a sample of S equally abundant species.

As originally proposed, these indices, (1) and (2), were to be used with density data, i.e., Pi= Ni/N, where Ni= the number of individuals in the ith species, and N= the total number of individuals in S species. However, various researchers have used biomass (Wilhm 1968, Tramer 1975) or coverage (Bazzaz 1975, Squiers and Wistendahl 1977) instead of density. When sampling vegetation, it is virtually impossible to recognize individuals when dealing with rhizomatous, stoloniferous, and caespitose plants. Daubenmire (1959, 1968:40,46), Rice (1967), and Mueller-Dombois and Ellenberg (1974:80-81) attach more ecological significance to coverage than density. Thus, in this study, the Shannon-Wiener and evenness indices were calculated using species coverage values for the ground stratum and species basal area values for the overstory stratum. Numerous woody sprouts precluded the measurement of dbh on a species basis in the transgressive stratum. As a consequence, density was relied on as a measure of species influence. Unlike the overstory stratum where there was a wide range in dbh, the narrow limits ($\geq$ 1 m total height and $\leq$ 2.54 cm dbh) imposed on transgressives added credibility to the use of density.

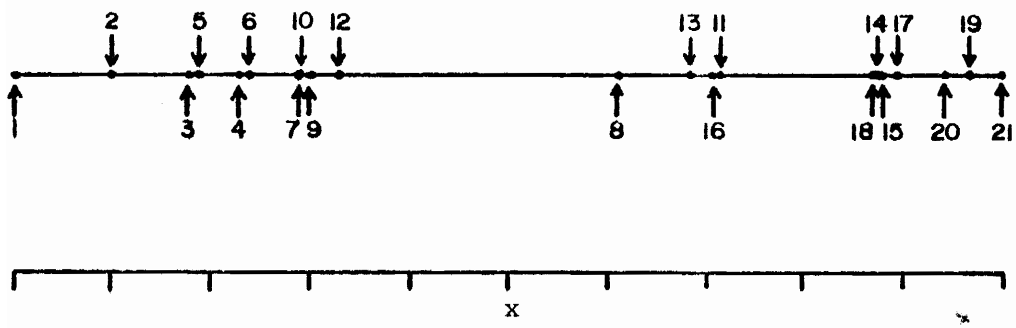
Calculations of richness, evenness, and diversity according to strata for each stand were averaged for each plantation age class, then graphed as a function of the time since planting of loblolly pine. Species richness values for various plant life forms found in the ground stratum were similarly treated, as were total coverages of plant species known to be food sources for white-tailed deer, wild turkey, and bobwhite quail.

Chapter V

RESULTS AND DISCUSSION

5.1 ORDINATION OF PINE PLANTATIONS

The spatial arrangement of stands in Fig. 3, resulting from polar ordination (Bray and Curtis 1957), represents a gradient of stand development. Stands 1 and 21, the youngest and oldest stands, were subjectively selected as end-points for the x axis. All other stands were positioned according to their relative similarity to these end-point stands. The graph was one dimensional due to an ORDIFLEX program (CEP-25A) routine--the y axis is not constructed if less than two stands are present in the center fifth of the x axis (Gauch 1977). An absence of stands in the central portion of the x axis suggested that stands can be divided into two groups based on compositional and structural differences. In general, the ordering of stands tended to be in accordance with their age; however, among intermediate aged stands, 5 to 19 years, additional factors seemed to be influencing community development since stand placement did not strictly conform to an age gradient. To provide insights into this lack of agreement between relative



Stand No.	Stand[a] I.D.	Age[b] (yrs)
1	C7-10	1
2	C20-38	1
3	C26-68	1
4	C20-38	3
5	BA27-61	3
6	BA27-59	3
7	C6-3	5
8	BA13-4	5
9	BA16-9&6	6
10	C7-13	9
11	BA7-38	9
12	C20-21	9
13	C26-61	15
14	BA5-14	15
15	C15-1	16
16	BA13-41	18
17	C26-31	18
18	C18-5	19
19	BA5-4	21-22
20	C25-20	22
21	C19-1	22

[a] Refer to Table 1.
[b] Age represents the time since planting with loblolly pine.

Fig. 3. Ordination of pine plantations (ground stratum).

position in the ordination and absolute age of stands, importance values (IVs) for selected species, i.e., those with at least one IV $\geq$ 10.0 for one stand were listed relative to the ordination sequence of stands (Table 3). Because the ordination was based on species IVs in the ground stratum, it was possible to associate the stand pattern with the pattern of species replacement over time.

Stands situated on the right half of the x axis in Fig. 3 were dominated by ericaceous plants (*Vaccinium vacillans*, *V. stamineum*, and *Gaylussacia baccata*), and *Nyssa sylvatica* (black gum), while those on the left side were characterized by old-field species. A further division was apparent among stands situated on the right side of the ordination: 8, 11, 13, and 16 seemed to be in a transitional phase, old-field species being displaced by the ericaceous- *Nyssa* complex (Fig. 3, Table 3). The offsetting of stand 8 from 11, 13, and 16, was attributed to its relatively high IVs for four old-field species-- *Rhus copallina* (winged sumac), *Andropogon virginicus* (broomsedge), *Rubus* spp. (blackberries-dewberries) and *Solidago juncea* (goldenrod). On the left half of the axis, there were two outliers from the main group of stands. Stand 1 was distinguished from the other stands by noticeably higher IVs for three annuals, *Digitaria ischaemum* (crabgrass), *Lespedeza stipulacea*

Table 3. Importance values of selected species in the ground stratum of various aged pine stands.

Species	Stand Number[a] 1	2	3	5	4	6	7	10	9	12	8	13	16	11	18	14	15	17	20	19	21
Time Since Planting (yrs)	1	1	1	3	3	3	5	9	6	9	5	15	18	9	19	15	16	18	22	22	22
Lespedeza stipulacea	10.6	3.8	2.7	1.3	0.2	0.4															
Conyza canadensis	25.1	7.4	6.9	2.4	2.2	0.7															
Cassia nictitans		2.1	22.1	2.7	4.4		5.3	1.9	2.2	0.8											
Potentilla canadensis	7.9	13.1	19.9	8.8	7.2	3.9	3.7	5.6	5.5	6.4	0.4	1.0	1.6	1.7							
Panicum commutatum	15.3		3.2	3.8	1.2	6.0	0.7		0.6	4.8			0.8	8.7							1.0
Rhus glabra	3.4	4.8	5.5	4.3		10.5	0.6				2.2										
Rhus copallina	5.0	19.9	20.2	27.8	3.6	21.0	0.3	4.7	9.9	7.2	10.6	2.3	1.5	8.8							
Andropogon virginicus	7.8	15.7	11.6	51.7	14.0	59.8	22.4	2.3	5.4	2.6	20.6			0.4							
Andropogon scoparius		6.7	16.6				5.2	1.8	46.4	9.3				2.9							
Rubus (*blackberry-dewberry*)	7.4	3.4	6.7	14.0	18.6	29.3	4.7	10.5	11.4	13.7	26.2	16.8	16.6	5.4	7.2	4.4		7.4	1.2		2.0
Solidago nemoralis	5.8	5.8	1.7	2.0	12.6	2.2	18.1	7.2	2.3	3.1	1.8			3.0							
Solidago juncea	0.3	0.5	1.1	4.2	1.1	15.4	3.6	8.1	6.0	3.8	9.0		0.8	2.7							
Lespedeza procumbens	5.8	7.4	5.6	9.7	3.3		1.9	10.3	23.5	3.5	1.1										
Lespedeza repens	1.7	0.6	1.9	2.8		0.4	0.7	6.3	2.8	10.7		1.0	2.4								
Danthonia spicata	4.5	21.2	0.5	2.9	18.2	1.6	8.2	16.6	4.1	18.8	4.1	4.1		1.0			1.4	0.9			
Campsis radicans			2.5				0.2	24.4	0.7												
Lyonia ligustrina				1.2							7.2		7.6	14.9							
Rhus radicans	0.3	0.6			3.0		0.9	2.1	2.3	0.4	0.4	1.0			17.5		1.4	1.8			
Liriodendron tulipifera	2.0			4.5	0.9	1.1	1.1	1.0	2.5	0.4		4.4	4.4		2.3						13.5
Vaccinium vacillans	0.8	0.6		2.2	4.7	1.3	6.3	2.6	3.0	6.8	13.8	13.7	45.8	38.4	39.8	45.6	17.4	19.7	50.4	69.4	43.0
Vaccinium stamineum			1.2	1.3		0.5		5.6	1.7	10.5	6.8	27.4	10.2	14.1	11.2	26.7	8.8	13.7	19.7	23.3	8.2
Gaylussacia baccata				0.4	0.4					2.6	13.9	3.4		26.1	3.3	36.8	13.0	17.1		38.8	16.0
Nyssa sylvatica	1.3	1.0	1.7	1.2	4.7	1.6	1.8	0.5	4.7	0.4	23.7	3.1	6.1	25.0	26.0	13.9	25.6	44.3	10.0	37.4	37.5
Acer rubrum	2.2		0.3	1.0	3.5	3.0	2.7	0.3	1.4	3.6	4.4	35.4	21.7	2.0	7.2	8.0	16.3	16.0	10.0	7.7	3.0
Carya glabra	1.8	6.0	4.5			1.9		1.4	1.1	3.3	1.5	23.8	6.3		3.3		10.2	1.8			1.0
Carya tomentosa	0.4	0.3	0.9		0.4				0.4	4.9	0.8				14.7		31.5		1.2		1.0
Cornus florida	1.5		1.2				2.0	0.3	3.9	1.7		5.4			13.6		13.4	2.6	2.0		2.6
Quercus alba	0.6	0.3		0.4	0.4			1.4	1.1	1.9	7.8	3.1	33.3		4.4		19.5	13.1	28.1	3.8	7.6
Quercus coccinea	0.4		2.0	0.9			0.3				3.8	9.7	0.8	3.7	6.6	0.9	7.5	6.0	2.4	4.2	10.7
Quercus prinus						2.0					3.9		2.3	1.8		0.9		5.3	20.4		
Sassafras albidum			1.2					2.2	0.2							2.1		9.8	16.7		14.5
Chimaphila maculata								1.1		2.0		7.2	1.6	0.4	12.4		5.8	3.7	14.5	2.1	14.9
Vaccinium-Gaylussacia Coverage (%)[b]	0.0	0.1	0.1	0.7	1.7	0.2	2.3	1.8	1.4	3.5	8.6	1.3	3.1	23.9	1.2	12.7	0.5	2.1	3.0	8.2	2.8
Site Index[c]	---	---	---	---	---	---	---	53	---	63	---	59	60	47	56	58	56	55	50	53	56

[a] Stands are arranged in order of their position along the x axis of the polar ordination (Fig. 3).
[b] Site quality is inversely correlated with the amount of *Vaccinium* and *Gaylussacia* cover (Lunt 1939, Sechrest and Cooper 1970).
[c] Loblolly pine base age 25.

Table 3. Importance values of selected species in the ground stratum of various aged pine stands.

Species	Stand Number[a]																				
	1	2	3	5	4	6	7	10	9	12	8	13	16	11	18	14	15	17	20	19	21
	Time Since Planting (yrs)																				
	1	1	1	3	3	3	5	9	6	9	5	15	18	9	19	15	16	18	22	22	22
Digitaria ischaemum	17.5		3.3																		
Lespedeza stipulacea	10.6	3.8	2.7	1.3	0.2	0.4															
Conyza canadensis	25.1	7.4	6.9	2.4	2.2	0.7															
Cassia nictitans		2.1	22.1	2.7	4.4		5.3	1.9	2.2	0.8											
Potentilla canadensis	7.9	13.1	19.9	8.8	7.2	3.9	3.7	5.6	5.5	6.4	0.4	1.0	1.6	1.7							
Panicum commutatum	15.3		3.2	3.8	1.2	6.0	0.7		0.6	4.8			0.8	8.7							1.0
Rhus glabra	3.4	4.8	5.5	4.3		10.5	0.6				2.2										
Rhus copallina	5.0	19.9	20.2	27.8	3.6	21.0	0.3	4.7	9.9	7.2	10.6	2.3	1.5	8.8							
Andropogon virginicus	7.8	15.7	11.6	51.7	14.0	59.8	22.4	2.3	5.4	2.6	20.6			0.4							
Andropogon scoparius		6.7	16.6				5.2	1.8	46.4	9.3				2.9							
Rubus (blackberry-dewberry)	7.4	3.4	6.7	14.0	18.6	29.3	4.7	10.5	11.4	13.7	26.2	16.8	16.6	5.4	7.2	4.4		7.4	1.2		2.0
Solidago nemoralis	5.8	5.8	1.7	2.0	12.6	2.2	18.1	7.2	2.3	3.1	1.8			3.0							
Solidago juncea	0.3	0.5	1.1	4.2	1.1	15.4	3.6	8.1	6.0	3.8	9.0		0.8	2.7							
Lespedeza procumbens	5.8	7.4	5.6	9.7	3.3				1.9	23.5		3.5		1.1			10.3				
Lespedeza repens	1.7	0.6	1.9	2.8		0.4	0.7	6.3	2.8	10.7		1.0	2.4								
Danthonia spicata	4.5	21.2	0.5	2.9	18.2	1.6	8.2	16.6	4.1	18.8	4.1	4.1		1.0			1.4	0.9			
Campsis radicans			2.5					24.4													
Lyonia ligustrina				1.2			0.2		0.7		7.2		7.6	14.9							
Rhus radicans	0.3	0.6			3.0		0.9	2.1	2.3	0.4	0.4	1.0			17.5		1.4	1.8			
Liriodendron tulipifera	2.0			4.5	0.9	1.1	1.1	1.0	2.5	0.4		4.4	4.4		2.3						13.5
Vaccinium vacillans	0.8	0.6		2.2	4.7	1.3	6.3	2.6	3.0	6.8	13.8	13.7	45.8	38.4	39.8	45.6	17.4	19.7	50.4	69.4	43.0
Vaccinium stamineum			1.2	1.3		0.5		5.6	1.7	10.5	6.8	27.4	10.2	14.1	11.2	26.7	8.8	13.7	19.7	23.3	8.2
Gaylussacia baccata				0.4	0.4					2.6	13.9	3.4		26.1	3.3	36.8	13.0	17.1		38.8	16.0
Nyssa sylvatica	1.3	1.0	1.7	1.2	4.7	1.6	1.8	0.5	4.7	0.4	23.7	3.1	6.1	25.0	26.0	13.9	25.6	44.3	10.0	37.4	37.5
Acer rubrum	2.2		0.3	1.0	3.5	3.0	2.7	0.3	1.4	3.6	4.4	35.4	21.7	2.0	7.2	8.0	16.3	16.0	10.0	7.7	3.0
Carya glabra	1.8	6.0	4.5			1.9		1.4	1.1	3.3	1.5	23.8	6.3		3.3		10.2	1.8			1.0
Carya tomentosa	0.4	0.3	0.9		0.4				0.4	4.9	0.8						31.5	14.7	1.2		1.0
Cornus florida	1.5		1.2				2.0	0.3	3.9	1.7		5.4			13.6		13.4	2.6	2.0		2.6
Quercus alba	0.6	0.3		0.4	0.4			1.4	1.1	1.9	7.8	3.1	33.3		4.4		19.5	13.1	28.1	3.8	7.6
Quercus coccinea	0.4		2.0	0.9			0.3				3.8	9.7	0.8	3.7	6.6	0.9	7.5	6.0	2.4	4.2	10.7
Quercus prinus						0.2					3.9		2.3	1.8		0.9		5.3	20.4		
Sassafras albidum			1.2					2.2	0.2							2.1		9.8	16.7		14.5
Chimaphila maculata								1.1		2.0		7.2	1.6	0.4	12.4		5.8	3.7	14.5	2.1	14.9
Vaccinium-Gaylussacia Coverage (%)[b]	0.0	0.1	0.1	0.7	1.7	0.2	2.3	1.8	1.4	3.5	8.6	1.3	3.1	23.9	1.2	12.7	0.5	2.1	3.0	8.2	2.8
Site Index[c]	---	---	---	---	---	---	---	53	---	63	---	59	60	47	56	58	56	55	50	53	56

[a] Stands are arranged in order of their position along the x axis of the polar ordination (Fig. 3).
[b] Site quality is inversely correlated with the amount of *Vaccinium* and *Gaylussacia* cover (Lunt 1939, Sechrest and Cooper 1970).
[c] Loblolly pine base age 25.

(Korean lespedeza), Conyza canadensis (horseweed), and a perennial, Panicum commutatum (panic grass), along with appreciably lower IVs for three successionally more advanced species-- Rhus copallina, Andropogon virginicus, and A. scoparius (little bluestem). Stand 2 was differentiated by a distinctly higher IV for Danthonia spicata (poverty grass).

In general, the species-stand pattern of IVs in Table 3, i.e., the annual to perennial to woody species progression, and the gradual change from species typical of old fields to those associated with the understories of pine plantations, denoted an ordering of stands along a temporal gradient. Deviations from the expected ordering by age were interpreted as follows: (1) The offsetting of stand 1 (C7-10) from the other one-year-old stands, may have been related to its later dates of site preparation and planting (Fig. 3, Table 1), and its more complete isolation, in contrast to stands 2 and 3, from areas occupied by mature old-field perennial species. (2) According to age, the order of stands 9 and 10 should have been reversed. The determining factor in their placement was the relatively large IV for Andropogon scoparius in stand 9. If A. scoparius had been lumped with A. virginicus, stand 9 would have appeared more like stand 7 in composition and thus, may have preceded stand 10. (3) Stands 8 and 11 are positioned well beyond their expected rank based on age. The relatively xeric conditions in these stands (site index 47 for stand 11), probably accounts for the abundant ericaceous cover (Table 3). Lunt (1939) and Sechrest and Cooper (1970) found that site quality is inversely correlated with the amount of _Vaccinium_ and _Gaylussacia_ cover. Together with _Nyssa sylvatica_, this was the same type of cover which dominated stands 15 to 22 years of age. Thus stands 8 and 11 appeared compositionally more advanced than their age would indicate, and they were ranked amongst the older stands. With the exclusion of stands 8 and 11, the order and age of stands within the ericaceous- _Nyssa_ phase of succession were: 13 (15 yrs), 16 (18 yrs), 18 (19 yrs), 14 (15 yrs), 15 (16 yrs), 17 (18 yrs), 20 (22 yrs), 19 (21-22 yrs), and 21 (22 yrs). The tight clustering of stands 14, 15, 17, and 18 (Fig. 3), despite differences in age and ericaceous cover (Table 3), as well as the general mixing of stands aged 15 to 19 years, implied that within the ground stratum: (i) vegetational development had become less dependent on site conditions; and (ii) successional changes were so subtle that stands aged 15 to 19 years could not be clearly differentiated.

5.2 STRUCTURAL DIFFERENCES AMONG STANDS

Ordination results showed that pine plantations similar in age could be appreciably different in vegetational composition within the ground stratum. Statistical tests were subsequently employed to determine whether structural differences among similarly aged stands within various age classes were significantly great to mask differences among age classes, thereby precluding the ability to discern successional trends.

Mean values computed for a diverse group of habitat structural variables are presented in Tables 4 to 7 according to age class, i.e., time since planting with loblolly pine. Changes in each variable over time were tested using a nested analysis of variance statistical design (0.05 level of significance). Variation among stands within classes was highly significant in nearly all cases. Exceptions included moss, fungi, and lichen coverages (Table 4), and vegetative density in certain profile layers in summer and winter (Table 7). However, variation among classes was significant in nearly all tests as well, i.e., the aging process had associated with it structural differences among classes which were discernable despite the heterogeneity among stands within classes. Exceptions were woody debris, moss, fungi, and rock coverages, and ground stratum tree density and coverage (Table 4).

Table 4. Mean values[a] of habitat structural variables for the ground stratum of various aged pine stands.

Variables	Level of Significance[b]: Among Age Classes	Level of Significance[b]: Among Stands Within Classes	Time Since Planting (yrs): 1	3	5	9	15	18	22
Vascular Plant			A	B	AB	C	D	D	D
Coverage (%)	P < .001 (S)	P < .001 (S)	79.4	64.1	65.6	43.2	9.8	7.9	11.1
Grass			A	A	A	B	B	B	B
Coverage (%)	P < .001 (S)	P < .001 (S)	27.1	28.4	22.8	5.6	0.0	0.0	0.0
Litter			D	CD	C	B	A	A	A
Coverage (%)	P < .001 (S)	P < .001 (S)	1.3	13.2	17.1	41.6	79.2	83.3	79.8
Bare Soil			A	AB	B	B	B	B	B
Coverage (%)	.01 < P < .025 (S)	P < .001 (S)	8.5	3.9	1.1	0.9	0.0	0.0	0.0
Woody Debris									
Coverage (%)	P > .75 (NS)	P < .001 (S)	4.5	5.4	5.3	4.4	5.0	4.0	4.2
Moss									
Coverage (%)	.05 < P < .10 (NS)	.25 < P < .50 (NS)	0.1	0.4	0.3	0.4	0.1	0.1	0.1
Fungi									
Coverage (%)	.50 < P < .75 (NS)	.50 < P < .75 (NS)	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Lichen			B	B	A	A	B	B	AB
Coverage (%)	.01 < P < .025 (S)	.10 < P < .25 (NS)	0.0	0.0	0.2	0.2	0.0	0.0	0.1
Rock									
Coverage (%)	.25 < P < .50 (NS)	P < .001 (S)	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Litter			C	BC	B	B	A	A	A
Depth (cm)	P < .001 (S)	P < .001 (S)	0.1	0.9	2.0	2.3	4.2	4.5	4.4
Tree									
Density[c]									
(no./ha)	.25 < P < .50 (NS)	.001 < P < .005 (S)	16833	10083	20417	15917	21000	17417	15500
Tree									
Coverage[c] (%)	.10 < P < .25 (NS)	P < .001 (S)	7.6	3.8	10.0	5.6	4.3	4.1	5.0
Areal Species									
Richness			A	A	A	A	B	B	B
(no./quadrat)	P < .001 (S)	P < .001 (S)	10.2	9.0	9.8	8.0	2.8	3.4	2.6

[a] Values were computed from a sample size of 120, i.e., 40 quadrats per stand, and three stands per age class.

[b] Means were tested at the 0.05 level of significance using a nested ANOVA design. P-values indicate the margin of acceptance (NS) or rejection (S). When variation among classes was found to be significant, means were tested using the Waller-Duncan multiple comparison procedure with a k-ratio value of 100; means with the same letter are not significantly different.

[c] Tree values were based only on those species which were also present in the overstory stratum.

Table 5. Mean values[a] of habitat structural variables for the transgressive stratum of various aged pine stands.

Variables	Level of Significance[b]		Time Since Planting (yrs)						
	Among Age Classes	Among Stands Within Classes	1	3	5	9	15	18	22
Transgressive Coverage (%)	$.001 < P < .005$ (S)	$P < .001$ (S)	C 7.6	B 21.9	AB 26.6	AB 28.9	A 37.7	AB 28.1	B 24.9
Transgressive Density (no/ha)	$.025 < P < .05$ (S)	$P < .001$ (S)	B 2854	AB 7594	A 10474	A 10906	A 10677	A 8464	AB 5901
Areal Species Richness (no./quadrat)	$P < .001$ (S)	$P < .001$ (S)	D 1.6	BC 4.1	ABC 5.0	A 6.2	AB 5.4	ABC 5.0	C 3.7

[a,b] Refer to Table 4.

Table 6. Mean values[a] of habitat structural variables for the overstory stratum of various aged pine stands.

Variables	Level of Significance[b]: Among Age Classes	Level of Significance[b]: Among Stands Within Classes	Time Since Planting (yrs): 1	3	5	9	15	18	22
Overstory			C	C	C	B	A	A	A
Basal Area[c] (m^2/ha)	P < .001 (S)	P < .001 (S)	0.00	0.29	5.42	15.72	33.04	38.47	32.31
Loblolly Pine			D	D	D	C	AB	A	B
Basal Area (m^2/ha)	P < .001 (S)	P < .001 (S)	0.00	0.24	4.70	13.73	27.11	30.67	22.34
Hardwood			B	B	B	B	A	A	A
Basal Area (m^2/ha)	P < .001 (S)	P < .001 (S)	0.00	0.03	0.14	1.40	4.54	5.22	4.62
Other Pines			B	B	B	B	B	AB	A
Basal Area[d] (m^2/ha)	.01 < P < .025 (S)	P < .001 (S)	0.00	0.03	0.58	0.60	1.39	2.58	5.34
Overstory			E	E	D	C	A	A	B
Density[c] (no./ha)	P < .001 (S)	P < .001 (S)	0	373	2030	2797	5087	5277	4070
Loblolly Pine			C	C	AB	AB	A	A	B
Density (no./ha)	P < .001 (S)	P < .001 (S)	0	313	1447	1503	1887	1810	1023
Hardwood			D	D	D	C	A	A	B
Density (no./ha)	P < .001 (S)	P < .001 (S)	0	30	160	1010	2930	3013	2233
Other Pines			B	B	AB	AB	AB	AB	A
Density[d] (no./ha)	.025 < P < .05 (S)	P < .001 (S)	0	30	423	283	270	453	813
Dead Tree			B	B	B	B	B	A	A
Basal Area (m^2/ha)	.001 < P < .005 (S)	P < .001 (S)	0.00	0.00	0.00	0.12	0.27	0.77	0.83
Dead Tree			B	B	B	B	B	A	A
Density (no./ha)	.001 < P < .005 (S)	P < .001 (S)	0	0	0	37	193	487	497
Canopy			D	D	C	B	A	A	AB
Closure[e] (%)	P < .001 (S)	P < .001 (S)	0.0	6.8	39.7	74.6	88.8	93.1	85.6
Pine Canopy			C	C	B	B	A	A	A
Closure[f] (%)	P < .001 (S)	P < .001 (S)	0.0	3.4	32.9	44.6	71.6	73.5	71.5
Areal Species									
Richness			D	D	C	B	A	A	A
(no./quadrat)	P < .001 (S)	P < .001 (S)	0.0	0.6	1.7	2.6	4.8	5.0	4.4

[a] Values were computed from a sample size of 120, i.e., 40 quadrats per stand, and three stands per age class, except for canopy closure variables which are based on 60 estimates per class.

[b] Refer to Table 4

[c] The overstory is comprised of loblolly, hardwoods, and other pines.

[d] Other pines are Virginia and shortleaf.

[e] Canopy closure represents overhead vegetative coverage; it is primarily a measure of overstory development.

[f] Pine canopy closure represents overhead coverage from pines only; it was estimated in winter.

ERRATUM

Table 7. Mean Vegetative density (%)[a] at successive strata between ground level and two meters above the ground in various aged pine stands.

Stratum	Level of Significance[b]: Among Age Classes	Among Stands Within Classes	Time Since Planting (yrs): 1	3	5	9	15	18	22
			Summer						
0-0.2 m	P < .001 (S)	P < .001 (S)	A 94.5	A 95.0	A 93.7	A 83.7	B 40.7	B 29.0	B 27.8
0.4-0.6 m	P < .001 (S)	.25 < P < .50 (NS)	B 60.5	A 72.0	A 72.3	C 42.5	D 22.8	DE 14.0	E 12.5
0.9-1.1 m	P < .001 (S)	.05 < P < .10 (NS)	C 22.2	B 41.2	A 67.2	B 40.2	C 17.8	C 15.3	C 15.2
1.4-1.6 m	P < .001 (S)	.01 < P < .025 (S)	D 6.2	C 19.2	A 48.8	B 36.2	CD 17.7	C 19.5	C 19.0
1.9-2.1 m	P < .001 (S)	.10 < P < .25 (NS)	D 5.0	CD 10.3	A 47.0	A 44.5	B 25.7	BC 20.0	BC 20.3
Mean for 5 Strata	-------	-------	37.7	47.5	65.8	49.4	24.9	19.6	19.0
Equitability[c] (Shannon-Wiener)	P < .001 (S)	.10 < P < .25 (NS)	C 1.02	B 1.20	A 1.40	A 1.37	A 1.36	A 1.42	A 1.34
			Winter						
0-0.2 m	P < .001 (S)	P < .001 (S)	AB 62.0	A 72.3	AB 57.0	BC 34.8	C 14.7	C 10.7	C 12.3
0.4-0.6 m	P < .001 (S)	.05 < P < .10 (NS)	BC 14.8	A 34.3	B 21.3	BC 12.3	C 11.8	C 9.5	C 9.5
0.9-1.1 m	P < .001 (S)	.01 < P < .025 (S)	C 5.7	B 16.2	A 28.2	BC 11.0	BC 9.8	BC 8.7	BC 8.5
1.4-1.6 m	P < .001 (S)	P > .75 (NS)	D 5.0	B 13.0	A 33.2	BC 10.0	CD 8.5	CD 8.0	CD 7.8
1.9-2.1 m	P < .001 (S)	.001 < P < .005 (S)	B 5.0	B 9.3	A 32.8	B 10.8	B 8.5	B 8.0	B 7.5
Mean for 5 Strata	-------	-------	18.5	29.0	34.5	15.8	10.7	9.0	9.1
Equitability[c] (Shannon-Wiener)	P < .001 (S)	P < .001 (S)	E 1.07	DE 1.13	DC 1.30	BC 1.35	AB 1.52	A 1.56	A 1.57

[a] Values were computed from a sample size of 60, i.e., 20 estimates per stand, and three stands per age class. Estimates were made of living vegetation in summer, and living/recently dead (from previous summer) in winter.

[b] Refer to Table 4

[c] Profile Equitability $= -\sum_{i=1}^{5} P_i \ln P_i$, where $P_i = N_i/N$ and N = summation of vegetative densitites for the five strata (N_1 to N_5)

Table 7. Vegetative density (%)[a] at successive strata between ground level and two meters above the ground in various aged pine stands.

Stratum	Level of Significance[b]: Among Age Classes	Level of Significance[b]: Among Stands Within Classes	Time Since Planting (yrs): 1	3	5	9	15	18	22
			Summer						
0-0.2 m	P < .001 (S)	P < .001 (S)	A 94.5	A 95.0	A 93.7	A 83.7	B 40.7	B 29.0	B 27.8
0.4-0.6 m	P < .001 (S)	.25 < P < .50 (NS)	B 60.5	A 72.0	A 72.3	C 42.5	D 22.8	DE 14.0	E 12.5
0.9-1.1 m	P < .001 (S)	.05 < P < .10 (NS)	C 22.2	B 41.2	A 67.2	B 40.2	C 17.8	C 15.3	C 15.2
1.4-1.6 m	P < .001 (S)	.01 < P < .025 (S)	D 6.2	C 19.2	A 48.8	B 36.2	CD 17.7	C 19.5	C 19.0
1.9-2.1 m	P < .001 (S)	.10 < P < .25 (NS)	D 5.0	CD 10.3	A 47.0	A 44.5	B 25.7	BC 20.0	BC 20.3
Mean for 5 Strata	-------	-------	37.7	47.5	65.8	49.4	24.9	19.6	19.0
Equitability[c] (Shannon-Wiener)	P < .001 (S)	.10 < P < .25 (NS)	C 1.02	B 1.20	A 1.40	A 1.37	A 1.36	A 1.42	A 1.34
			Winter						
0-0.2 m	P < .001 (S)	P < .001 (S)	AB 62.0	A 72.3	AB 57.0	BC 34.8	C 14.7	C 10.7	C 12.3
0.4-0.6 m	P < .001 (S)	.05 < P < .10 (NS)	BC 14.8	A 34.3	B 21.3	BC 12.3	C 11.8	C 9.5	C 9.5
0.9-1.1 m	P < .001 (S)	.01 < P < .025 (S)	C 5.7	B 16.2	A 28.2	BC 11.0	BC 9.8	BC 8.7	BC 8.5
1.4-1.6 m	P < .001 (S)	P > .75 (NS)	D 5.0	B 13.0	A 33.2	BC 10.0	CD 8.5	CD 8.0	CD 7.8
1.9-2.1 m	P < .001 (S)	.001 < P < .005 (S)	B 5.0	B 9.3	A 32.8	B 10.8	B 8.5	B 8.0	B 7.5
Mean for 5 Strata	-------	-------	18.5	29.0	34.5	15.8	10.7	9.0	9.1
Equitability[c] (Shannon-Wiener)	P < .001 (S)	P < .001 (S)	E 1.07	DE 1.13	DC 1.30	BC 1.35	AB 1.52	A 1.56	A 1.57

[a] Values were computed from a sample size of 60, i.e., 20 estimates per stand, and three stands per age class. Estimates were made of living vegetation in summer, and living/recently dead (from previous summer) in winter.

[b] Refer to Table 4

[c] Profile Equitability = $-\sum_{i=1}^{5} Pi \ln Pi$, where $Pi = Ni/N$ and N = summation of vegetative densitites for the five strata (N_1 to N_5)

For variables with significant differences among classes, a Waller-Duncan k-ratio t-test was used to compare means for the purpose of distinguishing where major changes occurred during succession. Results of the multiple comparison procedure (Tables 4 to 7) indicated a strong similarity among 1- and 3-year-old classes, and among 15-, 18-, and 22-year-old classes. Significant structural differences most often occurred between classes aged 9 and 15 years, followed by those aged 5 and 9 years, and finally by those aged 3 and 5 years. By integrating these results with those obtained from the ordination analysis, the development of converted stands could be described as a progression from an old-field phase (1 to 3 yrs) to a transitional phase (3 to 15 yrs) to a pine woodland phase (15 to 22 yrs).

At the state forests, natural forest stands are categorized as hardwood or natural pine-hardwood. Over the years these natural forest areas have been repeatedly thinned, especially the pine component, as a result of the shortleaf pine bark beetle infestation of the 1960's. Six natural forest stands, including three hardwood and three natural pine-hardwood stands, were selected with the intention of comparing pre-conversion sites, both compositionally and structurally, with the pine plantation sere. Before making this comparison, nested ANOVA tests were performed to detect any significant structural differences between the hardwood and natural pine-hardwood classes. Although significant variation with regard to structural variables was found among stands within classes, no significant differences were found between classes (Tables 8 to 11). As a result, mean values used for natural forest variables in the ensuing analyses were computed from the means of six stands. In contrast, the mean value used for each plantation age-class variable was calculated from the means of the three similarly aged stands within that class.

5.3 DESCRIPTIONS OF INDIVIDUAL DEVELOPMENTAL STAGES

5.3.1 Year 1

Noticeably high values of total vascular plant coverage (Fig. 4) and species richness (Fig. 5) were evident one year (second summer) following planting with loblolly pine. The proliferation of herbaceous plants accounted for these high levels (Fig. 6, Tables 12 and 13). In contrast to the pre-conversion natural forest stands, total vascular plant and grass coverages were substantially greater in the

Table 8. Mean values[a] of habitat structural variables for the ground stratum of hardwood and pine-hardwood forest stands.

Variables	Level of Significance[b]: Between Classes	Level of Significance[b]: Among Stands Within Classes	Class: Hardwood	Class: Pine-Hardwood
Vascular Plant Coverage (%)	.05 < P < .10 (NS)	.001 < P < .005 (S)	13.2	22.4
Grass Coverage (%)	P > .75 (NS)	.10 < P < .25 (NS)	0.2	0.2
Litter Coverage (%)	.10 < P < .25 (NS)	.001 < P < .005 (S)	75.5	66.2
Bare Soil Coverage (%)	.25 < P < .50 (NS)	.025 < P < .05 (S)	2.0	0.1
Woody Debris Coverage (%)	P > .75 (NS)	.05 < P < .10 (NS)	3.8	3.5
Moss Coverage (%)	.25 < P < .50 (NS)	P > .75 (NS)	0.4	0.6
Fungi Coverage (%)	.50 < P < .75 (NS)	.01 < P < .025 (S)	0.0	0.0
Lichen Coverage (%)	P > .75 (NS)	.05 < P < .10 (NS)	0.2	0.2
Rock Coverage (%)	.25 < P < .50 (NS)	.10 < P < .25 (NS)	0.0	0.0
Litter Depth (cm)	.05 < P < .10 (NS)	P < .001 (S)	3.0	4.3
Tree Density (no/ha)	.50 < P < .75 (NS)	P < .001 (S)	45250	52500
Tree Coverage (%)	.10 < P < .25 (NS)	.10 < P < .25 (NS)	8.4	11.3
Areal Species Richness (no./quadrat)	P > .75 (NS)	P < .001 (S)	4.6	4.8

[a]Values were computed from a sample size of 120, i.e., 40 quadrats per stand, and three stands per class.

[b]Means were tested at the 0.05 level of significance using a nested ANOVA design. P-values indicate the margin of acceptance (NS) or rejection (S).

Table 9. Mean values[a] of habitat structural variables for the transgressive stratum of hardwood and pine-hardwood forest stands.

Variables	Level of Significance[b]		Class	
	Between Classes	Among Stands Within Classes	Hardwood	Pine-Hardwood
Transgressive Coverage (%)	$P > .75$ (NS)	$.01 < P < .029$ (S)	16.1	15.7
Transgressive Density (no./ha)	$.25 < P < .50$ (NS)	$P < .001$ (S)	4609	5427
Areal species Richness (no./quadrat)	$P > .75$ (NS)	$P < .001$ (S)	3.2	3.2

[a,b] Refer to Table 8.

Table 10. Mean values[a] of habitat structural variables for the overstory stratum of hardwood and pine-hardwood forest stands.

Variables	Level of Significance[b]: Between Classes	Level of Significance[b]: Among Stands Within Classes	Class: Hardwood	Class: Pine-Hardwood
Overstory Basal Area (m^2/ha)	$.50 < P < .75$ (NS)	$.50 < P < .75$ (NS)	27.14	26.05
Hardwood Basal Area (m^2/ha)	$.10 < P < .25$ (NS)	$.10 < P < .25$ (NS)	25.19	19.31
Pine Basal Area[c] (m^2/ha)	$.05 < P < .10$ (NS)	$.001 < P < .005$ (S)	1.95	6.74
Overstory Density (no./ha)	$.10 < P < .25$ (NS)	$.01 < P < .025$ (S)	1668	1448
Hardwood Density (no./ha)	$.05 < P < .10$ (NS)	$.01 < P < .025$ (S)	1620	1293
Pine Density[c] (no./ha)	$.05 < P < .10$ (NS)	$.001 < P < .005$ (S)	48	155
Dead Tree Basal Area ($no.^2$/ha)	$.25 < P < .50$ (NS)	$.25 < P < .50$ (NS)	0.79	1.13
Dead Tree Density (no./ha)	$P > .75$ (NS)	$.25 < P < .50$ (NS)	187	185
Canopy Closure (%)	$.05 < P < .10$ (NS)	$.25 < P < .50$ (NS)	93.2	90.8
Areal Species Richness (no./quadrat)	$.25 < P < .50$ (NS)	$.01 < P < .025$ (S)	2.7	2.5

[a] Values were computed from a sample size of 240, i.e., 80 quadrats per stand, and three stands per class, except for canopy closure which was based on 60 estimates per class.

[b] Refer to Table 8.

[c] Pine includes Virginia and shortleaf.

Table 11. Vegetative density (%)[a] at successive strata between ground level and two meters above the ground in hardwood and pine-hardwood forest stands.

Stratum	Level of Significance[b]: Between Classes	Level of Significance[b]: Among Stands Within Classes	Class: Hardwood	Class: Pine-Hardwood
			Summer	
0-0.2 m	$.05 < P < .10$ (NS)	$.001 < P < .005$ (S)	28.0	53.0
0.4-0.6 m	$.50 < P < .75$ (NS)	$.10 < P < .25$ (NS)	15.7	17.5
0.9-1.1 m	$.25 < P < .50$ (NS)	$.10 < P < .25$ (NS)	20.7	15.2
1.4-1.6 m	$.10 < P < .25$ (NS)	$.50 < P < .75$ (NS)	18.2	12.7
1.9-2.1 m	$.10 < P < .25$ (NS)	$.50 < P < .75$ (NS)	22.7	16.0
Mean for 5 Strata	-------	--------	21.0	22.9
Equitability[c] (Shannon-Wiener)	$.25 < P < .50$ (NS)	$.01 < P < .025$ (S)	1.34	1.26
			Winter	
0-0.2 m	$.05 < P < .10$ (NS)	$.10 < P < .25$ (NS)	7.3	16.8
0.4-0.6 m	$.50 < P < .75$ (NS)	$.10 < P < .25$ (NS)	6.5	7.5
0.9-1.1 m	$.10 < P < .25$ (NS)	$.01 < P < .025$ (S)	5.5	8.5
1.4-1.6 m	$.10 < P < .25$ (NS)	$.25 < P < .50$ (NS)	5.7	8.8
1.9-2.1 m	$.10 < P < .25$ (NS)	$.50 < P < .75$ (NS)	5.5	8.0
Mean for 5 Strata	-------	--------	6.1	9.9
Equitability[c] (Shannon-Wiener)	$.05 < P < .10$ (NS)	$.01 < P < .025$ (S)	1.59	1.48

[a] Values were computed from a sample size of 60; i.e., 20 estimates per stand, and three stands per class.
[b] Refer to Table 8.
[c] Refer to Table 7.

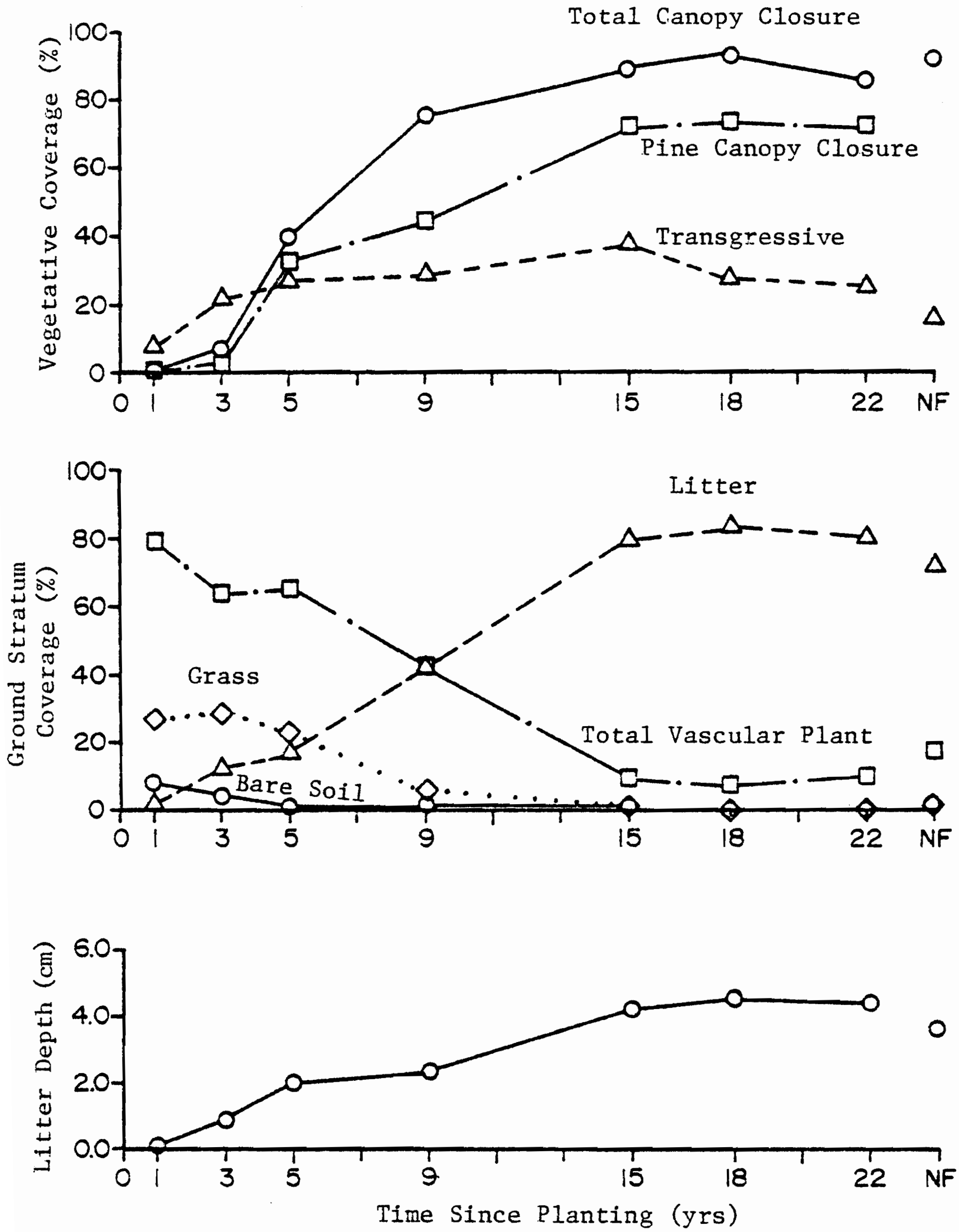


Fig. 4. Trends in selected structural variables (mean values) in pine plantations as a function of time since planting; natural forest values (NF) are presented for comparison.

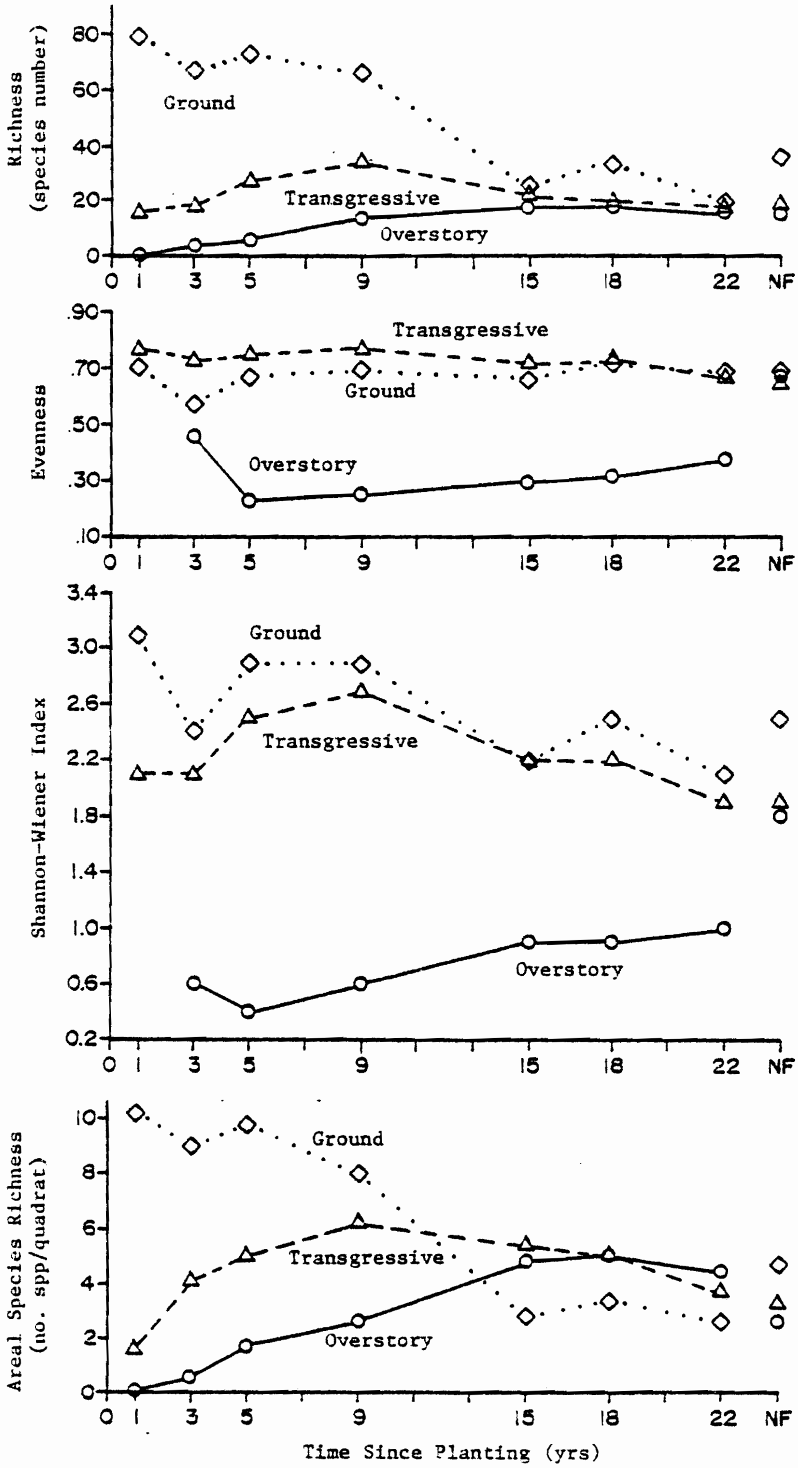


Fig. 5. Trends in richness, evenness, and diversity (mean values) for various strata within pine plantations as a function of time since planting; natural forest values (NF) are presented for comparison.

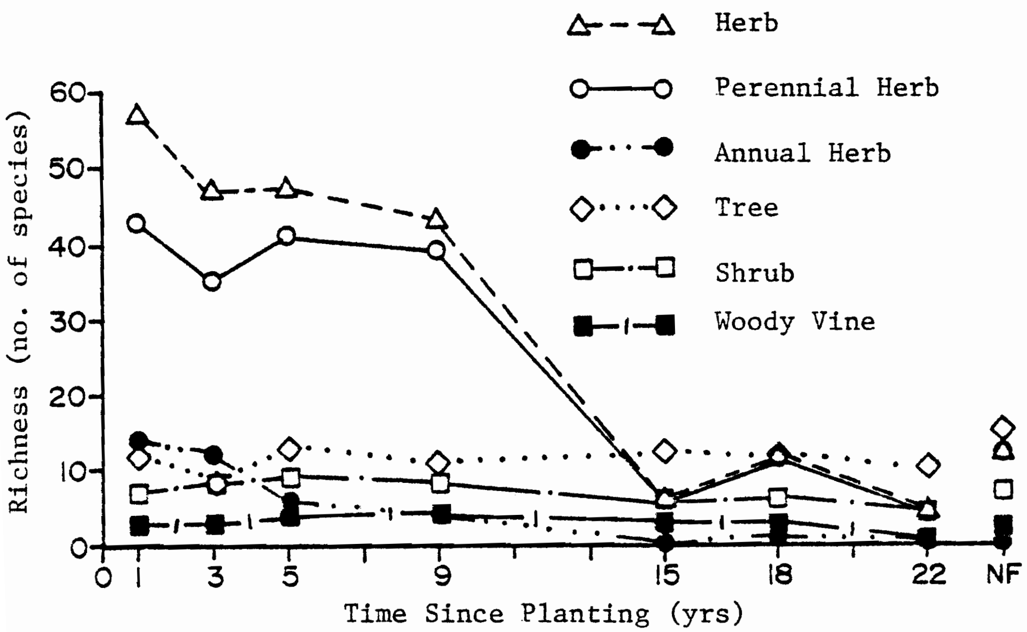


Fig. 6. Trends in species richness (mean values) of various plant life forms found in the ground stratum of pine plantations as a function of time since planting; natural forest values (NF) are presented for comparison.

Table 12. Species richness[a] of plant life forms[b] found in the ground stratum of various aged pine plantations and natural forest stands.

Life Form	Pine Plantations: Time Since Planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 Years
Tree	12	9	13	11	12	12	10	15
Shrub	7	8	9	8	5	6	5	7
Woody Vine	3	3	4	4	3	3	1	2
Herb	57	47	47	43	6	12	4	12
Fern	0	0	1	1	1	t	t	t
Clubmoss	0	0	t	0	0	0	0	t
Graminoid	16	13	11	11	1	1	1	3
Annual	2	1	1	1	0	0	0	t
Perennial	14	12	10	10	1	1	1	3
Forb	41	34	35	31	4	11	3	9
Annual-Biennial	12	11	5	3	0	1	0	0
Perennial	29	23	30	28	4	10	3	9
Total Woody Plants	22	20	26	23	20	21	16	24
All Life Forms	79	67	73	66	26	33	20	36

[a]Species richness values are rounded-off means; values appreciably less than one are signified by "t".

[b]Plant life form designations for individual species are presented in Appendix Table I.

Table 13. Mean coverage and frequency of selected plant species[a] found in the ground stratum of various aged pine plantations and natural forest stands.

Species	Coverage (%) Pine Plantations Time Since Planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 yrs	Frequency (%) Pine Plantations Time Since Planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 yrs
Erechtites hieracifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Digitaria ischaemum	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Conyza canadensis	4.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	69.2	15.0	0.0	0.0	0.0	0.0	0.0	0.0
Ambrosia artemisiifolia	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	9.2	6.7	0.8	0.0	0.0	0.0	0.0	0.0
Eupatorium spp.	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Potentilla canadensis	4.4	0.8	0.3	0.2	0.0	0.0	0.0	0.0	70.0	48.3	30.8	33.3	0.8	1.7	0.0	2.9
Aster spp.	0.7	1.1	0.6	0.3	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Desmodium spp.	0.5	0.0	2.4	0.5	0.0	0.0	0.0	0.1	---	---	---	---	---	---	---	---
Panicum spp.	4.9	4.3	2.3	0.8	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Rhus glabra	2.1	2.0	0.3	0.0	0.0	0.0	0.0	0.0	15.8	10.0	3.3	0.0	0.0	0.0	0.0	0.0
Rhus copallina	7.4	7.1	2.2	1.4	0.0	0.0	0.0	0.0	40.8	44.2	26.7	20.0	0.8	0.8	0.0	0.4
Rubus (*blackberry-dewberry*)	1.8	7.4	4.1	1.2	0.1	0.3	0.0	0.0	33.3	67.5	56.7	45.8	16.7	24.2	2.5	3.4
Andropogon virginicus	4.8	18.7	6.7	0.2	0.0	0.0	0.0	0.0	47.5	80.0	38.3	8.3	0.0	0.0	0.0	0.0
Andropogon scoparius	3.5	0.0	8.5	1.1	0.0	0.0	0.0	0.0	22.5	0.0	32.5	5.0	0.0	0.0	0.0	0.4
Solidago spp.	1.4	2.8	3.9	1.3	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Lespedeza spp.	6.5	2.0	4.0	1.8	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Danthonia spicata	4.2	3.0	1.3	2.4	0.0	0.0	0.0	0.1	30.8	27.5	32.5	33.3	4.2	0.8	0.0	7.0
Vaccinium vacillans	0.0	0.8	2.2	4.2	1.5	1.2	2.7	2.2	4.2	14.2	31.7	40.8	46.7	65.8	77.5	53.8
Gaylussacia baccata	0.0	0.0	1.0	2.8	1.8	0.3	0.8	2.3	0.0	1.7	16.7	19.2	20.8	9.2	29.2	20.8
Vaccinium stamineum	0.0	0.1	0.9	2.7	1.5	0.6	1.1	2.0	3.3	4.2	9.2	16.7	21.7	12.5	16.7	26.6
Nyssa sylvatica	0.4	0.7	3.5	2.4	0.8	1.2	2.1	2.2	8.3	12.5	25.8	21.7	15.0	27.5	23.3	20.2
Acer rubrum	0.4	0.6	0.8	0.1	0.4	0.3	0.3	1.2	3.3	13.3	12.5	11.7	37.5	38.3	10.8	43.8
Carya glabra	1.6	0.2	0.3	0.3	0.4	0.2	0.0	0.4	17.5	2.5	3.3	3.3	8.3	5.8	0.8	7.0
Carya tomentosa	0.2	0.0	0.0	0.3	0.3	0.2	0.0	0.8	2.5	0.8	2.5	3.3	5.8	5.8	1.7	8.6
Quercus alba	0.0	0.0	0.9	0.2	0.2	1.0	0.7	1.3	2.5	1.7	8.3	1.7	6.7	19.2	12.5	39.2
Quercus coccinea	0.3	0.1	0.4	0.4	0.2	0.1	0.3	0.9	3.3	0.8	5.0	2.5	5.0	7.5	7.5	24.2
Quercus velutina	0.2	0.0	0.1	0.0	0.1	0.1	0.3	1.2	1.7	0.8	1.7	0.0	7.5	4.2	5.0	17.1
Sassafras albidum	0.1	0.0	0.0	0.1	0.0	0.2	0.5	0.2	1.7	0.0	0.8	3.3	1.7	4.2	12.5	8.3
Chimaphila maculata	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	8.3	9.2	15.0	24.2	10.4
Cypripedium acaule	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	1.7	3.3	4.2	0.4

[a]Selected species had a mean IV (relative frequency + relative cover) $\geq$ 10 for at least one plantation stage or natural forest class. Exceptions were: *Erechtites hieracifolia*, *Digitaria ischaemum*, *Ambrosia artemisiifolia*, *Eupatorium* spp., *Aster* spp., *Desmodium* spp., *Rhus glabra*, and *Cypripedium acaule*.

Table 13. Mean coverage and frequency of selected plant species[a] found in the ground stratum of various aged pine plantations and natural forest stands.

Species	Coverage (%) Pine Plantations Time Since Planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 yrs	Frequency (%) Pine Plantations Time Since Planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 yrs
Erechtites hieracifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Digitaria ischaemum	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Conyza canadensis	4.6	0.1	0.0	0.0	0.0	0.0	0.0	0.0	69.2	15.0	0.0	0.0	0.0	0.0	0.0	0.0
Ambrosia artemisiifolia	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	9.2	6.7	0.8	0.0	0.0	0.0	0.0	0.0
Eupatorium spp.	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Potentilla canadensis	4.4	0.8	0.3	0.2	0.0	0.0	0.0	0.0	70.0	48.3	30.8	33.3	0.8	1.7	0.0	2.9
Aster spp.	0.7	1.1	0.6	0.3	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Desmodium spp.	0.5	0.0	2.4	0.5	0.0	0.0	0.0	0.1	---	---	---	---	---	---	---	---
Panicum spp.	4.9	4.3	2.3	0.8	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Rhus glabra	2.1	2.0	0.3	0.0	0.0	0.0	0.0	0.0	15.8	10.0	3.3	0.0	0.0	0.0	0.0	0.0
Rhus copallina	7.4	7.1	2.2	1.4	0.0	0.0	0.0	0.0	40.8	44.2	26.7	20.0	0.8	0.8	0.0	0.4
Rubus (blackberry-dewberry)	1.8	7.4	4.1	1.2	0.1	0.3	0.0	0.0	33.3	67.5	56.7	45.8	16.7	24.2	2.5	3.4
Andropogon virginicus	4.8	18.7	6.7	0.2	0.0	0.0	0.0	0.0	47.5	80.0	38.3	8.3	0.0	0.0	0.0	0.0
Andropogon scoparius	3.5	0.0	8.5	1.1	0.0	0.0	0.0	0.0	22.5	0.0	32.5	5.0	0.0	0.0	0.0	0.4
Solidago spp.	1.4	2.8	6.9	1.3	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Lespedeza spp.	6.5	2.0	4.0	1.8	0.0	0.0	0.0	0.0	---	---	---	---	---	---	---	---
Danthonia spicata	4.2	3.0	1.3	2.4	0.0	0.0	0.0	0.1	30.8	27.5	32.5	33.3	4.2	0.8	0.0	7.0
Vaccinium vacillans	0.0	0.8	2.2	4.2	1.5	1.2	2.7	2.2	4.2	14.2	31.7	40.8	46.7	65.8	77.5	53.8
Gaylussacia baccata	0.0	0.0	1.0	2.8	1.8	0.3	0.8	2.3	0.0	1.7	16.7	19.2	20.8	9.2	29.2	20.8
Vaccinium stamineum	0.0	0.1	0.9	2.7	1.5	0.6	1.1	2.0	3.3	4.2	9.2	16.7	21.7	12.5	16.7	26.6
Nyssa sylvatica	0.4	0.7	3.5	2.4	0.8	1.2	2.1	2.2	8.3	12.5	25.8	21.7	15.0	27.5	23.3	20.2
Acer rubrum	0.4	0.6	0.8	0.1	0.4	0.3	0.3	1.2	3.3	13.3	12.5	11.7	37.5	38.3	10.8	43.8
Carya glabra	1.6	0.2	0.3	0.3	0.4	0.2	0.0	0.4	17.5	2.5	3.3	3.3	8.3	5.8	0.8	7.0
Carya tomentosa	0.2	0.0	0.0	0.3	0.3	0.2	0.0	0.8	2.5	0.8	2.5	3.3	5.8	5.8	1.7	8.6
Quercus alba	0.0	0.0	0.9	0.2	0.2	1.0	0.7	1.3	2.5	1.7	8.3	1.7	6.7	19.2	12.5	39.2
Quercus coccinea	0.3	0.1	0.4	0.4	0.2	0.1	0.3	0.9	3.3	0.8	5.0	2.5	5.0	7.5	7.5	24.2
Quercus velutina	0.2	0.0	0.1	0.0	0.1	0.1	0.3	1.2	1.7	0.8	1.7	0.0	7.5	4.2	5.0	17.1
Sassafras albidum	0.1	0.0	0.0	0.1	0.0	0.2	0.5	0.2	1.7	0.0	0.8	3.3	1.7	4.2	12.5	8.3
Chimaphila maculata	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	8.3	9.2	15.0	24.2	10.4
Cypripedium acaule	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	1.7	3.3	4.2	0.4

[a]Selected species had an IV $\geq$ 10 for at least one plantation stage or natural forest class. Exceptions were: *Erechtites hieracifolia*, *Digitaria ischaemum*, *Ambrosia artemisiifolia*, *Eupatorium spp.*, *Aster spp.*, *Desmodium spp.*, *Rhus glabra*, and *Cypripedium acaule*.

one-year-old plantations (Fig. 4). At this time, the most prevalent grasses were Panicum spp., Andropogon virginicus, Danthonia spicata, Digitaria ischaemum, and A. scoparius (Table 13).

Woody species were also well represented in the one-year-old stands due to the abundant sprouting from cut stems, roots, and rhizomes (Fig. 6, Tables 12 and 13). The flush of growth from forbs, grasses, resprouting hardwoods, invading Virginia pine, and planted loblolly left little soil bare (Fig. 4).

The native forest stands (average age of 72 years) with their closed canopy and mat of litter (Fig. 4), had apparently suppressed ground stratum development. Burning of the litter layer, and the mechanical agitation of the soil during clear-cutting, site preparation, and planting phases probably resulted in moving dormant buried seeds closer to the soil surface where environmental conditions were conducive to germination. From the studies of Brenchley (1918), Oosting and Humphreys (1940), Toole and Brown (1946), Darlington and Steinbauer (1961), Livingston and Allessio (1968) and Kivilaan and Bandurski (1973), there are indications that the seeds of many herbaceous species are capable of remaining viable in the soil for a considerable period of time. With the history of the central Piedmont, it is quite possible that soils underlying these second-growth forests contain a seed pool which is representative of the entire successional sequence. Invading disseminules also undoubtedly contributed to re-vegetation of the denuded conversion sites. The influence of these pioneer species was likely governed in part by the degree to which converted stands were isolated within forest tracts.

5.3.2 Year 3

Total vascular plant coverage and species richness within the ground stratum decreased somewhat when compared to one-year-old plantations (Figs. 4 and 5). The decline in richness was due mainly to the disappearance of a number of perennial herbs (Fig. 6, Table 12) such as *Chrysogonum virginianum* (green-and-gold) and *Clitoria mariana* (butterfly pea), which had existed in the natural forest, and weedy species like *Rumex acetosella* (sheep-sorrel), *Plantago lanceolata* (English plantain), *Setaria geniculata* (foxtail grass), *Elymus virginicus* (wild rye), and *Festuca rubra* (red fescue). The existence of many of these herbaceous species appeared to be marginal in the one-year-old stands. Coverage losses by many herbaceous species were offset by the gains of *Andropogon virginicus* and *Rubus* spp. (Table

13). Grass coverage was maintained at the level reached in the one-year-old stands (Fig. 4); however, there was a change from a fairly even proportionment among several species to a strong dominance by A. virginicus (Table 13). These changes in richness and coverage were reflected in a reduction in species evenness (Fig. 5)--the result of extensive coverages by A. virginicus, and to a lesser extent Rubus spp. and Rhus copallina (Table 13). Aster spp. coverage peaked at this stage, but their contribution to total coverage was minor. Part of the loss in total vascular plant coverage in the ground stratum (Fig. 4) may have been due to the growth of woody species into the transgressive stratum (Figs. 4 and 7).

Other Piedmont successional studies have noted a decline in species richness associated with Andropogon dominance (Oosting 1942, Nicholson and Monk 1974). Oosting (1942) attributed the decrease in species numbers of three year fields to the monopolization of water and nutrients, and shading created by the profusely spreading Andropogon spp. A factor not considered by Oosting was the allelopathic effects of Andropogon. The dominance and persistence of A. virginicus in old fields has been ascribed in part to its toxic decay products which inhibit the growth of other species (Rice 1972). However, strong supporting

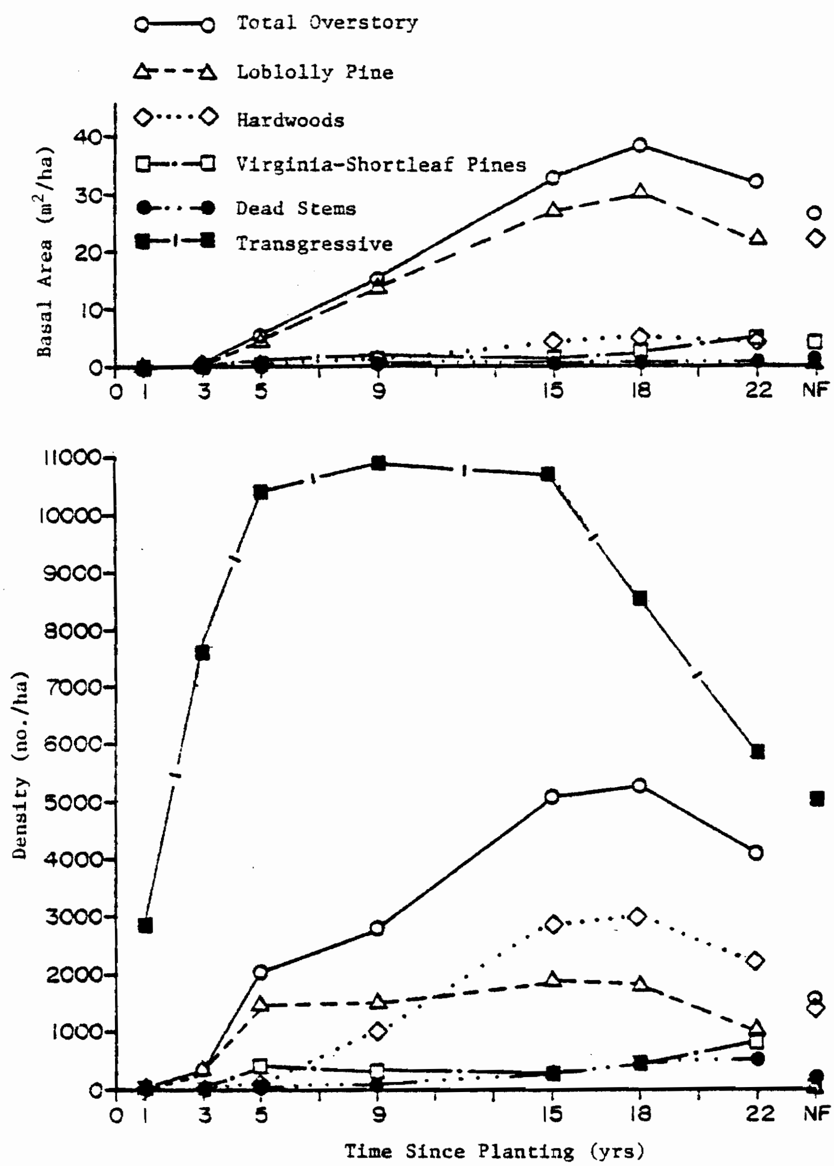


Fig. 7. Trends in stem basal area and density (mean values) in pine plantations as a function of time since planting; natural forest values (NF) are presented for comparison.

evidence for the role of allelopathy in succession is still lacking (Bazzaz 1979, Stowe 1979, Barbour et al. 1980:233-234). Pinder (1975) has provided evidence that forb growth during the period of *Andropogon* spp. dominance was principally limited by competition amongst living individuals rather than decomposing vegetative matter.

5.3.3 Year 5

The rapid development of loblolly pine was responsible for increases in overstory basal area and density in five-year-old stands, while the co-developing hardwoods were the main contributors to increases in transgressive stratum density and coverage (Figs. 4 and 7). Correspondingly, there was a continuation of the gradual rise in species richness within these strata (Fig. 5). The abrupt decline in overstory evenness, a function of basal area apportionment among species, was a direct result of the heavy influx of loblolly pine into this stratum (Figs. 5 and 7).

There was still a relatively low degree of canopy closure in five-year-old plantations (Fig. 4). As a consequence, total vascular plant coverage within the ground stratum remained at a fairly high level (Fig. 4). Compared to the previous stage of development, ground stratum evenness exhibited a slight gain (Fig. 5). This change was related to decreasing coverages of *Andropogon virginicus*, *Rhus* spp., and *Rubus* spp., being offset by increasing coverages for *A. scoparius*, *Solidago* spp., *Lespedeza* spp. (bush clovers), *Desmodium* spp. (tick trefoils), ericaceous shrubs, and various tree species (Table 13). The decline of *A. virginicus* may have initiated the slight increase in ground stratum richness (Fig. 5) which was attributed to an increase in perennial forb species (Fig. 6, Table 12).

5.3.4 Year 9

From five to nine years, the degree of canopy closure nearly doubled (Fig. 4). Subordinate hardwoods were a significant component of total canopy closure and overstory density, although their basal area was comparatively small (Figs. 4 and 7). This movement of hardwoods into the overstory was responsible for the higher species richness in the overstory stratum of nine-year-old plantations when compared to five-year-old plantations (Fig. 5). The increase of hardwood stems within the overstory had little effect on species evenness (Fig. 5); collectively, hardwoods comprised a small portion of the total basal area (Fig. 7). Basal area of the dominant loblolly pine had increased at the same rate as in the three to five year period, even though its growth into the overstory stratum had ceased (Fig. 7).

Total vascular plant coverage and species richness values for the ground stratum declined from the levels attained in five-year-old stands (Figs. 4 and 5). Grasses were no longer a dominant life form (Fig. 4, Table 13), although the number of species had not changed (Table 12). An exception to this trend was Danthonia spicata, a more shade tolerant species (Ehrenreich and Crosby 1960), which showed a slight increase in coverage (Table 13). Chimaphila maculata (spotted wintergreen), an upland forest species (Billings 1938, Oosting 1942, Chamberlain and Crandall 1964, Radford et al. 1978), appeared for the first time (Table 13).

Transgressive coverage and density remained fairly constant relative to levels in the five-year-old stands (Figs. 4 and 7), while species richness increased slightly (Fig. 5). This slight increase in the number of species in the transgressive stratum at nine years may be a growth lag response to peak woody species numbers in the ground stratum at five years (Table 12).

At this point in time, the successional process appeared to be in a transitional phase, i.e., drastic reductions in the once dominant old-field species accompanied by an increase in cover of the more tolerant ericaceous plants (Table 13). Reductions in *Andropogon* spp. biomass in old-field pine stands have been related to shading and root competition from pines; pine litter deposition does not seem to be a limiting factor (Gabrielson 1968). In hardwood stands with dense crown cover, Ehrenreich and Crosby (1960) found grass coverage was severely suppressed; however, species responses differed--*Danthonia spicata* was more abundant than *Andropogon scoparius* and *A. virginicus*, which were marginally persistent. As for the shift to dry site species such as the ericads, dense pine stands typically exhibit a xerophytic herb-shrub stratum, resulting from intense competition with the dominant pines whose roots form a closed network within the upper six inches (15.2 cm) of soil (Billings 1938). The dry surface soil and a thick litter mat which prevents seeds from reaching mineral soil, are apparently inhibitory to the establishment and persistence of herbaceous species (Billings 1938). In such an environment, *Chimaphila maculata* was well adapted for survival, heavily cutinized to lessen water loss from transpiration, deeply rooted, and capable of vegetative propagation by rhizomes (Billings 1938). It should be noted that *Vaccinium vacillans* and *Gaylussacia baccata* are also rhizomatous (Radford et al. 1978).

5.3.5 Year 15

The most significant structural development in the transition from 9- to 15-year-old plantations was the nearly complete closure of the canopy (Fig. 4). Loblolly pine still accounted for the major portion of overstory canopy closure and basal area (Figs. 4 and 7), but hardwood density now exceeded that of loblolly (Fig. 7). Competition among tree species had apparently intensified since appreciable numbers of dead trees began to appear in the overstory (Fig. 7).

Reduced light, root competition and the build-up of litter (Fig. 4) apparently resulted in low levels of total vascular plant coverage and species richness (Figs. 4 and 5) within the ground stratum (Billings 1938, Gabrielson 1968). The decline in richness was due to the disappearance of many herbaceous species (Fig. 6, Tables 12 and 13). Annual plants were no longer present (Fig. 6, Table 12), and grass coverage had dropped to zero (Fig. 4). Ericaceous plants and *Nyssa sylvatica* were the principal species, but even their coverages had been reduced (Table 13). *Cypripedium acaule* (moccasin flower), a rhizomatous species whose habitat is described as being dry, acid pine woodlands (Radford et al. 1978), appeared for the first time (Table 13).

In old-field successional studies conducted in the Piedmont, Billings (1938), Oosting (1942), and Nicholson and Monk (1974), reported gradual declines in the number of herbaceous species from the period of *Andropogon* dominance up to crown closure; herbaceous species numbers remained moderately stable during the pine forest seral stage. Data gathered by Billings (1938) indicated an inverse correlation between the thickness of the organic layer and the number of old-field species over time. The progressive accumulation of pine litter apparently prevents the seeds of these herbs from reaching mineral soil and germinating (Billings 1938). As a result, persistent old-field species are usually those capable of vegetative propagation (Billings 1938).

Species evenness in the ground stratum differed slightly from the levels attained in five- and nine-year-old stands (Fig. 5). Although total vascular plant coverage and species richness were significantly reduced in progressively older stands (Figs. 4 and 5), residual coverage continued to be divided in similar proportions among the remaining species.

Transgressive species richness had decreased (Fig. 5), but density remained at the plateau first reached at five years (Fig. 7). The slight increase in transgressive coverage (Fig. 4) relative to nine-year-old plantations may have been due to a horizontal spreading in form by these understory species to intercept more light.

5.3.6 Year 18

Overstory canopy closure and density were mostly unchanged over levels in the 15-year-old stands, while basal area (mainly loblolly pine) increased at approximately the same rate as the 9 to 15 year period (Figs. 4 and 7). The stabilization of hardwood density and basal area, and the abrupt decline of transgressive density marked the culmination of hardwood growth into the overstory (Fig. 7). The enlarged dead tree component of the overstory (Fig. 7) consisted of Virginia pines and to a lesser degree hardwoods.

The only significant changes in the understory were the declines in transgressive coverage and density (Figs. 4 and 7), and the rise in richness and evenness in the ground stratum (Fig. 5). These ground stratum changes were mainly attributed to the appearance of perennial woodland forbs (Table 12) such as *Polygonatum biflorum* (Solomon's seal), *Desmodium nudiflorum*, *Mitchella repens* (partridge berry), *Hieracium venosum* (hawkweed), and *Aster paternus*.

5.3.7 Year 22

Declines in overstory density and basal area from the 18th to the 22nd year were deceptive (Fig. 7). The spacing of loblolly was greater than the average 7x8 ft (2.1x2.4 m) in two of the three stands sampled. As a consequence, more Virginia pine became established and successfully competed with loblolly pine (Fig. 7). It was assumed that losses in hardwood and transgressive densities were the result of natural mortality (Fig. 7).

Species richness in the ground stratum had dropped to its lowest level due mainly to a loss of perennial forbs and some woody species (Table 12), including *Potentilla canadensis* (cinquefoil), *Lespedeza repens*, *Galium circaezans* (bedstraw), *Eupatorium rotundifolium* (thoroughwort), *Lysimachia quadrifolia* (whorled loosestrife), *Rhus copallina*, *Rhus radicans* (poison ivy), and *Lonicera japonica* (Japanese honeysuckle). *Danthonia spicata* was also absent from this stage of development (Table 13). The presence of *Rubus* spp. at this time as well as the two preceding stages (15 and 18 yrs) (Table 13), was attributed to widely spaced clusters of small seedlings, apparently disseminated by birds. Otherwise, conditions had remained relatively constant under the intense shading of the hardwood midstory-pine overstory.

5.3.8 Natural forest

Conditions in the native forest stands were similar to the post-canopy closure plantations (15 to 22 yrs) (Figs. 4 to 7, Tables 12 and 13). The most notable differences were: (1) a lower overstory basal area in the natural forest, due to the repeated "salvage" thinnings in the past (Fig. 7); (2) a lower hardwood overstory basal area in plantations because of their younger age and competition with loblolly pine (Fig. 7); (3) a greater overstory total stem density, overstory hardwood density, and transgressive density in plantations due to their younger age and the numerous sprouts amongst the planted pines (Fig. 7); (4) a lower overstory species evenness in pine plantations, the result of basal area dominance by loblolly pine (Figs. 5 and 7); and (5) a higher ground stratum species richness (Fig. 5) in the natural forest owing to more herbaceous perennial species and tree species (Fig. 6, Table 12). This higher richness was probably a response to greater environmental heterogeneity (microhabitats) coupled with seed input from mature hardwoods.

5.3.9 Tree species community changes

Insight to community dynamics was acquired by interrelating density changes of tree species within the ground, transgressive, and overstory strata. Tree species densities and basal areas are shown in Table 14 as a function of time since planting.

Dominant overstory trees within the natural forest were *Quercus alba* (white oak), *Pinus virginiana*, and *Q. coccinea* (scarlet oak), with basal areas of 10.20, 2.82, and 2.33 m^2/ha, respectively. Although *Acer rubrum* (red maple), *Nyssa sylvatica*, and *Cornus florida* (flowering dogwood) had overstory densities which surpassed those of *P. virginiana* and *Q. coccinea*, their size was more typical of understory trees, as indicated by comparisons of species basal area with density (Table 14). In Table 15, *N. sylvatica*, *C. florida*, and, *A. rubrum* showed maximum densities in the smallest diameter size class. Their numbers rapidly decreased in successively larger diameter classes, with few individuals exceeding 12.7 cm dbh. Billings (1938) and Oosting (1942) observed that these species rarely attained dominance in the overstory. Oosting found these three species, along with *Oxydendrum arboreum* (sourwood), to be characteristic of upland hardwood forests of the North Carolina Piedmont. Density and basal area values presented by Oosting indicated that *O. arboreum* and *C. florida* were the most dominant of the four species. In the present study, *O. arboreum* was infrequently encountered, and the

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Table 14. Mean stem density and basal area by strata for selected species[a] in various aged pine plantations and natural forest stands.

Species	Density (no./ha)							
	Natural Forest (72 yrs)	Time Since Planting (yrs)						
		1	3	5	9	15	18	22
	Ground Stratum							
Quercus alba	8833	167	83	750	250	1250	833	2250
Acer rubrum	6958	917	2333	1750	3250	6333	5917	1250
Nyssa sylvatica	4542	1250	2250	6833	5667	2167	3750	3883
Quercus coccinea	3500	583	250	583	333	667	2250	1083
Cornus florida	3042	2417	0	2083	1500	2083	1500	1000
Liriodendron tulipifera	2542	1000	1250	417	333	167	167	583
Quercus velutina	2500	333	167	250	0	833	500	500
Quercus prinus	1542	0	167	1333	333	3500	83	1417
Pinus virginiana	1334	833	583	2333	750	0	0	0
Sassafras albidum	1334	417	0	83	333	333	583	2500
Carya tomentosa	1250	333	83	250	333	500	500	167
Carya glabra	834	3583	167	167	417	917	417	83
Diospyros virginiana	250	583	250	250	250	667	250	83
Quercus stellata	42	1167	1833	500	0	0	0	0
Pinus echinata	0	83	0	0	0	0	0	0
Rhus spp.[b]	0	#1	#1	#2	#2	0	0	0
Pinus taeda	0	1000	0	0	0	0	0	0
	Transgressive Stratum							
Quercus alba	161	104	78	469	229	823	1021	672
Acer rubrum	693	177	922	1474	1161	1724	849	630
Nyssa sylvatica	1958	0	1266	2328	1729	1349	1760	2203
Quercus cocinea	104	88	47	432	495	536	589	385
Cornus florida	737	203	141	698	620	1094	1354	260
Liriodendron tulipifera	102	135	771	260	432	880	812	240
Quercus velutina	135	57	10	83	21	260	198	161
Quercus prinus	50	0	73	162	281	1083	188	411
Pinus virginiana	31	36	156	1667	453	52	5	0
Sassafras albidum	26	10	0	5	47	62	89	36
Carya tomentosa	349	10	52	83	203	937	766	73
Carya glabra	195	78	208	109	156	437	385	391
Diospyros virginiana	23	208	36	161	187	94	120	151
Quercus stellata	8	224	94	135	104	62	5	5
Pinus echinata	0	5	0	0	0	0	0	0
Rhus spp.	0	1057	1771	854	1604	31	5	0
Pinus taeda	0	172	1375	99	21	10	0	0
	Overstory Stratum							
Quercus alba	337	0	10	0	150	300	537	457
Acer rubrum	248	0	3	50	130	607	557	373
Nyssa sylvatica	219	0	0	3	27	47	27	100
Quercus coccinea	58	0	0	30	270	133	247	263
Cornus florida	195	0	0	0	107	347	383	140
Liriodendron tulipifera	14	0	7	7	37	430	723	120
Quercus velutina	29	0	0	3	3	170	143	173
Quercus Prinus	48	0	7	27	133	320	123	377
Pinus virginiana	68	0	30	423	283	200	357	807
Sassafras albidum	8	0	0	0	0	13	0	23
Carya tomentosa	122	0	0	0	10	210	87	20
Carya glabra	66	0	0	3	17	17	17	57
Diospyros virginiana	7	0	0	0	7	13	37	30
Quercus stellata	19	0	0	20	23	20	13	33
Pinus echinata	33	0	0	0	0	70	97	7
Rhus spp.	0	0	0	0	0	0	0	0
Pinus taeda	0	0	313	1447	1503	1887	1810	1023
	Basal Area (m^2/ha)							
	Overstory Stratum							
Quercus alba	10.20	0.00	0.01	0.00	0.22	0.53	0.85	0.78
Acer rubrum	1.06	0.00	0.00	0.05	0.16	0.80	1.42	0.62
Nyssa sylvatica	1.12	0.00	0.00	0.00	0.02	0.04	0.02	0.09
Quercus coccinea	2.33	0.00	0.00	0.03	0.44	0.23	0.38	0.50
Cornus florida	0.36	0.00	0.00	0.00	0.09	0.33	0.32	0.13
Liriodendron tulipifera	0.76	0.00	0.01	0.01	0.04	0.76	1.12	0.30
Quercus velutina	1.47	0.00	0.00	0.00	0.00	0.22	0.22	0.29
Quercus prinus	0.90	0.00	0.01	0.02	0.20	0.79	0.45	1.56
Pinus virginiana	2.82	0.00	0.03	0.58	0.60	1.06	2.26	5.24
Sassafras albidum	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.02
Carya tomentosa	1.14	0.00	0.00	0.00	0.03	0.21	0.08	0.02
Carya glabra	1.00	0.00	0.00	0.00	0.02	0.03	0.03	0.08
Diospyros virginiana	0.01	0.00	0.00	0.00	0.01	0.01	0.03	0.03
Quercus stellata	0.53	0.00	0.00	0.02	0.02	0.02	0.01	0.05
Pinus echinata	1.52	0.00	0.00	0.00	0.00	0.33	0.32	0.09
Rhus spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pinus taeda	0.00	0.00	0.24	4.70	13.73	27.11	30.66	22.35

[a] Species selected had a mean IV ≥ 10 for at least one plantation stage or natural forest class in at least one of the strata.

[b] *Rhus* spp. stems were not counted within the ground stratum; the numbers appearing signify its ranking relative to the other species based on a comparison of coverage values.

IV = relative frequency + relative cover for ground, rel. freq. + rel. density for transgressive, rel. freq. + rel. density + rel. basal area for overstory

Table 14. Mean stem density and basal area by strata for selected species[a] in various aged pine plantations and natural forest stands.

Species	Natural Forest (72 yrs)	1	3	5	9	15	18	22
	Density (no./ha)							
	Natural	Time Since Planting (yrs)						
	Ground Stratum							
Quercus alba	3833	167	83	750	250	1250	833	2250
Acer rubrum	6958	917	2333	1750	3250	6333	5917	1250
Nyssa sylvatica	4542	1250	2250	6833	5667	2167	3750	3883
Quercus coccinea	3500	583	250	583	333	667	2250	1083
Cornus florida	3042	2417	0	2083	1500	2083	1500	1000
Liriodendron tulipifera	2542	1000	1250	417	333	167	167	583
Quercus velutina	2500	333	167	250	0	833	500	500
Quercus prinus	1542	0	167	1333	333	3500	83	1417
Pinus virginiana	1334	833	583	2333	750	0	0	0
Sassafras albidum	1334	417	0	83	333	333	583	2500
Carya tomentosa	1250	333	83	250	333	500	500	167
Carya glabra	834	3583	167	167	417	917	417	83
Diospyros virginiana	250	583	250	250	250	667	250	83
Quercus stellata	42	1167	1833	500	0	0	0	0
Pinus echinata	0	83	0	0	0	0	0	0
Rhus spp.[b]	0	#1	#1	#2	#2	0	0	0
Pinus taeda	0	1000	0	0	0	0	0	0
	Transgressive Stratum							
Quercus alba	161	104	78	469	229	823	1021	672
Acer rubrum	693	177	922	1474	1161	1724	849	630
Nyssa sylvatica	1958	0	1266	2328	1729	1349	1760	2203
Quercus cocinea	104	88	47	432	495	536	588	386
Cornus florida	737	203	141	698	620	1094	1354	260
Liriodendron tulipifera	102	135	771	260	432	880	812	240
Quercus velutina	135	57	10	83	21	260	198	162
Quercus prinus	50	0	73	162	281	1083	188	411
Pinus virginiana	31	36	156	1667	453	52	5	0
Sassafras albidum	26	10	0	5	47	63	89	37
Carya tomentosa	349	10	52	83	203	938	766	73
Carya glabra	195	78	208	109	156	438	385	391
Diospyros virginiana	23	208	36	162	188	94	120	151
Quercus stellata	8	224	94	135	104	62	5	5
Pinus echinata	0	5	0	0	0	0	0	0
Rhus spp.	0	1057	1771	854	1605	31	5	0
Pinus taeda	0	172	1375	99	21	10	0	0
	Overstory Stratum							
Quercus alba	337	0	10	0	150	300	537	457
Acer rubrum	248	0	3	50	130	607	557	373
Nyssa sylvatica	219	0	0	3	27	47	27	100
Quercus coccinea	58	0	0	30	270	133	247	263
Cornus florida	195	0	0	0	107	347	383	140
Liriodendron tulipifera	14	0	7	7	37	430	723	120
Quercus velutina	29	0	0	3	3	170	143	173
Quercus Prinus	48	0	7	27	133	320	123	377
Pinus virginiana	68	0	30	423	283	200	357	807
Sassafras albidum	8	0	0	0	0	13	0	23
Carya tomentosa	122	0	0	0	10	210	87	20
Carya glabra	66	0	0	3	17	17	17	57
Diospyros virginiana	7	0	0	0	7	13	37	30
Quercus stellata	19	0	0	20	23	20	13	33
Pinus echinata	33	0	0	0	0	70	97	7
Rhus spp.	0	0	0	0	0	0	0	0
Pinus taeda	0	0	313	1447	1503	1887	1810	1023
	Basal Area (m^2/ha)							
	Overstory Stratum							
Quercus alba	10.20	0.00	0.01	0.00	0.22	0.53	0.85	0.78
Acer rubrum	1.06	0.00	0.00	0.05	0.16	0.80	1.42	0.62
Nyssa sylvatica	1.12	0.00	0.00	0.00	0.02	0.04	0.02	0.09
Quercus coccinea	2.33	0.00	0.00	0.03	0.44	0.23	0.38	0.50
Cornus florida	0.36	0.00	0.00	0.00	0.09	0.33	0.32	0.13
Liriodendron tulipifera	0.76	0.00	0.01	0.01	0.04	0.76	1.12	0.30
Quercus velutina	1.47	0.00	0.00	0.00	0.00	0.22	0.22	0.29
Quercus prinus	0.90	0.00	0.01	0.02	0.20	0.79	0.45	1.56
Pinus virginiana	2.82	0.00	0.03	0.58	0.60	1.06	2.26	5.24
Sassafras albidum	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.02
Carya tomentosa	1.14	0.00	0.00	0.00	0.03	0.21	0.08	0.02
Carya glabra	1.00	0.00	0.00	0.00	0.02	0.03	0.03	0.08
Diospyros virginiana	0.01	0.00	0.00	0.00	0.01	0.01	0.03	0.03
Quercus stellata	0.53	0.00	0.00	0.02	0.02	0.02	0.01	0.05
Pinus echinata	1.52	0.00	0.00	0.00	0.00	0.33	0.32	0.09
Rhus spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pinus taeda	0.00	0.00	0.24	4.70	13.73	27.11	30.67	22.34

[a] Species selected had an IV ≥ 10 for at least one plantation stage or natural forest class in at least one of the strata.

[b] *Rhus spp.* stems were not counted within the ground stratum; the numbers appearing signify its ranking relative to the other species based on a comparison of coverage values.

Table 15. Mean stem density of selected species according to dbh class in the overstory stratum of natural forest stands.

	Density (no./ha)					
DBH (cm)	*Quercus alba*	*Quercus coccinea*	*Pinus virginiana*	*Nyssa sylvatica*	*Acer rubrum*	*Cornus florida*
> 2.5 ≤ 5.1	50.0	13.3	1.7	166.7	118.3	155.8
> 5.1 ≤ 7.6	50.8	2.5	5.0	27.5	65.8	27.5
> 7.6 ≤ 10.2	36.7	5.0	5.8	6.7	27.5	6.7
> 10.2 ≤ 12.7	35.8	5.0	2.5	5.8	22.5	2.5
> 12.7 ≤ 15.2	26.7	1.7	4.2	1.7	4.2	1.7
> 15.2 ≤ 17.8	26.7	3.3	4.2	0.8	5.0	0.8
> 17.8 ≤ 20.3	19.2	2.5	9.2	3.3	2.5	0.0
> 20.3 ≤ 22.9	14.2	1.7	9.2	0.8	0.0	0.0
> 22.9 ≤ 25.4	8.3	5.0	5.8	0.8	1.7	0.0
> 25.4 ≤ 27.9	20.0	4.2	3.3	0.8	0.0	0.0
> 27.9 ≤ 30.5	8.3	4.2	6.7	0.0	0.0	0.0
> 30.5 ≤ 33.0	9.2	1.7	5.0	0.0	0.0	0.0
> 33.0 ≤ 35.6	5.8	2.5	4.2	0.8	0.0	0.0
> 35.6 ≤ 38.1	3.3	0.0	0.0	0.8	0.0	0.0
> 38.1 ≤ 40.6	5.8	1.7	0.0	1.7	0.0	0.0
> 40.6 ≤ 43.2	6.7	1.7	0.8	0.8	0.0	0.0
> 43.2 ≤ 45.7	0.8	1.7	0.0	0.0	0.0	0.0
> 45.7 ≤ 48.3	1.7	0.0	0.0	0.0	0.0	0.0
> 48.3 ≤ 50.8	0.8	0.0	0.8	0.0	0.0	0.0
> 50.8 ≤ 53.3	2.5	0.8	0.0	0.0	0.0	0.0
> 53.3 ≤ 55.9	1.7	0.0	0.0	0.0	0.0	0.0
> 55.9 ≤ 58.4	0.8	0.0	0.0	0.0	0.0	0.0
> 58.4 ≤ 61.0	0.8	0.0	0.0	0.0	0.0	0.0

density-basal area values listed in Table 14 depict N. sylvatica and A. rubrum as being more prevalent than C. florida. Similar findings were reported by Chamberlain and Crandall (1964) for the white oak forest type in the central Piedmont of Virginia.

Quercus alba and Q. coccinea were at their highest densities in the smallest dbh classes (Table 15); however, larger individuals were also present--dbh ranged from 2.5 to 61.0 cm. Unlike the three understory species which exhibited a continuous decline in densities with progressively larger diameter classes, the densities of the oaks oscillated with higher densities occurring around 22.9 to 27.9 cm. The fluctuations at the higher levels may have reflected the selective removal of poorly formed trees in previous thinning operations. In contrast to the hardwoods, Pinus virginiana density appeared to peak within the 17.8 to 22.9 cm dbh range. Low numbers in the smaller size classes are typical of pines in a mature hardwood forest as seedlings are highly intolerant to shade and root competition from the dominant overstory trees (Billings 1938, Coile 1940, Ferrell 1953).

Q. alba, A. rubrum, N. sylvatica, Q. coccinea, and C. florida also dominated the tree component of the ground stratum (Table 14). Going from the ground to the transgressive stratum, there was a substantial reduction in stem densities, especially among the oaks. Oosting (1942) noted that A. rubrum, N, sylvatica, and C. florida reproduced freely and had high densities in the seedling stage (<1 ft) (<0.3 m) but experienced high mortality as transgressives (>1 ft) (>0.3 m). In his study, Q.alba density was also much lower in the transgressive stratum. The less tolerant oaks and Liriodendron tulipifera (yellow poplar) are capable of existing under a forest canopy for many years as seedling sprouts--the roots remain alive while the stems die back to the base every few years (Billings 1938, Merz and Boyce 1956). Such an adaptation may explain the differences in species stem densities between the ground and transgressive layers.

One year (second summer) following conversion high ground stratum densities were observed for the profusely sprouting Rhus spp (Rhus copallina and R. glabra), Carya glabra (pignut hickory), and Cornus florida (Table 14). The sumacs were virtually nonexistent in the natural forest; however, with the removal of the overstory, these rhizomatous shrubs spread rapidly within the lower strata. Rhus spp. continued to dominate the ground and transgressive strata in three-year-old stands, but appreciable density gains were made by the vigorously sprouting Acer rubrum, Nyssa sylvatica, Quercus stellata (post oak), and Liriodendron tulipifera. Pinus taeda numbers had been subordinate to sprouting hardwood growth in the one-year-old stands, but by the third year they had grown en masse into the transgressive stratum, with some rapidly growing individuals reaching the overstory.

Five-year-old plantations were characterized by a decline in Rhus spp. numbers within the lower strata, and the appearance of Pinus virginiana in relatively significant numbers within all strata. Unlike planted loblolly and sprout hardwoods, the establishment of P. virginiana occurs over an extended period of time. This cumulative effect resulted in the emergence of P. virginiana in numbers no longer subordinate to hardwoods.

The completion of canopy closure in stands aged 15 years marked the absence of intolerant Rhus spp. and Pinus virginiana in the ground stratum. Contorted, "leggy" Rhus copallina remnants persisted in the transgressive stratum. In stands aged 5 to 15 years, Nyssa sylvatica, Acer rubrum, and Cornus florida densities were maintained at high levels in the lower strata. By the 15th year, the densities of A. rubrum, C. florida, and other hardwoods had increased appreciably within the overstory; collectively they exceeded Pinus taeda density for the first time (Fig. 7, Table 14).

As indicated by its basal area, P. taeda dominated the overstory stratum, but the suppressed hardwoods had formed a clearly definable midstory canopy (Table 16). Hardwood density at 15 years was most concentrated in the smallest diameter class (2.5 to 5.1 cm), with appreciable numbers ranging upwards to 10.2 cm (Table 16). As expected, the planted Pinus taeda displayed an even-aged diameter distribution centered at 10.2 to 15.2 cm. The diameter distributions of Pinus virginiana and P. echinata were somewhat like that of the hardwoods, being mostly confined to a 2.5 to 10.2 cm dbh range. The infrequent occurrence of P. echinata in loblolly pine stands aged 15 to 22 years, and its virtual absence in younger stands (Tables 14 and 16), was probably related to the lack of seed trees resulting from the salvage removal of P. echinata during the bark beetle infestation of the 1960's. Plantations of P. echinata still exist in the state forests but their contribution to total acreage has been greatly reduced. Scattered, older individuals of P. echinata persist within the thinned natural forest stands; however, conditions in these hardwood dominated stands are not conducive to the growth of pine seedlings (Table 14).

Species densities within all strata were not appreciably different in 15- and 18-year-old stands.

Table 16. Mean stem density of pines and hardwoods according to dbh class in the overstory stratum of various aged pine plantations.

	Density (no./ha)																											
	Loblolly Pine							Hardwoods							Virginia Pine							Shortleaf Pine						
	Time Since Planting (yrs)																											
DBH (cm)	1	3	5	9	15	18	22	1	3	5	9	15	18	22	1	3	5	9	15	18	22	1	3	5	9	15	18	22
>2.5 ≤ 5.1	0	313	347	77	33	53	7	0	30	160	850	2417	2520	1710	0	30	370	177	63	60	127	0	0	0	0	40	47	0
>5.1 ≤ 7.6	0	0	890	197	173	190	27	0	0	0	143	403	327	337	0	0	40	90	60	103	287	0	0	0	0	10	33	0
>7.6 ≤ 10.2	0	0	207	413	320	197	90	0	0	0	17	80	97	110	0	0	13	17	40	113	187	0	0	0	0	10	13	0
>10.2 ≤ 12.7	0	0	3	523	410	283	170	0	0	0	0	17	30	50	0	0	0	0	20	57	120	0	0	0	0	3	0	3
>12.7 ≤ 15.2	0	0	0	263	440	330	183	0	0	0	0	7	17	17	0	0	0	0	17	17	63	0	0	0	0	0	3	3
>15.2 ≤ 17.8	0	0	0	30	310	373	207	0	0	0	0	7	17	3	0	0	0	0	0	0	10	0	0	0	0	7	0	0
>17.8 ≤ 20.3	0	0	0	0	143	233	133	0	0	0	0	0	7	3	0	0	0	0	0	0	7	0	0	0	0	0	0	0
>20.3 ≤ 22.9	0	0	0	0	43	110	123	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
>22.9 ≤ 25.4	0	0	0	0	10	37	57	0	0	0	0	0	0	3	0	0	0	0	0	0	7	0	0	0	0	0	0	0
>25.4 ≤ 27.9	0	0	0	0	3	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
>27.9 ≤ 30.5	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
>30.5 ≤ 33.0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Conspicuous changes in Quercus prinus (chestnut oak) numbers reflected more xeric site conditions in one of the replicate 15-year-old stands (Table 14). In 22-year-old plantations, the increase in density exhibited by Quercus alba in the ground stratum was due in part to numerous small seedlings. The seedlings could have been die-back sprouts since transgressive density of Q. alba in 22-year-old stands was lower than that of stands aged 18 years, or they may have germinated from acorns disseminated by animals from adjacent hardwood stands. Gray squirrels (Sciurus carolinensis) and blue jays (Cyanocitta cristata), both acorn cachers, were encountered in post-canopy closure stands. Seed dissemination by birds may have caused the abrupt increase in Sassafras albidum in the ground stratum. With regard to stem density, Nyssa sylvatica dominated the lower strata. In form, this ubiquitous species appeared more like a shrub than a tree, with profuse horizontal branching rather than vertical growth, an evident response to heavy shading by the hardwood midstory-pine overstory. The reappearance of Pinus virginiana at a dominant density level in the overstory in 22-year-old plantations (Tables 14 and 16) has already been noted as probably due to the wider spacing of Pinus taeda. The decline in hardwood overstory density, but not basal area, in these older plantations, was assumed to be the result of mortality, as suggested by the number of dead stems (Fig. 7). It seemed that the loss in hardwood density was confined to trees within the 2.5 to 5.1 cm dbh class (Table 16). The magnitude of the density reduction could not be accounted for by growth into the larger diameter classes. Reductions in total stem numbers also occurred in the transgressive (Fig.7) and ground (Table 4) strata.

Tree species changes in loblolly pine plantations on converted sites in Virginia were not appreciably different from those of old-field pine stands of the North Carolina Piedmont. Billings (1938) described the formation of a distinct secondary arborescent stratum by subdominant hardwoods in pine stands aged 50 to 60 years. Cornus florida was the dominant tree in this layer; other species were Oxydendrum arboreum, Liquidambar styraciflua (sweet gum), Liriodendron tulipifera, and Acer rubrum. Oosting (1942) divided the hardwood midstory into two layers; an upper layer composed of L. styraciflua, A. rubrum, Nyssa sylvatica, and L. tulipifera, and a slightly lower level of C. florida and O. arboreum. C. florida, A. rubrum, L. tulipifera, oaks, and hickories became more numerous with increasing stand age (Billings 1938). Though never abundant in the understory, N. sylvatica responded similarly (Billings 1938).

As a result of sprout regeneration, a well defined hardwood midstory was present at 15 years of age in loblolly pine stands of the central Piedmont of Virginia (Tables 14 and 16). Principal midstory trees at 22 years were *Quercus alba*, *Q. prinus*, *A. rubrum*, and to a lesser extent, *Q. coccinea*, *Q. velutina* (black oak), *C. florida*, and *L. tulipifera*. In the transgressive and ground strata, the primary species was *N. sylvatica*, followed by *Q. alba* and *A. rubrum*.

5.4 SUMMARY OF SUCCESSIONAL TRENDS

Within the ground stratum, species richness and vegetative coverage showed the same trend. To illustrate, high values were associated with stands 1 to 5 years of age followed by a continual decline from 5 to 15 years, at which point canopy closure was complete and these variables were relatively stable for the next seven years (Figs. 4 and 5). Deviations in this general trend occurred at (1) 3 years, where temporary reductions in species numbers and coverage were associated with dominance by *Andropogon virginicus* ; and (2) 18 years, where a slight increase in richness was related to the appearance of various woodland forbs. Species evenness in the ground layer was fairly constant over time (Fig. 5), except for three-year-old stands where a decline occurred due to extensive coverages by A. virginicus and to lesser degree, Rubus spp., and Rhus copallina.

The structure (density and coverage) of the transgressive stratum was at its maximum level from 5 to 15 years, diminishing thereafter (Figs. 4 and 7). Species richness in the transgressive and overstory strata increased gradually with stand age as woody species grew into these layers (Fig. 5). A peak in transgressive stratum richness in the ninth year was followed by a decline which, like ground stratum richness, leveled-off between 15 and 22 years (post-canopy closure). Species evenness in the transgressive layer changed minimally throughout the 22 year period (Fig. 5). A slight decline from 9 to 22 years was probably caused by the gradual loss of Rhus spp. and Pinus virginiana, the continued growth of many hardwoods into the overstory, and the increasing density of the shrub-like Nyssa sylvatica.

Loblolly pine dominated the overstory stratum throughout the successional period studied, consistently accounting for most of the total overstory basal area (Fig. 7). With regard to overstory density, hardwood density surpassed that of loblolly between the 9th and 15th years (Fig. 7). By the 15th year, two distinct tree layers were evident--a uniform canopy of suppressed hardwoods beneath a pine canopy. Overstory stratum species richness reached a plateau at 15 years (Fig. 5) which coincided with the aforementioned density dominance of hardwoods in the overstory. Species evenness in the overstory dropped markedly from the third to the fifth year because of the disproportionate amount of basal area in loblolly pine. Subsequently, evenness increased at a slow rate as native woody species grew into the overstory stratum (Fig. 5).

From year 15 to 22, understory compositional and structural variables stabilized (Figs. 4 to 7). With the completion of canopy closure at 15 years, the transition from old field to woodland conditions ended. Vegetative variables indicate relatively stable environmental conditions. A saturation level had been reached, i.e., the monopolization of resources by loblolly pine resulted in consistently low levels of light, water, and nutrients available to other species (Billings 1938, Gabrielson 1968). Such conditions, together with litter fall, probably kept the understory in a suppressed state. There was constancy in composition as well as structure--intolerant species were replaced by those adapted to pine woodland conditions. Oosting (1942) noted a middle-aged (31 years) stabilization in composition and structure for all strata which lasted until the pines were succeeded by hardwoods.

To allow comparisons with other successional studies, heterogeneity indices such as Shannon-Wiener information content (H') (Pielou 1966a,b) and areal species richness (ASR) (Squiers and Wistendahl 1977), both purported as being integrators of species richness and evenness, were utilized (Fig 5). For the ground and transgressive strata, both indices were more indicative of varietal changes because of the relative constancy of the evenness component. ASR for the overstory stratum appeared to be related to species numbers while H' reflected changes in species evenness from the 3rd to the 22nd year. No overstory existed in the one-year-old stands; consequently, species richness was zero, and both the evenness and H' indices were undefined. The strong similarity between richness and ASR tends to support the opinion of Peet (1974) and others who consider ASR to be simply a richness measure.

Functional relationships among structural-compositional variables are evident from Figs. 4 to 7. Vegetative variables exhibiting similar responses included total canopy closure, litter coverage, litter depth, total overstory basal area, loblolly pine basal area, total overstory density, and hardwood overstory density. These variables appeared to be inversely related to a number of ground stratum variables, including total vascular plant coverage, grass coverage, species richness, total number of herbaceous species, number of perennial herb species, and number of annual herb species.

Canopy closure and overstory basal area were closely related because they both varied in accordance with the crown cover and basal area of loblolly pine, the dominant species in the overstory (Figs. 4 and 7). Loblolly pine density changed only slightly from 5 to 18 years (Fig. 7); as a consequence, it was the increasing density of the subdominant hardwoods which influenced the total overstory density curve.

In studies dealing with herbage production (grasses, forbs, and in some cases woody plants) relative to changes in overstory structural variables, inverse relationships have been established between understory vegetative biomass and overstory basal area, canopy cover, and density (Pase and Hurd 1958, Blair 1960, Ehrenreich and Crosby 1960, Halls and Schuster 1965, Blair 1967, Jameson 1967, Blair and Enghardt 1976, Brender et al. 1976, Blair and Feduccia 1977, Wiggers et al. 1978). These overstory variables have also been directly related to litter production (Pase and Hurd 1958, Williston 1965, Brender et al. 1976). Experimental tests conducted by Gabrielson (1968) have related reductions in herbaceous biomass, individuals, and species numbers to a combination of root competition, shade, and litter. Billings (1938) showed a negative correlation between litter depth and the number of old-field herbaceous species over time.

5.5 COMPARISON OF PIEDMONT SUCCESSIONAL STUDIES

Studies of old-field succession in the Georgia Piedmont by Nicholson and Monk (1974) indicated that stages of development are later and of longer duration than comparable stages in the converted stand sequence in the Virginia Piedmont. In contrast, the timing of events in the North Carolina Piedmont studies of Billings (1938) and Oosting (1942) did not differ appreciably from the present study of converted stands up to the time of canopy closure.

In the present study, vegetational sampling was initiated one year (second summer) after the planting of pine. As a result, the characteristic first year dominance by annual plants was not observed. The first growing season following the abandonment of cultivated land in the North Carolina Piedmont, Conyza canadensis and Digitaria sanguinalis were conspicuous dominants (Oosting 1942, Keever 1950). In old fields aged two years, these species were still abundant but the predominant species were clearly Aster ericoides and Ambrosia artemisiifolia (ragweed)

(Oosting 1942, Keever 1950). At converted sites in the central Piedmont of Virginia, perennial herbs dominated in both species numbers and coverage: 43 perennial species as compared to 14 annual species, and 33.0 percent perennial coverage as compared to 15.8 percent annnual coverage. Dominance as measured by coverage was shared among a number of perennial and annual species (Table 13). Conyza canadensis was well distributed throughout the converted stands, but individuals were small and overtopped by perennial herbs and woody sprouts. In these stands, the form of C. canadensis matched a description given by Keever (1950) for two year fields. Digitaria ischaemum, Ambrosia artemisiifolia, and Aster species were present at converted sites but their contribution to total vascular plant coverage was minor (Table 13).

Converted stand studies by Chamberlain and Crandall (1964) in the Virginia Piedmont and Atkeson and Johnson (1979) in the Georgia Piedmont, were begun the first summer following the establishment of loblolly pine. Site preparation of stands investigated in both studies was more intensive than those analyzed in the present study. Each described first year stands of tall herbaceous plants interspersed with bare ground. Annual plants dominated the Georgia sites, Conyza canadensis, Ambrosia artemisiifolia, and _Eupatorium capillifolium_ (dog fennel) being the most prominent. At the Virginia site of Chamberlain and Crandall (1964), coverages for the first two summers were 66.6 and 81.3 percent, respectively, for total vascular plants, and 26.3 and 10.3 percent, respectively, for bare soil. High cover values in the first summer were recorded for perennial _Panicum_ spp., and the annuals, _Erechtites hieracifolia_ (fireweed) and _Conyza canadensis_. In the present study, coverage in the first year (second summer) was 79.4 percent and 8.5 percent for total vascular plants and bare soil, respectively. Assuming a coverage value for the first summer similar to that of Chamberlain and Crandall (1964), the curve of total vascular plant coverage as a function of time in the present study (Fig. 4) resembled the graph of an equation developed by Brender et al. (1976) depicting the weight of green vegetation at ground level as a function of stand age (1 to 23 yrs) and basal area for unthinned loblolly pine plantations in the Georgia Piedmont . It also approximated a curve of stem density relative to community age--the first 22 years--presented by Nicholson and Monk (1975) for old-field succession in the Georgia Piedmont.

Litter deposition during succession was monitored by Billings (1938) in the North Carolina Piedmont, and Nicholson and Monk (1975) and Brender et al. (1976) in the

Georgia Piedmont. The first appearance of a humus layer, in addition to the litter and fermentation layers, occurred between the ages of 20 and 30 years (Billings 1938, Brender et al. 1976). The time at which increasing forest floor weight and depth began to level-off was 23 years (1794 g/m^2) (Brender et al. 1976) to 30 years (1200g/m^2) (Nicholson and Monk 1975) and 56 years (3.3 cm) (Billings 1938), respectively. In converted stands studied, litter accumulation reached a plateau at 15 years--a depth of 4.2 cm (Fig. 4). The more rapid accumulation and leveling-off may be related to the simultaneous development of pines and sprout hardwoods in converted stands, i.e., greater total leaf fall input and faster breakdown since hardwood litter generally decomposes more quickly than pine litter (Coile 1940, Metz 1954, Ovington 1954, 1962:136-138, Gabrielson 1968). As for differences in litter production due to pine spacing, Williston (1965) found little variation in forest floor weight among the more common spacings (1.8x1.8, 2.1x2.1, and 2.4x2.7 m). He concluded that "increased crown volume and needle size compensated for decreases in density."

5.5.1 Richness

Successional changes in species richness for all strata in the old-field sere exhibited a common response, an initial phase of rapid accretion followed by a prolonged period of increase at a progressively lower rate (Nicholson and Monk 1974). The species richness trend for the ground stratum of converted stands was almost the inverse of the old-field situation, e.g., a general decline from the 1st to the 22nd year (Fig. 5). Considering the time span monitored, the richness trend for converted stands might be regarded as a slight alteration of early succession (early forb to pine stages) in old fields. Data presented by Billings (1938), Oosting (1942), and Nicholson and Monk 1974, 1975), showed a reduction in herbaceous species numbers coincident with the gradual closure of the pine canopy. This loss in herb species was more than offset by the invasion of woody species. The completion of canopy closure marked the beginning of a period of pine dominance where ground stratum richness stabilized and then marginally declined (Nicholson and Monk 1974, 1975). It was not until hardwoods began to replace senescent pines that ground layer richness increased as hardwood forest species invaded (Nicholson and Monk 1974, 1975).

In converted stands, augmentation of species richness by invading woody disseminules was most likely minimal. Virtually all woody species were present in the form of sprouts at the start of succession (Fig. 6, Table 12). Initial dominance by herbaceous plants was short-lived owing to the rapid growth of the uniformly planted pines and interspersed hardwoods. As the monopolization of resources by pines escalated, species numbers dwindled in the ground stratum (Figs. 5 and 6, Table 12). Ground stratum richness had been at its maximum level the second summer after site conversion. Unlike the old-field sere, there was no compensation for the loss of herbaceous species. Ground stratum richness in 15- to 22-year-old pine stands was distinctly lower than the natural forest stands (Fig. 5).

The timing of the occurrennce of maximum species richness within the transgressive and overstory strata was simply a reflection of the growth rate of hardwoods. Peak densities at 9 years for the transgressive stratum and 15 to 18 years for the overstory coincided with peaks in richness (Figs. 5 and 7). From the 9th to the 22nd year, there was no further input of new species to the transgressive stratum; hence, richness declined as intolerant species were eliminated. Perhaps the similar richness values for the transgressive and overstory strata of 22-year-old pine and

72-year-old natural forest stands (Fig. 5) were an indication of species equilibria within these strata for young forested areas in the locale.

5.5.2 Evenness

Trends in species evenness were quite similar for the lower strata in converted stands. Evenness values for the ground and transgressive strata were relatively constant for the 22 year successional period; the only significant deviation occurred in the third year when Andropogon virginicus dominated the ground stratum (Fig. 5). High, stable values for evenness were viewed by Nicholson and Monk (1974) as being typical of older communities where intense competition for limited space and resources results in a more equitable and consistent sharing. During the pre-forest stages of old-field succession, they had found species evenness to be low and variable. It was only after the canopy closed completely that evenness was maintained at a high level.

In this study, intense competition was maintained throughout the 22 year successional sequence of converted stands. Limited resources and space resulted from dominance first by Andropogon virginicus and then loblolly pine. Evidence of such dominance was exemplified by ground stratum evenness at three years, and overstory evenness from the 3rd to the 22nd year (Fig. 5). Evenness was sustained by consistent proportioning of residual ground cover and transgressive density among the persisting species. Species evenness values for the three strata in natural forest stands and the ground and transgressive strata of the 22-year-old pine stands were clustered around a level of 0.68 (Fig. 5). Apparently overstory composition had little effect on species evenness within these understory strata, provided resources were still limited. Results from Nicholson and Monk (1975) also demonstrated that species evenness in the various strata tended to converge over time to a level of 0.8 exhibited by 125- to 200+-year-old hardwood forests. The 0.68 evenness value reported here more closely matched that of the pine forest stage (30 to 90 years old) of Nicholson and Monk, which converged around 0.64. For comparative purposes, a table for species evennness which conforms to that of Nicholson and Monk (1975) is presented in Appendix Table II.

5.6 PINE PLANTATIONS AND NATURAL FOREST AS WILDLIFE HABITAT

There was an inverse relationship between canopy closure and food plant coverages within the ground stratum for white-tailed deer, wild turkey, and bobwhite quail food plants (Fig. 8). In the nine-year-old stands, the first significant closure of the overstory canopy coincided with low vegetative coverages of food plant species for deer (28.0 percent), turkey (16.0 percent), and quail (6.6 percent) (Tables 17, 18, and 19). At 15 years, quail food plants were practically nonexistent (0.2 percent) while deer and turkey food plant coverages were 7.4 and 2.0 percent, respectively. The higher coverage levels for deer and turkey food plants were due in part to the more general classification of herbaceous food plants (Appendix Tables III, IV, and V). For quail, specific grasses, legumes, composites, etc., were known to be staple foods in the Piedmont province (Landers and Johnson 1976) (Appendix Table VI). The persistence of deer and turkey food plants beyond the 15th year, when canopy closure was complete, was mainly the result of browse plants being available for deer, and the presence of <u>Gaylussacia</u> <u>baccata</u> (huckleberry) whose fruit is eaten by turkeys (USDA-FS 1971). Herbaceous food plants were especially scarce in stands 15 years and older and in the natural forest (Tables 17, 18, and 19). For quail, annual food plant coverage was substantially lower in the three-year-old stands as compared to one-year-old stands; herbaceous perennials remaining in stands aged five and nine years were principally legumes (Table 19).

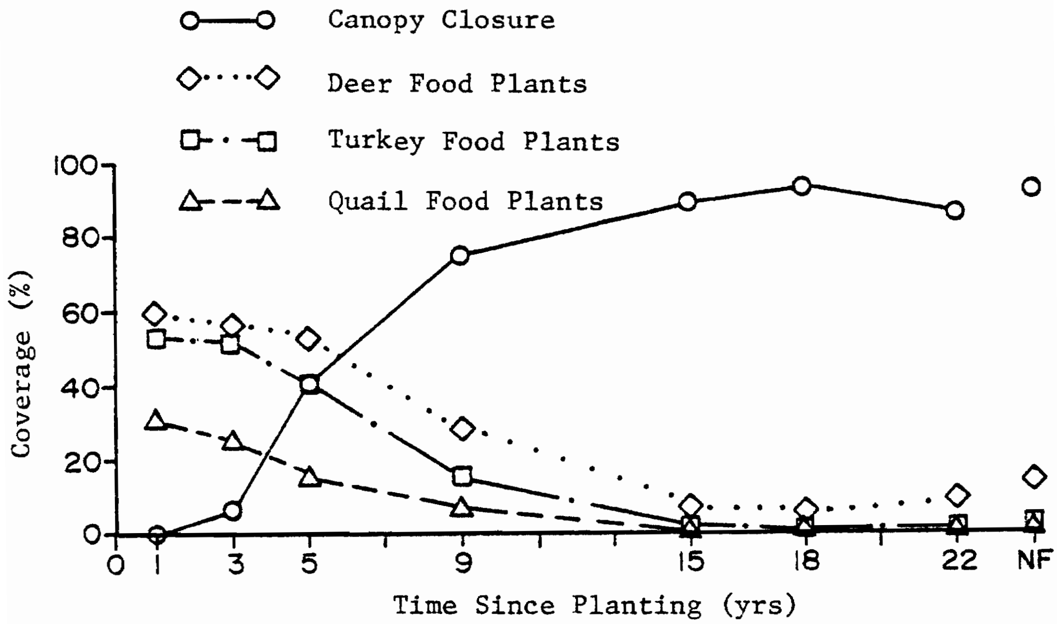


Fig. 8. Ground stratum food plant coverage and overstory canopy closure (mean values) in pine plantations as a function of the time since planting; natural forest values (NF) are presented for comparison.

Table 17. Mean coverage of white-tailed deer food plants in the ground stratum of various aged pine plantations and natural forest stands.

Food Categories	Coverage (%)							
	Pine Plantations Time since planting (yrs)							Natural Forest
	1	3	5	9	15	18	22	72 yrs
Total Food Plants	59.3	56.7	51.9	28.0	7.4	6.1	9.1	13.7
Woody Food Plants	17.3	21.4	20.0	18.8	7.3	5.8	8.9	13.2
Herbaceous Food Plants	42.0	35.2	31.9	9.2	0.1	0.2	0.1	0.5
Legumes (herbaceous)	11.1	2.8	6.5	2.4	t	t	t	0.2
Composites	7.8	5.3	6.1	1.9	t	0.1	t	t
Grasses	22.1	26.3	19.0	4.7	t	t	t	0.2
Sedges-Rushes	1.1	0.8	0.4	0.0	0.0	0.0	0.0	0.0
Ferns	0.0	0.0	0.1	0.1	t	0.1	t	0.1
Miscellaneous Herbaceous	0.1	0.1	0.2	0.1	t	0.1	0.1	0.1

Values ≤ 0.05 are signified by "t".

Table 17. Mean coverage of white-tailed deer food plants in the ground stratum of various aged pine plantations and natural forest stands.

	Coverage (%)							
	Pine Plantations Time since planting (yrs)							Natural Forest
Food Categories	1	3	5	9	15	18	22	72 yrs
Total Food Plants	59.5	56.7	52.6	28.0	7.4	6.1	9.1	13.7
Woody Food Plants	17.3	21.5	20.0	18.7	7.3	5.8	8.9	13.2
Herbaceous Food Plants	42.3	35.2	32.7	9.3	0.1	0.2	0.1	0.5
Legumes	11.1	2.8	6.9	2.4	0.0	0.0	0.0	0.2
Composites	7.8	5.3	6.1	1.9	0.0	0.0	0.0	0.0
Grasses	22.1	26.3	19.0	4.7	0.0	0.0	0.0	0.2
Sedges-Rushes	1.1	0.8	0.4	0.0	0.0	0.0	0.0	0.0
Ferns	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.1
Miscellaneous Herbaceous	0.1	0.0	0.2	0.1	0.0	0.1	0.1	0.1

Table 18. Mean coverage of wild turkey food plants in the ground stratum of various aged pine plantations and natural forest stands.

Food categories	Coverage (%) Pine Plantations Time since planting (yrs) 1	3	5	9	15	18	22	Natural Forest 72 yrs
Total food plants	53.4	52.4	40.7	16.0	2.0	1.0	0.9	2.8
Grasses	22.1	26.3	19.0	4.7	t	t	t	0.2
Honeysuckle-Greenbrier	0.1	0.2	0.6	1.4	t	t	t	0.1
Sumacs (includes poison ivy)	9.5	9.5	2.7	1.6	t	0.3	0.0	t
Legumes	11.1	2.8	6.9	2.4	t	t	t	0.2
Strawberries	t	0.0	0.2	t	0.0	0.0	0.0	0.0
Huckleberries	0.0	t	1.0	2.8	1.8	0.3	0.8	2.3
Blackberries-Dewberries	1.8	7.4	4.1	1.2	0.1	0.3	t	t
Composites	7.8	5.3	6.1	1.9	t	0.1	t	t
Grapes	t	t	t	t	t	0.1	t	t
Sedges	0.9	0.8	t	0.0	0.0	0.0	0.0	0.0

Values ≤0.05 are signified by "t".

Table 18. Mean coverage of wild turkey food plants in the ground stratum of various aged pine plantations and natural forest stands.

	Coverage (%)							
	Pine Plantations Time since planting (yrs)							Natural Forest
Food categories	1	3	5	9	15	18	22	72 yrs
Total food plants	53.4	52.4	40.7	16.0	2.0	1.1	0.9	2.8
Grasses	22.1	26.3	19.0	4.7	0.0	0.0	0.0	0.2
Honeysuckle-Greenbrier	0.1	0.2	0.6	1.3	0.0	0.0	0.0	0.1
Sumacs	9.5	9.5	2.7	1.6	0.0	0.3	0.0	0.0
Legumes	11.1	2.8	6.9	2.4	0.0	0.0	0.0	0.2
Strawberries	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Huckleberries	0.0	0.0	1.0	2.8	1.8	0.3	0.8	2.3
Blackberries-Dewberries	1.8	7.4	4.1	1.2	0.1	0.3	0.0	0.0
Composites	7.8	5.3	6.1	1.9	0.0	0.0	0.0	0.0
Grapes	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Sedges	0.9	0.8	0.0	0.0	0.0	0.0	0.0	0.0

Table 19. Mean coverage of bobwhite quail food plants in the ground stratum of various aged pine plantations and natural forest stands.

Food Categories	Coverage (%)							
	Pine Plantations Time since planting (yrs)							Natural Forest
	1	3	5	9	15	18	22	72 yrs
Total Food Plants	30.9	24.9	16.4	6.6	0.2	0.4	t	0.3
Sumacs	9.4	9.1	2.5	1.5	t	t	0.0	t
Blackberries-Dewberries	1.8	7.4	4.1	1.2	0.1	0.3	t	t
Grapes	t	t	t	t	t	0.1	t	t
Legumes	10.7	2.8	6.9	2.3	t	t	0.0	0.1
Grasses	8.6	4.3	2.3	0.8	t	t	t	t
Miscellaneous	0.3	1.3	0.5	0.8	t	t	0.0	0.0
Herbaceous annuals	10.4	1.8	0.5	0.3	0.0	0.0	0.0	t
Herbaceous perennials	9.2	6.5	8.3	2.8	t	t	t	0.2

Values ≤ 0.05 are signified by "t".

Table 19. Mean coverage of bobwhite quail food plants in the ground stratum of various aged pine plantations and natural forest stands.

	Coverage (%)							
	Pine Plantations Time since planting (yrs)							Natural Forest
Food Categories	1	3	5	9	15	18	22	72 yrs
Total Food Plants	30.9	24.9	16.3	6.6	0.2	0.4	0.0	0.2
Sumacs	9.4	9.2	2.5	1.5	0.0	0.0	0.0	0.0
Blackberries-Dewberries	1.8	7.4	4.1	1.2	0.1	0.3	0.0	0.0
Grapes	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Legumes	10.7	2.8	6.9	2.3	0.0	0.0	0.0	0.1
Grasses	8.7	4.3	2.3	0.8	0.0	0.0	0.0	0.0
Miscellaneous	0.3	1.3	0.5	0.8	0.0	0.0	0.0	0.0
Herbaceous annuals	10.4	1.8	0.5	0.3	0.0	0.0	0.0	0.0
Herbaceous perennials	9.2	6.5	8.4	2.8	0.0	0.0	0.0	0.2

In stands one to nine years of age, grasses accounted for the main portion of herbaceous food plant coverage for deer and turkey (Tables 17 and 18).

For deer and turkey, additional indicators of available food sources were the basal area and density of hard and soft mast-bearing trees, and the number of mast-producing species (Table 20). Oak species within the plantations were too young to produce acorns. In natural forest stands, six species of reproductively mature oaks accounted for 44.4 percent of the total overstory basal area. Soft mast trees comprised a minor component of total overstory basal area in both forests and plantations. Among plantations, the highest basal area and density levels attained by soft mast trees were in 15- and 18-year-old stands. In comparison, soft mast basal area in natural forest areas was three times as great while density was equivalent. One soft mast species, the intolerant <u>Prunus serotina</u> (black cherry), was absent in the natural forest stands and was on the verge of disappearing in the 22-year-old pine plantations (Table 20).

Browse is consumed by white-tailed deer throughout the year; with green leaves the principal vegetative material selected (Harlow and Hooper 1972, Halls 1973, Blair and Brunett 1980). Woody stems are an important food item in the spring when they are green and succulent (Harlow and

Table 20. Mean basal area and density of mast producing trees in various aged pine plantations and natural forest stands.

	Basal Area (m^2/ha)							
	Pine plantations Time since planting (yrs)							Natural Forest
	1	3	5	7	15	18	22	72 yrs
Total Overstory[a]	0.0	0.3	5.4	15.7	33.0	38.5	32.3	26.6
White Oak Group[b]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.8
Black Oak Group[b]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
Hard Mast[c]	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8
Soft Mast[a]	0.0	0.0	0.0	0.1	0.5	0.4	0.2	1.5
	Hard Mast[c] Density (no./ha)							
Quercus alba	0	0	0	0	0	0	0	69
Quercus prinus	0	0	0	0	0	0	0	5
Quercus stellata	0	0	0	0	0	0	0	10
Quercus coccinea	0	0	0	0	0	0	0	19
Quercus falcata	0	0	0	0	0	0	0	8
Quercus velutina	0	0	0	0	0	0	0	4
	Soft Mast[a] Density (no./ha)							
Cornus florida	0	0	0	107	347	383	140	195
Nyssa sylvatica	0	0	3	27	47	27	100	219
Prunus serotina	0	0	3	7	33	37	3	0
	Number of Mast Producing Species							
	0	0	2	3	3	3	3	8

[a] Stems > 2.54 cm dbh
[b] Stems ≥ 25.4 cm dbh
[c] Hard Mast = white and black oak groups

Hooper 1972, Halls 1973, Blair and Brunett 1980). If alternative food sources are available, hardened woody twigs are seldom eaten at any time of the year (Harlow and Hooper 1972, Halls 1973, Blair and Brunett 1980). In extensive plantations with closed canopies, which are common on corporate land holdings in the central Piedmont, minimal browse and fruit yields from suppressed understory plants are virtually the only food source. In Fig. 9, the stem density of transgressives, with 50 percent or more of their foliage within the 0 to 1.5 m feeding zone of deer, was at its highest levels in pine stands aged three to nine years. From 15 to 22 years, the food and cover provided by transgressives within the feeding zone gradually diminished as vegetation was shaded out or grew beyond the reach of deer. The availability of transgressive food and cover under the closed canopy of the hardwood forest was comparable to the heavily shaded 15- to 22-year-old stands and the newly developing one-year-old stands.

Changes in vegetative density at five heights above the ground were examined over time (Fig. 10). Vegetation profiles have been used to explain differences in small mammal abundance, distribution, species composition, and diversity (Rosenzweig and Winakur 1969, M'Closkey 1975, M'Closkey and Fieldwick 1975, M'Closkey and Lajoie 1975,

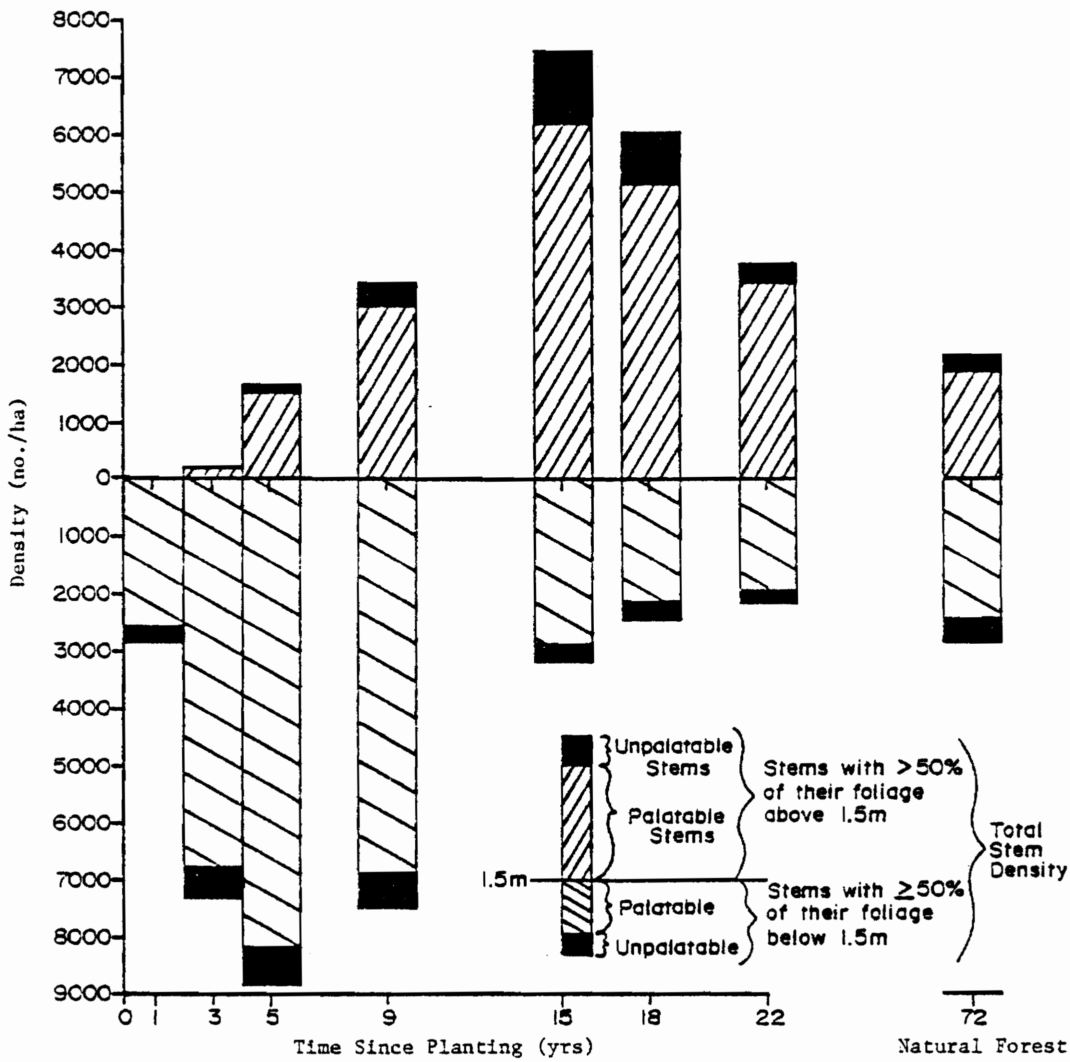


Fig. 9. Transgressive mean stem density in various aged pine plantations and natural forest stands partitioned according to availability and palatability to deer.

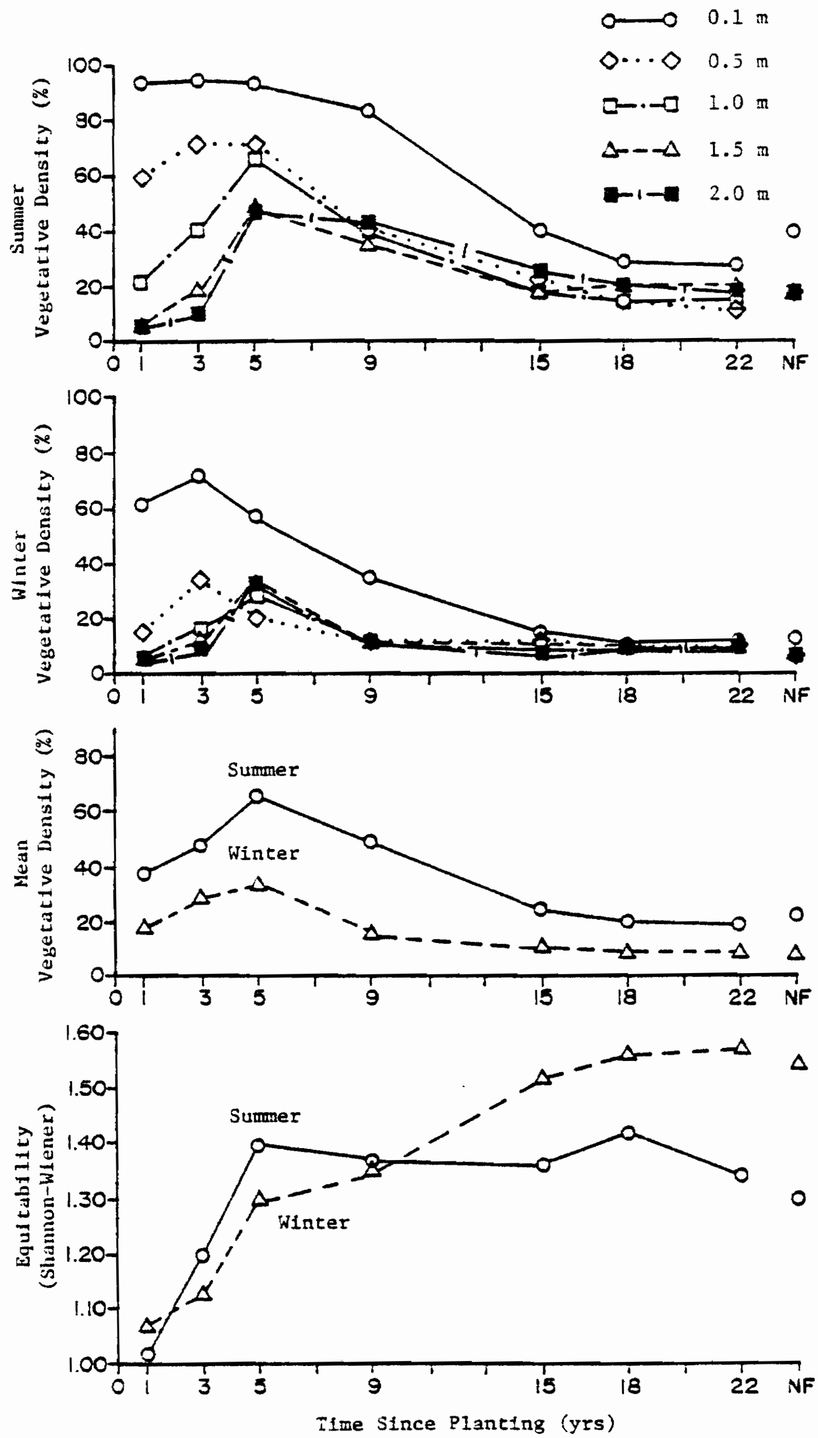


Fig. 10. Vegetative density at various strata, and equitability in pine plantations as a function of time since planting; the natural forest vegetative density profile (NF) is presented for comparison. Variables are defined in Tables 7 and 11.

Schreiber et al. 1976, Langley and Shure 1980), and songbird density and diversity (MacArthur and MacArthur 1961, Dickson and Segelquist 1979) among various habitats. This method of quantifying the structure of vegetation has also been proposed for evaluating deer habitat (cover for bedding and feeding) (Nudds 1977), and probably has applicability for quail and turkey habitat evaluation.

Low herbaceous plant growth in stands aged one year (second summer after planting of loblolly) was responsible for the high vegetative densities at the 0.1 and 0.5 m heights (Fig. 10). At three years, further increases in density within the 0.1 and 0.5 m layers marked the full development of grasses--primarily Andropogon virginicus (broomsedge). Rapidly developing loblolly and Virginia pines, and hardwood sprouts had begun to occupy the 1.0, 1.5, and 2.0 m levels; the main mass of sprout growth was still less than 1.0 m in height (Fig. 10, Table 14).

Mean vegetative density for the summer profile, an average of the densities for all five layers, peaked at five years (Fig. 10). Herbaceous plants still provided uniform cover from 0 to 0.5 m. Invading Virginia pine was at its greatest abundance, a substantial number of hardwood sprouts occupied the 2.0 m level, and self-pruning was minimal. At this point in time, total vegetative density and the evenness of its distribution among the five layers (equitability) were at a maximum (Fig. 10). Equitability was fairly constant from 9 to 22 years as vegetative density losses occurred within all layers as a result of the disappearance of many herbaceous plants, the suppression of persisting understory species, self-pruning by pines and hardwoods, and the mortality of native pines and hardwoods. The 0.1 m level still had the highest density of vegetation among all strata due to the remaining low cover provided by scattered ericaceous plants and Nyssa sylvatica (black gum).

Mean vegetative density in the natural forest and 15- to 22-year-old pine stands was similar (Fig. 10). Lower summer equitability in the natural forest was due to the disproportionate amount of vegetative density at the 0.1 m level. As indicated by transgressive coverage and density (Figs. 4 and 7), the understory of the forest stands was quite open.

In winter, there was a reduction in vegetative density at all levels within the various aged stands when compared to summer values (Fig. 10). Equitability increased in the natural forest and in stands aged 15 to 22 years as a result of foliage losses at 0.1 m layer, i.e., vegetation was equally scarce at all levels. Lower equitability in stands aged three and five years resulted from the abundance of dead grass (*Andropogon* spp.) at the 0.1 m level and foliage losses at the higher levels. In one-year-old stands, there was virtually no vegetation above 0.5 m. Hence, in winter, the only reduction in biomass occurred below 0.5 m, thereby increasing equitability.

5.6.1 Pine plantations

5.6.1.1 Bobwhite quail

Annual food plant coverage for quail totaled 10.4 percent the first year (second summer) following the planting of loblolly pine (Table 19). By the third year, annual food plant coverage was greatly reduced as perennial herbs, most notably *Andropogon virginicus*, and woody species predominated. In Georgia Piedmont plantations aged one to three years, quail exhibited a preference for annual over perennial food plants (Brunswig and Johnson 1973). Line occupancy percentages of 13.9, 18.0, and 16.6 were recorded for annual food plants during the first three growing seasons in these converted stands (Brunswig and Johnson 1973). The fourth season was characterized by a drop in annnual food plant occupancy to 3.0 percent as overall conditions for quail worsened (Brunswig and Johnson 1973).

The higher annual plant coverages in the Georgia study may have been related to the more intensive site treatment prior to planting with pine. Perkins (1973) noted a deterioration in quail feeding conditions by the third year on converted sites in Mississippi.

Legume and grass food plants of quail were most prominent in one-year-old stands (Table 19). Low coverages for these food types were coincident with significant canopy closure in the ninth year (Fig. 8). An analysis of quail crops by Brunswig and Johnson (1973) showed leguminous seeds to be a major food item. Byrd and Holbrook (1974) rated grasses as the next most important food source after legumes. Another important seed source for quail, Ambrosia artemisiifolia (ragweed) (Brunswig and Johnson 1973), was present in stands aged one to five years, but at very low coverage levels (Table 13). The presence of A. artemisiifolia in appreciable quantities is indicative of optimal quail habitat; protective cover is provided at this early forb stage yet it is open enough to allow quail to move freely (Ellis et al. 1969). Klimstra and Roseberry (1975) considered this stage of development to be most important for food production, but they found that quail utilization of intermediate successional stages (perennial weed and early shrub-bramble) was greater owing to much better nesting habitat.

Grasses, a prime material for nest construction and cover (Klimstra and Roseberry 1975), were most prevalent in one- to five-year-old stands (Table 17 or 18). According to Klimstra and Roseberry (1975), grasses commonly used for nesting material and protective cover were *Andropogon virginicus* (broomsedge), *Bromus* spp. (cheat grass), *Poa* spp. (blue grass), and *Panicum* spp. (panic grass). *Rubus* spp. (blackberry) and *Lonicera* spp. (honeysuckle) also furnish protective cover (USDA-FS 1971). In the present study, significant amounts of *Lonicera japonica* (Japanese honeysuckle) cover were seldom encountered in these upland stands (Table 18). *Andropogon virginicus* and *Rubus* spp. were most prominent in the three- and five-year-old plantations (Table 13). Although *A. virginicus* is a preferred nesting material, dense stands of this grass are avoided by quail (Klimstra and Roseberry 1975).

The average height of surrounding vegetation at nesting sites in Illinois was 49.5 cm (Klimstra and Roseberry 1975) while the cover at roosting sites usually ranged from 30 to 90 cm (Klimstra and Ziccardi 1963) or 30 to 60 cm (Ellis et al. 1969). In the present study, vegetative cover in one-year-old converted stands was mostly concentrated at 0.1 and 0.5 m above the ground (Fig. 10). At this point in time, vegetative coverage within the ground stratum (<1 m) may have become too thick for quail activities since quail prefer to nest (Rosene 1969:63, Klimstra and Roseberry 1975) and roost (Klimstra and Ziccardi 1963, Ellis et al. 1969) in areas where the soil is only partially covered by vegetation. Bare soil coverage rannged from 15 to 36 percent for good quail habitat in Illinois (Ellis et al. 1969). In converted stands in the present study aged one and three years, bare soil coverage was 8.5 and 3.9 percent (Fig. 4), respectively.

Based on habitat features such as bare soil, ragweed and annual food plant coverages, peak coverages of legume and grass food plants, and the vegetation profile, it appears that one-year-old stands (second growing season) still satisfy, though perhaps marginally, the habitat requirements of bobwhite quail. Stands three and five years of age lacked sufficient annual food plants and were probably too densely vegetated. Ground cover was sparse in post-canopy closure plantations, 15 to 22 years, but they were devoid of food plants (Table 19).

5.6.1.2 Wild turkey

Coverages of grasses and legumes, important food sources for the wild turkey (USDA-FS 1971), were at fairly high levels in stands aged one to five years (Table 18).

Substantial reductions in the coverages of these food plants co-occured with significant pine crown cover (Fig. 8) in nine-year-old stands. Desirable food grasses such as _Digitaria ischaemum_ (crab grass) and _Panicum_ spp. (panic grasses) (Mosby and Handley 1943:159) were never as abundant as the _Andropogon_ spp. (Table 13). _D. ischaemum_ was not found in stands older than one year (second growing season). _Panicum_ spp. coverage exhibited the same trend as total grass coverage, i.e., persistence in stands aged one to five years, and virtual elimination in nine-year-old stands. A distinct drop in coverages for legumes and composites in three-year old stands (Table 18) may have been a response to peak coverage for _Andropogon virginicus_ (Table 13). _Andropogon_ spp. dominated the ground stratum in stands aged three and five years (Table 13); these grasses have little, if any, food value, and their monopolization of a site results in the loss of many herbaceous food plant species (Mosby and Handley 1943:79). In the three-year-old stands, vegetation had grown to heights which would probably discourage usage by turkeys; vegetative densities of 72.0 and 41.2 percent at 0.5 and 1.0 m above the ground (Fig. 10) would prevent long range visibility and hamper movement.

Pine stands aged 15 to 22 years had little food value for turkeys (Table 18); however, during stressful weather conditions they could serve as protective cover (USDA-FS 1971). As for utilization as roosting sites, turkeys would have to penetrate a dense hardwood midstory to reach the overstory pines which at 22 years averaged 15.5 m in height and 16.0 cm dbh. According to Mosby and Handley (1943:166), pines attractive to wild turkeys for roosting sites typically have a 10 to 20 in (25.4 to 50.8 cm) dbh and a clean bole for the first 20 to 30 ft (6.1 to 9.1 m).

One-year-old stands (second growing season) would probably be frequented by turkeys since food plants were fairly abundant, Andropogon spp. had not yet dominated the ground layer, and vegetative growth had not reached the stage where it would obstruct movement and vision. Stands aged three years still might furnish satisfactory nesting habitat (Johnson et al. 1974).

5.6.1.3 White-tailed deer

Woody and herbaceous food plant coverages were fairly stable from one to five years (Table 17). From the fifth to the ninth year, woody plant coverage was only slightly altered; however, there was a substantial reduction in herbaceous food plant coverage. Under the closed canopy of 15-year-old plantations, herbaceous food species were quite scarce while many browse species had grown above the 1.5 m feeding zone of deer (Table 17, Fig. 9). In the Piedmont province, major food categories of the white-tailed deer as determined by rumen samples were the green leaves of woody plants, forbs, grasses-sedges, mushrooms, and dry leaves (Harlow and Hooper 1972). Individual food items which dominated samples at various times of the year were: green leaves of Lonicera spp.; fruit and green leaves of Smilax spp. (greenbrier), Rubus spp. (blackberry), Vitis spp. (grape), and Vaccinium spp. (blueberry); Rhus spp. (sumac) fruit; and acorns (Harlow and Hooper 1972). In the present study, food items such as Lonicera japonica, Smilax spp., and Vitis spp. were never abundant on these converted upland sites (Table 18). Rhus spp. and Rubus spp. colonies gradually disappeared as the overstory canopy closed (Table 18), but Vaccinium spp. persisted, albeit suppressed and scattered (Table 13). Understory fruit production in converted stands aged 15 to 22 years was likely minimal due to the two layered overstory--a midstory of hardwoods beneath the dominant pines (USDA-FS 1971). Total overstory basal areas for 15-, 18-, and 22-year-old stands were 33.04, 38.47, and 32.31 m^2/ha, respectively. These levels generally preclude moderate fruit yields within the understory (USDA-FS 1971).

Stands one, three, and five years of age provided forage and cover (bedding and feeding) for white-tailed deer. Nine-year-old stands would likely receive some use since browse was still fairly abundant within the 1.5 m feeding zone of deer (Table 17, Fig. 9). Stands 15 to 22 years of age may serve as cover or escape areas (Peery and Coggin 1978).

5.6.1.4 Future use of pine plantations by wildlife

As for the future utilization of converted stands by wildlife, the first commercial thinning at 23 to 25 years of age is expected to significantly alter understory structure and composition. Thinning operations will increase the amount of light reaching the ground level and create new sprout growth. As a result, there will probably be a resurgence of woody plant growth within the ground and shrub strata which should attract certain wildlife species. Herbaceous plant growth will probably remain minimal unless mineral soil is exposed. Burning of the litter mat would create favorable conditions for seed germination. The rate at which the system reverts to the post-canopy closure conditions of stands aged 15 to 22 years will depend on the extent to which midstory hardwoods are removed.

5.6.2 Natural forest

In some respects, the natural forest stands were quite similar to pine stands aged 15 to 22 years. Woody food plant coverages were somewhat higher under the closed canopy of the native forest stands, but as for herbaceous food plants, these stands were just as depauperate as the older pine stands (Tables 17, 18, 19). Vegetative cover within the ground stratum was sparse, e.g., a vascular plant coverage of 17.8 percent, grass coverage of 0.2 percent, and summer vegetative densities around 17 percent at heights of 0.5, 1.0, 1.5, and 2.0 m above the ground. Such openness within the understory complements the wild turkey's acute vision (USDA-FS 1971) and allows gallinaceous birds to move freely; however, these conditions deprive these game birds of the forage, fruit, seeds, and insects typically supplied from a well vegetated ground layer (USDA-FS 1971).

Unlike the pine plantations, the natural forest stands were mature enough to produce hard mast (Table 20). Averaging 72 years in age, the stands studied were within the 50 to 100 year range for optimal acorn production (USDA-FS 1971). Basal area for oaks with stems $\geq$ 25.4 cm dbh, the diameter at which most oaks are capable of reproduction (USDA-FS 1971), was 11.8 m^2/ha--a more than adequate level for supporting deer, turkey, and wildlife populations in general. The USDA-FS (1971) advised at least 20 ft^2/acre (4.6 m^2/ha) of mast species to maintain a population of one deer per 15 to 35 acres (6.1 to 14.2 ha). Assuming normal competition from other species which utilize mast, good turkey range (10 birds/mi^2) requires 8800 ft^2 of oak basal area/mi^2 (3.2 m^2/ha) (USDA-FS 1971). To support wildlife populations in general, Yoakum et al. (1980:402) suggested a basal area of 5.7 to 6.9 m^2/ha of oaks with a dbh of 25.4 cm or greater. In terms of density, 115 oaks/ha (dbh $\geq$ 25.4 cm) were present in these natural stands, which exceeds the density estimate of 19 oaks/acre (47 oaks/ha) recommended by Halls (1978) as necessary for good deer habitat.

As a guard against complete mast failure, Speake (1971), USDA-FS (1971), and Halls (1978) advocated mixed species management in forest stands. Six species of oaks with an adequate dbh for mast production could be found in the native forest stands under study. However, total stem density was not evenly distributed amongst these species (Table 20). With the major portion of potential mast production in _Quercus alba_ (white oak), these stands were susceptible to substantial fluctuations in annual yields. Using basal area values from Table 20, the ratio of black/red oaks to white oaks was approximately 1:2, just the reverse of the USDA-FS (1971) recommendation. Favorable qualities of the black/red oak group are more stable annual yields (USDA-FS 1971) and a lower rate of acorn deterioration (USDA-FS 1971, Halls 1973).

Soft mast is a supplement to acorn production. In Virginia, Mosby and Handley (1943:207) and Culbertson (1948) found that the primary mast species of the wild turkey were Quercus spp., Cornus florida (flowering dogwood), Fagus grandifolia (beech), and Nyssa sylvatica (black gum); fruits of these species are also consumed by deer (Halls 1978). For the soft mast species, Nyssa sylvatica and Cornus florida, total basal area for stems greater than 2.54 cm was 1.5 m^2/ha and total density was 414 stems/ha in natural stands (Table 20). The productivity of these soft mast species would likely be enhanced by more open growing conditions (USDA-FS 1971). A total overstory basal area of 26.6 m^2/ha (stems > 2.54 cm dbh) in natural forest stands surpassed the basal area range of 60 to 80 ft^2/acre (13.8 to 18.4 m^2/ha) specified by the USDA-FS (1971) for adequate fruit yields.

The value of natural forest stands to wildlife may be enhanced by interspersion with various aged pine plantations and other cover types. A heterogeneous landscape can more adequately meet the various needs of animal species. The deficiencies noted for native forest stands as well as converted stands could be minimized by proper juxtaposition, e.g., productive young converted stands adjacent to mature hardwood forest would be complementary. Further improvements in wildlife habitat could be made in conjunction with interspersion and juxtaposition by manipulating the size and shape of stands to maximize "edge effect".

Chapter VI

SUMMARY AND CONCLUSIONS

6.1 SUCCESSION IN CONVERTED STANDS

Significant stages in the vegetative development of converted stands are described in Fig. 11. Stages are not discrete entities, rather, they intergrade along a temporal gradient (Fig. 12). The initiation of succession in converted stands was quite unlike that in old fields. Typically, after many years in cultivation, the abandoned field is heavily dependent on external seed sources for revegetation. In clear-cut second-growth forest sites planted to pine, there was a diverse reservoir of propagative units. Despite such differences in initial conditions, the seral stages typical of old-field succession were likewise expressed in converted stand succession (Figs. 11 and 12), though somewhat abbreviated and masked by the abundance and diversity of reproductive units. The developmental process in converted stands was much like the one proposed by Egler (1954) in his "initial floristic composition" model. Virtually all species, i.e., the entire successional sequence, are present following the abandonment

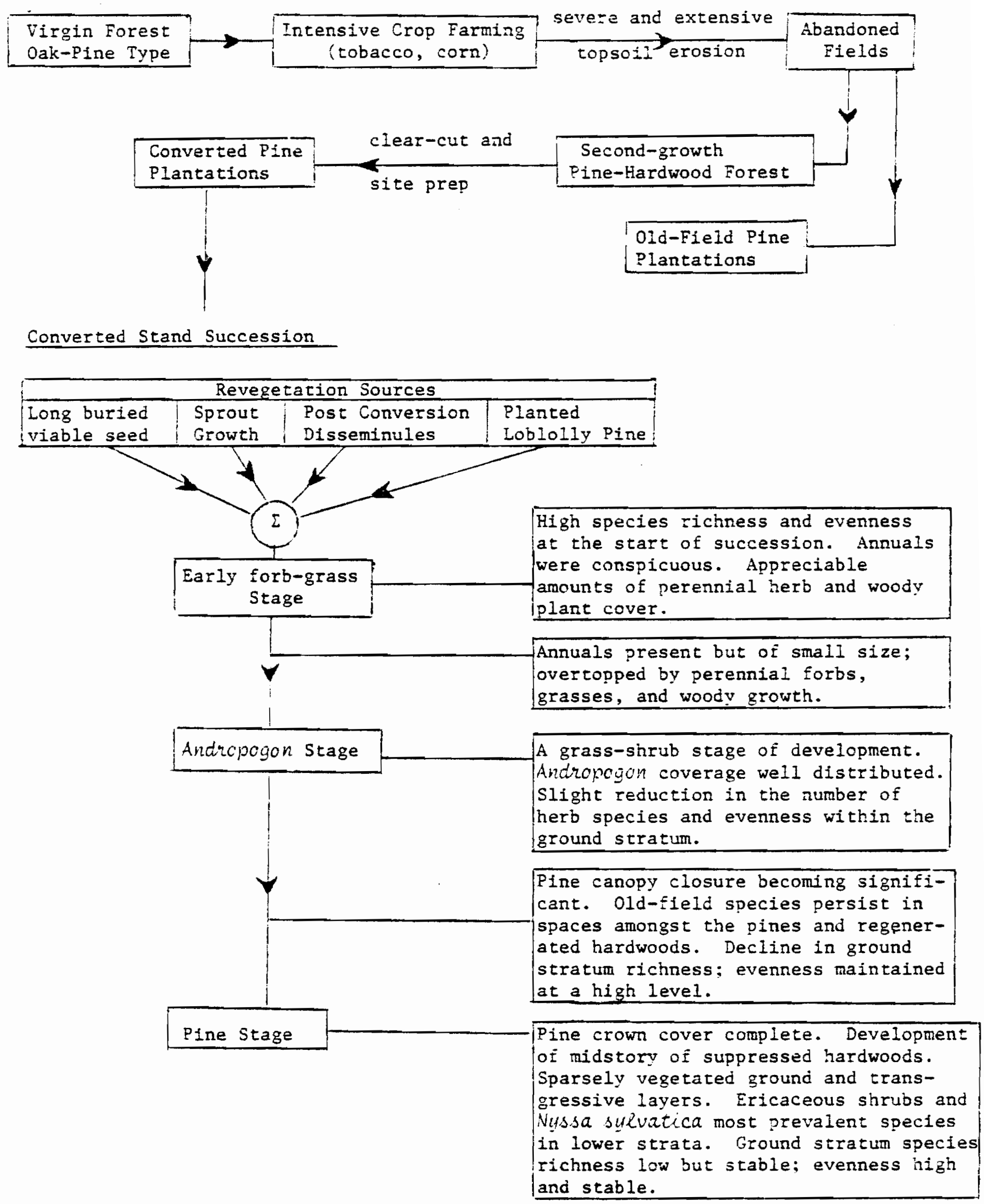
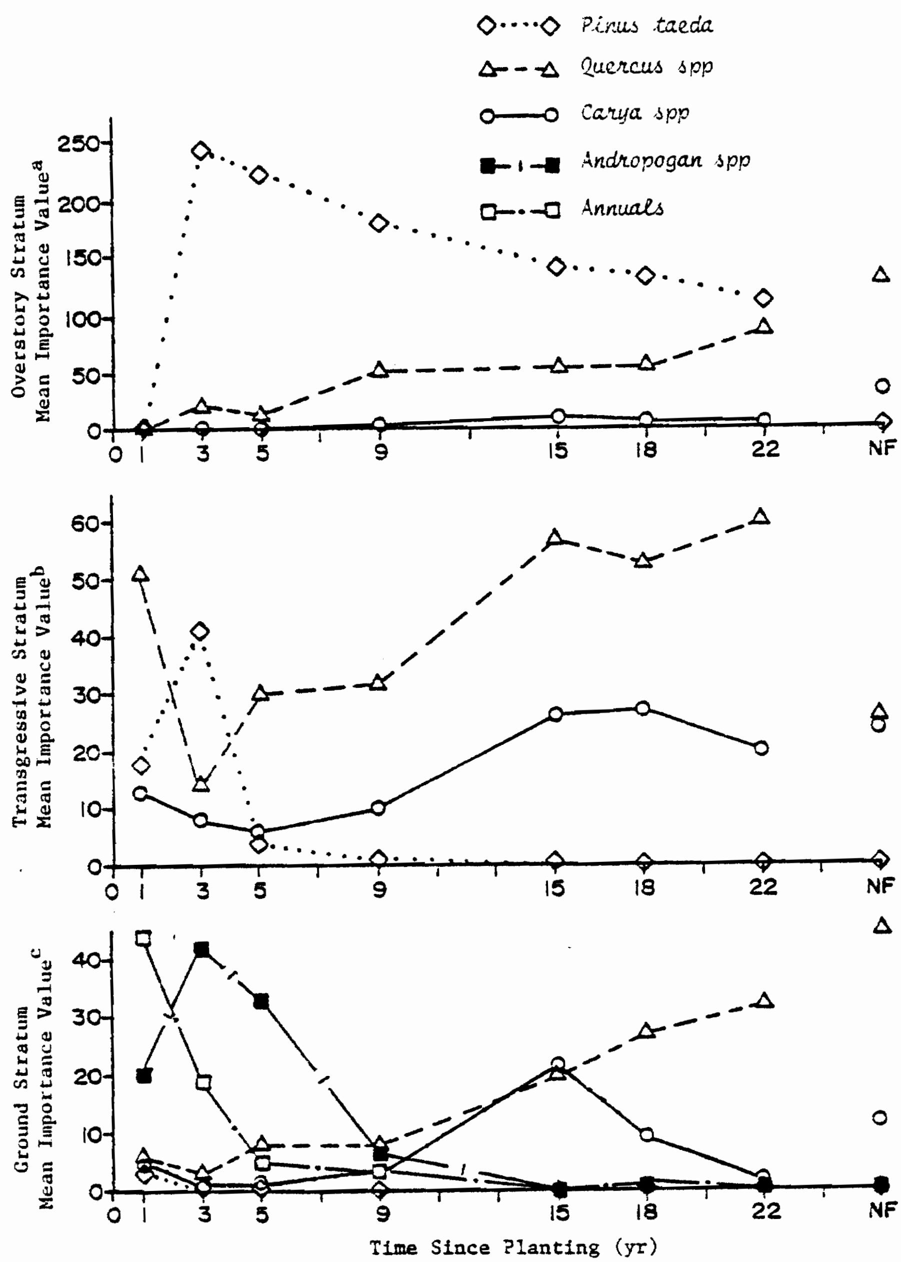


Fig. 11. Conceptual model of succession on converted sites in the central Piedmont of Virginia.



[a] IV = Relative Frequency + Relative Density + Relative Basal Area
[b] IV = Relative Frequency + Relative Density
[c] IV = Relative Frequency + Relative Coverage

Fig. 12. Mean importance values of diagnostic plant species by strata in pine plantations as a function of time since planting; natural forest values (NF) are presented for comparison.

of farm land. As time passes, various plant life forms predominate for varying periods. "As each successive group drops out, a new group of species, there from the start assumes predominance. Eventually only the trees are left (Egler 1954)."

The uniform planting of loblolly pine seedlings increases this introduced species' competitive advantage over the native tree species. Space and resources were monopolized by loblolly as its root system and canopy closed (Billings 1938, Gabrielson 1968). In the years preceding dominance by loblolly pine, the delay in dominance by <u>Andropogon virginicus</u> until the third year (fourth growing season) was probably due to an inadequate seed supply the first growing season following conversion. Keever (1950) reported that the few seedlings which appeared in first-year fields did not produce seeds until the fall of the second year. With the proliferation of <u>Andropogon</u> spp., other herbaceous plants were outcompeted for the available space and resources (Oosting 1942, Pinder 1975). <u>Andropogon</u> spp. were in turn eliminated by root competition and shading from the developing pines (Billings 1938, Gabrielson 1968). Suppressed hardwoods formed a midstory beneath the uniform pine canopy. Only upon the loss of loblolly pine will the oaks and hickories likely dominate the overstory. Such changes in the vegetative community of converted stands conform with Odum's (1960) observation that "secondary succession seems to involve a series of temporary steady-states each associated with a major life form."

6.2 WILDLIFE HABITAT

A secondary thrust of this study was directed towards an evaluation of habitat suitability for selected wildlife species in natural forest and converted stands in the Virginia Piedmont. Accordingly, an appraisal was made of the habitat conditions for bobwhite quail, wild turkey, and white-tailed deer. Assessments were made from an analysis of habitat variables considered by various sources to be indicative of food and cover conditions. The resulting habitat quality assessments provide a basic framework for the initiation of more intensive studies dealing with the habitat requirements of individual wildlife species. As such, this study is viewed as the initial phase of a long-term project aimed at determining the influences of the conversion process on wildlife indigenous to the central Piedmont of Virginia.

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APPENDIX

Table I. Species sampled[a].

Trees

Acer rubrum	*Pinus echinata*
Amelanchier arborea	*Pinus taeda*
Carpinus carolinianus	*Pinus virginiana*
Carya glabra	*Platanus occidentalis*
Carya tomentosa	*Prunus avium*
Cornus florida	*Prunus serotina*
Crataegus flabellata	*Quercus alba*
Diospyros virginiana	*Quercus coccinea*
Fagus grandifolia	*Quercus falcata*
Fraxinus americana	*Quercus marilandica*
Fraxinus pennsylvanica	*Quercus phellos*
Ilex opaca	*Quercus prinus*
Juniperus virginiana	*Quercus rubra*
Liquidambar styraciflua	*Quercus stellata*
Liriodendron tulipifera	*Quercus velutina*
Morus rubra	*Robinia pseudoacacia*
Nyssa sylvatica	*Sassafras albidum*
Oxydendrum arboreum	*Ulmus alata*
Paulownia tomentosa	*Ulmus americana*

[a]Nomenclature follows that of Gleason (1963). Life form designations are from Radford *et al.* (1978).

APPENDIX

Table I. Species sampled. (continued).

Shrubs

Alnus serrulata
Aralia spinosa
Aronia arbutifolia
Ascyrum hypericoides
Castanea dentata
Castanea pumila
Ceanothus americana
Cercis canadensis
Chionanthus virginicus
Corylus americana
Crataegus uniflora
Elaeagnus umbellata
Euonymus americanus
Gaylussacia baccata
Ilex decidua
Ilex verticillata
Kalmia latifolia
Lespedeza bicolor
Lyonia ligustrina
Lyonia mariana
Prunus virginiana
Rhododendron nudiflorum
Rhus copallina
Rhus glabra
Rosa carolina
Rubus spp. (*allegheniensis*, *argutus*, *enslenii*, *flagellaris*)
Rubus occidentalis
Symphoricarpos orbiculatus
Vaccinium corymbosum
Vaccinium stamineum
Vaccinium vacillans
Viburnum acerifolium
Viburnum prunifolium

APPENDIX

Table I. Species sampled. (continued).

Woody Vines

Campsis radicans	*Vitis aestivalis*
Lonicera japonica	*Vitis baileyana*
Parthenocissus quinquefolia	*Vitis labrusca*
Rhus radicans	*Vitis riparia*
Smilax glauca	*Vitis vulpina*
Smilax rotundifolia	

Forbs (annuals-biennials)

Acalypha gracilens	*Gnaphalium purpureum*
Ambrosia artemisiifolia	*Hypericum gentianoides*
Amphicarpa bracteata	*Ipomoea lacunosa*
Bidens frondosa	*Lactuca canadensis*
Cassia nictitans	*Lespedeza stipulacea*
Cirsium pumilum	*Lobelia inflata*
Conyza canadensis	*Polygala incarnata*
Crotalaria sagittalis	*Prenanthes serpentaria*
Diodia teres	*Pyrrhopappus carolinianus*
Erechtites hieracifolia	*Solanum nigrum*
Erigeron annuus	*Trichostema dichotomum*
Gerardia tenuifolia	*Verbascum thapsus*
Gnaphalium obtusifolium	

APPENDIX

Table I. Species sampled. (continued).

Forbs (perennials)	
Achillea millefolium	*Cypripedium acaule*
Aletris farinosa	*Desmodium ciliare*
Anemone virginiana	*Desmodium glabellum*
Angelica venenosa	*Desmodium laevigatum*
Antennaria plantaginifolia	*Desmodium marilandicum*
Apocynum cannabinum	*Desmodium nudiflorum*
Asclepias variegata	*Desmodium paniculatum*
Aster dumosus	*Desmodium rotundifolium*
Aster grandiflorus	*Desmodium viridiflorum*
Aster patens	*Dioscorea quarternata*
Aster paternus	*Eupatorium album*
Aster pilosus	*Eupatorium aromaticum*
Aster solidagineus	*Eupatorium fistulosum*
Aster undulatus	*Eupatorium hyssopifolium*
Aureolaria virginica	*Eupatorium rotundifolium*
Baptisia tinctoria	*Eupatorium saltuense*
Centrosema virginianum	*Eupatorium sessilifolium*
Chimaphila maculata	*Euphorbia corollata*
Chrysanthemum leucanthemum	*Fragaria virginiana*
Chrysogonum virginianum	*Galactia volubilis*
Chrysopsis mariana	*Galium circaezans*
Clitoria mariana	*Gentiana villosa*
Coreopsis verticillata	*Gillenia trifoliata*
	Goodyera pubescens

APPENDIX

Table I. Species sampled. (continued).

Helianthus atrorubens	*Monotropa hypopithys*
Hexastylis virginica	*Oenothera fruticosa*
Hieracium gronovii	*Oxalis europaea*
Hieracium venosum	*Oxalis stricta*
Houstonia purpurea	*Phytolacca americana*
Hypericum punctatum	*Plantago lanceolata*
Ipomoea pandurata	*Polygonum scandens*
Lechea racemulosa	*Polygonatum biflorum*
Lechea tenuifolia	*Potentilla canadensis*
Lespedeza cuneata	*Prunella vulgaris*
Lespedeza hirta	*Pycnanthemum flexuosum*
Lespedeza intermedia	*Pycnanthemum icanum*
Lespedeza nuttallii	*Rumex acetosella*
Lespedeza procumbens	*Scutellaria integrifolia*
Lespedeza repens	*Senecio smallii*
Lespedeza stuevei	*Smilacina racemosa*
Lespedeza virginica	*Solanum carolinense*
Liatris squarrosa	*Solidago altissima*
Linum virginianum	*Solidago arguta*
Lobelia puberula	*Solidago bicolor*
Ludwigia alternifolia	*Solidago curtisii*
Lysimachia quadrifolia	*Solidago erecta*
Mecardonia acuminata	*Solidago graminifolia*
Mitchella repens	*Solidago juncea*

APPENDIX

Table I. Species sampled. (continued).

Solidago nemoralis	*Tephrosia virginiana*
Solidago odora	*Uvularia perfoliata*
Solidago pinetorum	*Vernonia glauca*
Solidago rugosa	*Viola emarginata*
Strophostyles umbellata	*Viola sororia*
Stylosanthes biflora	
Graminoids (annuals)	
Agrostis hyemalis	*Panicum miliaceum*
Digitaria ischaemum	*Panicum philadelphicum*
Graminoids (perennials)	
Agrostis perennans	*Hystrix patula*
Andropogon scoparius	*Juncus effusus*
Andropogon virginicus	*Juncus secundus*
Carex bushii	*Juncus tenuis*
Carex pensylvanica	*Paspalum floridanum*
Cyperus ovularis	*Panicum angustifolium*
Danthonia spicata	*Panicum boscii*
Elymus virginicus	*Panicum clandestinum*
Eragrostis spectabilis	*Panicum commonsianum*
Festuca rubra	*Panicum commutatum*
Gymnopogon brevifolius	*Panicum consanguineum*

APPENDIX

Table I. Species sampled. (continued).

Panicum depauperatum	*Panicum polyanthes*
Panicum dichotomum	*Panicum sphaerocarpon*
Panicum lanuginosum	*Panicum villosissimum*
Panicum latifolium	*Scirpus cyperinus*
Panicum laxiflorum	*Scleria pauciflora*
Panicum linearifolium	*Setaria geniculata*
Panicum oligosanthes	*Triodia flava*
Ferns	
Polystichum acrostichoides	*Pteridium aquilinum*
Clubmoss	
Lycopodium complanatum	

ERRATUM

APPENDIX

standard deviation

Table II. Mean evenness ($\bar{J}' \pm 2$ SD) according to strata and developmental stage.

Stage of Development	Number of Stands	Stratum: Ground	Transgressive	Overstory
Pine (1 yr)	3	.712 ± .056	.771 ± .177	------
Pine (3 yrs)	3	.574 ± .265	.732 ± .100	.457 ± .141
Pine (5 yrs)	3	.680 ± .194	.750 ± .037	.229 ± .136
Pine (9 yrs)	3	.700 ± .162	.763 ± .119	.247 ± .286
Pine (15 yrs)	3	.670 ± .238	.717 ± .041	.299 ± .152
Pine (18 yrs)	3	.717 ± .094	.735 ± .039	.316 ± .052
Pine (22 yrs)	3	.690 ± .072	.670 ± .262	.377 ± .175
Natural Forest ($\bar{x}$ = 72 yrs)	6	.703 ± .051	.652 ± .137	.667 ± .207

APPENDIX

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Pine (9 yrs)	3	.700 ± .162	.763 ± .119	.247 ± .286
Pine (15 yrs)	3	.670 ± .238	.717 ± .041	.299 ± .152
Pine (18 yrs)	3	.717 ± .094	.735 ± .039	.316 ± .052
Pine (22 yrs)	3	.690 ± .072	.670 ± .262	.377 ± .175
Natural Forest ($\bar{x}$ = 72 yrs)	6	.703 ± .051	.652 ± .137	.667 ± .207

APPENDIX

Table III. White-tailed deer food plants (Harlow and Hooper 1972) sampled.

Woody plants (green leaves, succulent twigs and buds, hardened twigs and buds)	
honeysuckle (*Lonicera japonica*)	flowering dogwood (*Cornus florida*)
blackberries-dewberries (*Rubus spp.*)	persimmon (*Diospyros virginiana*)
oaks (*Quercus spp.*)	American hornbeaum (*Carpinus caroliniana*)
greenbriers (*Smilax spp.*)	pines (*Pinus spp.*)
red maple (*Acer rubrum*)	azalea (*Rhododendron spp.*)
blueberries (*Vaccinium spp.*)	red cedar (*Juniperus virginiana*)
black cherry (*Prunus serotina*)	American holly (*Ilex opaca*)
elms (*Ulmus spp.*)	black gum (*Nyssa sylvatica*)
grapes (*Vitis spp.*)	hawthorns (*Crataegus spp.*)
yellow poplar (*Liriodendron tulipifera*)	trumpet creeper (*Campsis radicans*)
sumacs (*Rhus spp.*)	viburnums (*Viburnum spp.*)
sassafras (*Sassafras albidum*)	Mt. laurel (*Kalmia latifolia*)
Herbaceous plants (stems and leaves)	
	miscellaneous:
legumes	plantains (*Plantago spp.*)
composites	violets (*Viola spp.*)
grasses	strawberries (*Fragaria spp.*)
sedges	pipsissewa (*Chimaphila spp.*)
rushes	partridge berry (*Mitchella repens*)
ferns	

APPENDIX

Table IV. Plants foraged by white-tailed deer at the Buckingham-Appomattox and Cumberland state forests.

Acer rubrum	red maple
Angelica venenosa	angelica
Aureolaria virginica	false foxglove
Ceanothus americanus	New Jersey tea
Euonymus americanus	strawberry bush
Gillenia trifoliata	Indian physic
Helianthus atrorubens	sunflower
Lactuca canadensis	wild lettuce
Nyssa sylvatica	black gum
Quercus coccinea	scarlet oak
Rubus argutus/allegheniensis	blackberry
Sassafras albidum	sassafras
Smilax glauca	catbrier
Viburnum prunifolium	black haw

APPENDIX

Table V. Wild turkey food plants (USDA-FS 1971, Baskett *et al.* 1980) sampled.

grasses	strawberries (*Fragaria spp.*)
honeysuckle (*Lonicera japonica*)	huckleberries (*Gaylussacia spp.*)
greenbriers (*Smilax spp.*)	blackberries-dewberries (*Rubus spp.*)
sumacs (*Rhus spp.*)	composites
poison ivy (*Rhus radicans*)	grapes (*Vitis spp.*)
legumes	sedges

APPENDIX

Table VI. Bobwhite quail food plants (prominent seed foods for the Piedmont province) (Landers and Johnson 1976) sampled.

	Legumes:
tick trefoils (*Desmodium spp.*)	wild beans (*Strophostyles spp.*)
Lespedezas (*Lespedeza spp.*)	hog peanuts (*Amphicarpa spp.*)
partridge peas (*Cassia spp.*)	spurred butterfly peas (*Centrosema spp.*)
milk peas (*Galactia spp.*)	
	Grasses:
panic grasses (*Panicum spp.*)	paspalums (*Paspalum spp.*)
crabgrasses (*Digitaria spp.*)	foxtail grasses (*Setaria spp.*)
	Miscellaneous:
ragweeds (*Ambrosia spp.*)	wood sorrels (*Oxalis spp.*)
honeysuckle (*Lonicera japonica*)	nut-rushes (*Scleria spp.*)
buttonweed (*Diodia teres*)	beggar-ticks (*Bidens spp.*)
sumacs (*Rhus spp.*)	blackberries-dewberries (*Rhus spp.*)
grapes (*Vitis spp.*)	

VITA

Tony Felix was born in Fall River, Massachusetts on September 29, 1951. He graduated from B.M.C. Durfee High School with high honors in 1969, and thereupon attended Southeastern Massachusetts University from which he graduated with high distinction and a B.S. degree in Electrical Engineering in 1973. From 1973 to 1975, he was employed as an engineer at the Naval Underwater Systems Center in Newport, Rhode Island. In 1975 he resigned to return to college on a full time basis in order to pursue a course of study suited to his interests. He matriculated at the University of Rhode Island in 1975, graduating with highest distinction and a B.S. degree in Resource Development in 1977. While at the University of Rhode Island, he was inducted into the Phi Kappa Phi Honor Society. He became a candidate for an M.S. degree in Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University in 1977. An Environmental Conservation Fellowship was awarded to him by the National Wildlife Federation in 1978. During the 1978-79 academic year, he was a recipient of a graduate teaching assistantship.

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VEGETATIONAL CHANGES RESULTING FROM FOREST CONVERSION IN THE CENTRAL PIEDMONT OF VIRGINIA AND THEIR IMPLICATIONS FOR WILDLIFE

by

Antone Costa Felix, III

(ABSTRACT)

Conversion of natural forest to loblolly pine plantations has become a common practice on commercial forest land in the central Piedmont of Virginia. To gain insight as to how habitat conditions for wildlife vary over time, vegetation composition and structure were quantified in 21 converted stands at two state forests. The stands represented three replications of seven developmental stages ranging in age from 1 to 22 years. Six natural forest stands which typify sites presently being converted were selected for comparison.

The seral process can be exemplified by comparing vegetative changes in species richness, evenness, and vegetative coverage in the ground stratum (<1m). Richness and vegetative coverage showed the same trends: high values in stands 1 to 5 years of age followed by a decline from 5 to 15 years, at which point canopy closure was complete and these variables were relatively stable for the next seven years. Evenness over time was fairly constant, except for three-year-old stands where a decline occurred due to predominance by _Andropogon virginicus_. Trends in richness

and evenness differed from the old-field successional model due to a diverse reservoir of propagative units at the initiation of succession and the rapid closure of the canopy by co-developing pines and sprout hardwoods.

From an analysis of habitat variables, it appeared that one-year-old stands satisfied requirements of bobwhite quail and wild turkey; stands aged three years were deficient in food plants and probably too densely vegetated. Nine-year-old stands still provided browse for white-tailed deer. Post-canopy closure stands (15 to 22 yrs) were of little value to wildlife. In native forest stands (72 yrs), understory forage production was comparable to the post-canopy closure stands, while mast production, as estimated by oak basal area and density, was more than adequate for good deer and turkey habitat.

The present value of converted stands to wildlife depends on their size and interspersion with native forest and other cover types. Their future value could vary significantly depending on the silvicultural treatments applied.