RELATIONSHIP OF UNDERSTORY DEVELOPMENT IN THINNED LOBLOLLY PINE PLANTATIONS TO OVERSTORY STRUCTURE AND SITE CHARACTERISTICS IN THE VIRGINIA PIEDMONT

by

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INTRODUCTION

Management efforts in the southeastern loblolly pine *(Pinus taeda)*[1] type are being intensified in order to meet increased demand for softwood products (Wheeler 1967). In the south-central Piedmont of Virginia over 120,000 ha are classified as loblolly pine, comprising approximately 30 percent of the commercial softwood acreage (Sheffield 1976). Most of this is planted, since the region is almost entirely outside the natural range of loblolly pine (Nelson and Zilgitt 1969). Thinning is commonly practiced in these stands in order to salvage potential mortality and to improve stand development.

Recently there has been much concern over the effects of intensive pine management on other forest resources. Wildlife species in particular are dependent on vegetation structure and composition for food and cover. Although understory vegetation in loblolly pine plantations may include plants valuable as forage (Krochmal and Kologoski 1974), crown closure in unthinned stands will ultimately limit understory growth, and hence the production of food and cover for wildlife (Halls 1974). Changes in overstory density due to thinning result in concurrent changes in the understory vegetation. Forest managers need to be able to predict these changes in order to determine the effects of thinning on wildlife populations. Thinned plantations on old-field sites can present an opportunity to study the influence of overstory trees on vegetation development patterns, since accurate stand histories are often available.

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[1] Common and scientific plant names are according to Gleason (1963).

In order to be useful to forest managers, information on vegetation response to thinning must be related to commonly used forest measurements. Blair and Brunett (1976) studied phytosociological changes in an all-aged loblolly-shortleaf *(P. echinata)* pine ecosystem in relation to overstory density and time since selective timber harvest. They made no attempt to develop prediction equations relating these factors, nor did they consider site variability as a factor. No studies exist relating the effects of thinning in planted loblolly pine stands of the Piedmont to changes in community structure, production, and species composition. Furthermore, there are no previous studies in the southeastern pine ecosystem which would enable managers to predict these changes using standard forest measurements, such as basal area and site index. Predictive information of this type would be extremely useful to forest managers, and could also be incorporated into existing growth and yield models for loblolly pine (Daniels and Burkhart 1975; Burkhart et al. 1972).

Objectives

The objectives of this study are:

1. To develop equations for predicting understory production, based on easily obtainable overstory and site characteristics.
2. To analyze understory species composition with respect to environmental gradients (light, moisture, and time) as expressed indirectly by overstory structure and site measurements.
3. To evaluate the quality of wildlife habitat in old-field pine plantations, with particular emphasis on white-tailed deer *(Odocoileus*

virginianus) forage needs, and to compare habitat quality across the above-mentioned gradients.

Hypotheses Concerning Understory Development in Pine Stands

Aside from site quality, the dominant factors affecting understory and midstory biomass increment are changes in shading and rain throughfall caused by variations in overstory density (Blair and Enghardt 1976, Anderson et al. 1969). Forage and fruit production for wildlife species such as white-tailed deer are generally inversely related to timber stand density (Blair 1969). Opening the forest canopy creates an environment conducive to the production of understory forage species, providing a dependable energy source for wildlife (Blair and Enghardt 1976, Blair 1971). Although understory production is initially increased by thinning, production will again decrease with increasing canopy closure. On mesic sites a multilayered shrub and hardwood community may develop following thinning, growing out of reach of deer and other ground foragers, and shading out forage plants beneath. The midstory increases with the intensity of pine removal, and on mesic sites in Louisiana it is the principal deterrent to growth of forage species (Blair and Enghardt 1976). Repeated thinning on such sites will have limited impact on understory plants, unless the midstory is controlled.

Changes in production caused by thinning are important, both because of the impact of forage production on wildlife populations, and because production can be considered an expression of community function (Skeen 1973). However, the potential effects of thinning on other aspects of vegetation structure should not be overlooked. Thinning may have significant effects on nutrient mobility and uptake, and consequently on the quality of forage for wildlife. Thinning appears to increase the rate of litter decomposition and the amount of available nutrients, especially nitrogen (Boggess 1959); however, these effects may only be temporary (Wells and Jorgensen 1975). Forage protein and phosphorus concentrations tend to be higher in areas under canopies than in adjacent clearcut areas (Wolters 1973). Studies by Crawford et al. (1975) indicated that forage species eaten most often by deer in selectively cut areas had a higher percent dry matter, crude protein, phosphorus, and gross energy content than plants in adjacent clearcut areas. Thus, in very sparse canopies the benefits of increased forage production may be partially negated by accelerated nutrient losses.

Overstory spatial pattern is another aspect of structure which may be influenced by management, and which may in turn influence understory vegetation. Pattern diversity (patchiness) is highest when individuals of different species are present in any small area (Pielou 1966). Pielou also found that natural thinning in forest stands (resulting from competition among trees) apparently increases community pattern diversity. Soil under canopy trees develops properties (pH, cation exchange capacity) which vary spatially in relation to the location of the trees (Zinke 1961). Thus, the spatial pattern of the trees may be an important factor in determining environmental patterns, and in turn may affect understory patchiness. Species diversity in old-field successional communities appears to be particularly high when there is a high degree of both vertical and horizontal heterogeneity (Bazzaz 1975). Thus, in a patchy environment--with patchiness perhaps induced by clumped overstory patterns--one might expect higher diversity of successional species. Reice (1974) demonstrated that the community level process of leaf litter breakdown is unevenly distributed in space, suggesting a patch-specific community component. He further predicted that the rates of other community level processes such as primary production will increase in proportion to the spatial heterogeneity of their environments.

It is clear that many environmental and biotic factors in addition to overstory structure may greatly influence understory developmental patterns. Soil parent material and moisture relationships will largely determine the potential of the site to produce vegetation. Different preabandonment land uses may produce markedly different species invasion strategies, which in turn will affect the development of floristic composition (Tramer 1975). The floristic composition of the site prior to stand establishment (planting) and adjacent seed sources may also greatly influence later development (Egler 1954, Nicholson and Monk 1974).

The above review of field evidence and hypotheses in succession dynamics suggests several predictions regarding understory structural and compositional changes in thinned old-field pine stands having similar land-use histories and site characteristics. Understory production and species composition should be related to and hence predictable from overstory density, time since planting, and time since thinning. Production should be higher in open stands that have had enough time to develop productive understories, but have not developed vigorous midstories. Low overstory densities should promote the coexistence of moderately shade-tolerant forest species with old-field successional species. As crown closure increases, intolerant species should be suppressed; on mesic sites this suppression may be enhanced by the development of a hardwood midstory. Concentrations of nutrients such as nitrogen should be higher in understory plants beneath sparse canopies than in those beneath full canopies. Understory production, diversity of successional species, and nutrient concentrations should be highest in patchy environments, and low in homogeneous environments. In pine stands a major factor promoting patchiness should be tree spatial pattern, with clumped patterns resulting in more patchiness than random or regular patterns. While plantations may start out with essentially regular spatial patterns, patchy site conditions and the uneven application of management practices such as thinning may ultimately result in stands which deviate significantly from regular patterns.

STUDY AREAS

Location

The Buckingham-Appomattox State Forest, located in the west-central Piedmont of Virginia, and the Cumberland State Forest, located approximately 35 km east, were chosen as study areas (Fig. 1). These areas were selected because they contain the major sites and ranges of thinning that are encountered in old-fields of the region planted in pine (S. Warner, pers. comm.). In addition, they have well documented stand histories and are easily accessible.

Site Description

The principal rock formations in this region are quartz serecite, schist, greenstone, and granite gneiss. Most old-field pine plantations in the study area were located over slight to moderately eroded well-drained soils on 2 to 15 percent slopes, such as Cecil, Tatum, Lloyd, and Appling. These sites are considered to be favorable for the growth of loblolly, Virginia *(P. virginiana)*, and shortleaf pine, as well as several other commercial species (U.S.D.A. 1966). Loblolly pine plantations on these sites develop with little competition from hardwoods and other undesirable species, but often Virginia pine invades plantations and becomes established as a major component of the overstory and midstory. Other overstory and midstory species may include *Liriodendron tulipifera, Liquidambar styraciflua, Acer rubrum, Juniperus virginiana,* and *Nyssa sylvatica.* Understory development in these stands ranges from very sparse (0 to 5 percent) to moderate (10 to 20 percent) coverage, depending on overstory canopy closure and on specific site characteristics. Typical understory species include *Lonicera japonica, Rubus* spp.,

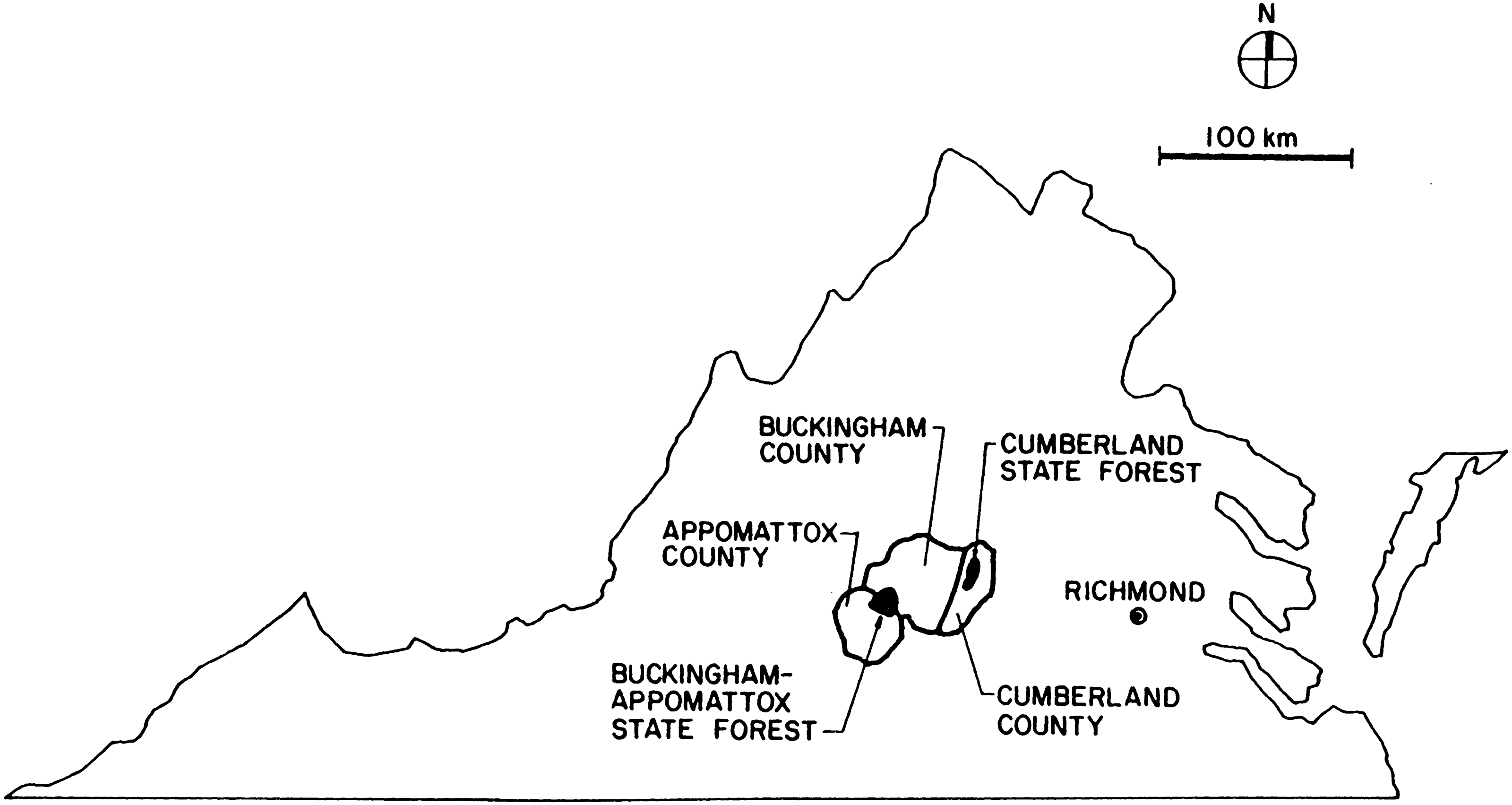

Figure 1. Location of study areas for overstory-understory relationships in loblolly pine plantations in the Virginia Piedmont.

Acer rubrum, Pinus spp., *Panicum* spp., *Quercus* spp., and *Vaccinium* spp. A number of stands are planted on well-drained to somewhat poorly drained soils on 2 to 15 percent slopes, such as Iredell and Elbert. These sites are somewhat less productive for pines than the previously described sites, and understory competition seems to be more vigorous, although including many of the same species. A few stands are located on alluvial or mixed alluvial sites on 0 to 2 percent slopes. These sites tend to be quite productive for pines, but also are characterized by a vigorous growth of hardwoods and other competitors. In open canopied stands, the understory strata may be extremely productive, comprised of *Lonicera japonica, Rhus radicans,* grasses, sedges, and a large variety of herbaceous plants. Closed canopied stands on these sites tend to have somewhat sparser understories, but may have a vigorous growth of hardwoods such as *Liriodendron tulipifera, Acer rubrum,* and *Platanus occidentalis* in the midstory and overstory.

Site History

The old-field sites in question were abandoned from agriculture during the period 1937 to 1956 and subsequently planted to loblolly pine. Prior to abandonment these sites were predominantly in corn, with some in wheat. Pine planting was generally completed within one year of abandonment, with occasional lapses of two to three years before planting. Site preparation was minimal, generally involving only the burning of broomsedge *(Andropogon* spp.*)*. Nursery stock was hand-planted in rows at various spacings in order to provide 250 to 259 seedlings per ha. There was no fertilization or control of hardwood or other plant competition on these sites. Depending on the vigor of the trees, the stands were first commercially thinned between 20 and 40 years of age. In some cases earlier salvage cuts may have been made, with the purpose of removing trees damaged by ice, wind, fire, or insects (S. Warner, pers. comm.) Records of the actual basal areas removed in thinnings are not available, but an examination of stands in a wide range of conditions indicated that prethinning basal areas probably did not exceed 50 m^2/ha, while post-thinning basal areas were probably not less than 15 m^2/ha.

MATERIALS AND METHODS

Field Methodology

Overstory Stand and Plot Sampling

The overstory data were used primarily to predict changes in understory dynamics. Therefore, stands were purposefully selected with the objective of establishing a wide range in basal areas and times since thinning. Fourteen stands ranging in times since thinning from 1 to 12 years were selected. All stands except two had been thinned once; the remaining two were thinned lightly about 10 years prior to the most recent thinning. Ten stands were on soils formed from granite gneiss or schist, two were on soils of dark-colored basic rock origin, and two were on alluvial or mixed alluvial soils (U.S.D.A. 1966). Past cultural disturbances of these soils probably override textural considerations in many cases, and make these soils classifications of limited utility.

Prior information on site quality and stand basal areas was generally lacking or inadequate. Therefore, stands were visited and subjectively divided into two to five substands based on overstory density and height, and topography (slope, aspect, and slope position). In each substand, one 400 m^2 (20 m by 20 m square) plot was established with a permanently staked center. This size of plot was considered by Mueller-Dombois and Ellenberg (1974:48) to be sufficient to adequately represent overstory structural and species compositional characteristics. To the greatest extent possible, each plot was representative of the substand, and sharp changes or edge influences were avoided.

Measurements on 29 overstory plots were taken during January to April, 1978. On each plot, all overstory (5 m or taller) trees were tallied by species, and the diameters measured to the nearest mm at 1.4 m above ground line (d.b.h.) to obtain numbers per ha and basal area (m^2/ha) for each plot. The total heights of the three dominant or co-dominant loblolly pines closest to the plot center were measured to the nearest 0.5 m and used to calculate site index values (Burkhart et al. 1972). Increment cores were obtained from the site index trees to check the ages of the stands against records. Slope percent and aspect in degrees azimuth were measured at the plot center. Slope position was classified as being: floodplain-terrace, toe slope, foot slope, back slope, shoulder, and summit (Smith and Burkhart 1976).

Relevé Plots

The relevé method (Benninghoff 1966; Mueller-Dombois and Ellenberg 1974:45) was used to provide an overall structural and compositional evaluation for each 400 m^2 plot, and to enable comparisons among plots. A tentative species list and voucher collection were obtained by repeated visits to the plots during April to June, 1978. The contribution of each species to the herb (less than 1 m), shrub (1 m to less than 5 m) and tree (5 m or greater) strata was quantified during 29 June to 3 July, using a modification of Benninghoff's (1966) cover-abundance scales (Table 1).

Forage Production Plots

Understory forage production and structure for the herb (0 m to less than 1 m) and low shrub (1 m to less than 2 m) strata were measured during 3 July to 20 August, 1978, using 20 1 m by 1 m square plots randomly located in each 400 m^2 plot. The 2 m maximum height for these

Table 1. Cover and abundance scales used in vegetation analyses for loblolly pine stands in the Virginia Piedmont.

Cover Scale		Abundance Scale	
Scale Value	Percent Cover	Scale Value	Description
0	0	0	absent
1	0-0.25	1	growing singly
2	0.25-1	2	small groups
3	1-4	3	distinct groups
4	5-9	4	small colonies, rather dense
5	10-24		
6	25-32	5	solid stands, dense
7	33-49		
8	50-74		
9	75-99		
10	100		

strata was chosen because most forage production available to herbivores would occur below this height. Twenty replicates in each overstory plot were chosen as a compromise between a sample size beyond which the variance of mean forage production would not be significantly lowered, and one which was allowed by resource and time restrictions. To avoid confounding time trends over the course of the sampling period, the order in which each 400 m^2 plot was sampled was randomized with respect to time. Current annual leaf production, shoot extension, and fruit production of trees and shrubs, and all aboveground biomass of herbs and grasses, were collected as a measure of forage production. Whittaker (1961) has shown that such measures may also be directly related to net primary production. To retain maximum flexibility in later analyses, the plant materials were collected by species in each 1 m stratum, and fruits were sorted separately from leaf and twig production. In many cases, production in a given category was insufficient (less than 1 percent of plot production) to warrant separate collection. In such cases, several species of plant parts were combined and the relative proportions of each by weight were estimated ocularly. Numbers of tree stems originating in the 1 m^2 plot were tallied by species. Vertical stratification of vegetative cover was measured at the center of each 1 m^2 plot, using a modification of Wight's (1938:106) density board method. A board composed of four 20 cm high by 50 cm wide backdrops centered at 0.5 m, 1.0 m, 1.5 m, and 2.0 m was used to measure percent cover (Table 1) at a fixed distance of 2 m. The direction that the board faced was changed systematically according to the four cardinal directions from one plot to the next, in order to obtain a uniform representation of cover.

To provide an accurate reflection of the relationship between canopy coverage and understory dynamics, canopy coverage was measured at the same time the understory plots were sampled, using a spherical densiometer (Strickler 1959) located at the plot center. In addition, the 20 1 m^2 plot centers were used as random points from which the distances to the nearest dominant or codominant tree were measured to the nearest cm. These values were used in conjunction with the density information collected from the overstory plots to estimate overstory spatial pattern using Pielou's (1959) index.

Laboratory Procedures

Understory production samples were oven-dried at 65 C for 72 hours and then weighed to the nearest 0.01 g. A list of key species or species groups was developed, using those species determined by Harlow and Hooper (1971) to comprise the bulk of deer diet in the southeastern Piedmont, and which were relatively abundant on these study areas. Vegetation samples from all plots were pooled according to these groups and according to plant part (leaves, twigs, and fruit). Species of particular importance and abundance such as honeysuckle *(Lonicera japonica)* were kept separated according to the stands in which they occurred. Dry weights were obtained for these pooled groups in order to obtain relative proportions of each plant part for the species occurring in the study plots. Vegetative material in each pooled group was thoroughly mixed and from each random samples of approximately 10 g were ground in a Wiley mill to pass a 30 mesh screen. Three replicates from each sample, pooled across stands, and one replicate for the species separated by stand, were analyzed for percent nitrogen using a micro-Kjeldahl procedure. Percent nitrogen was converted to percent crude protein by multiplying by 6.25 (McKenzie and Wallace 1954). Two replicates from each sample, pooled across stands, were analyzed for gross energy (cal/g) in a Parr adiabatic oxygen bomb calorimeter. Gross energy was determined on a stand basis only for honeysuckle leaves. Three replicates from each sample (pooled across stands and separated by stand) were analyzed for percent dry matter digestibility (referenced to deer) by Carlile's (1978) modification of Palmer et al.'s (1976) method.

Quantitative Techniques

Prediction Equations for Forage Production

Two basic approaches were taken to the development of prediction equations for forage production. First, theoretical models based on differential equations were developed, and the parameters of these were estimated using the sample data. The second was empirical in that no underlying model form was assumed. In this approach, the data were used in an exploratory fashion to develop a model form and to screen predictor variables.

Development of a theoretical growth model for forage production. The theoretical growth model used was based on the general Von Bertalanffy (1957) model for biological growth (Beverton and Holt 1957; Pienaar and Turnbull 1973). Von Bertalanffy developed the following model, based on a metabolic hypothesis:

$$\frac{dW_t}{dt} = nW_t^{m} - vW_t \qquad (1)$$

where:

W_t = the mass or volume of an organism or group of organisms at time t,

n = the anabolic or self-accelerating growth rate,

v = the catabolic or self-decelerating growth rate,

m (nonnegative) = a constant relating, for example, volume to surface area.

This equation, when integrated with respect to time, gives:

$$W_t = [\, \frac{n}{v} - (\frac{n}{v} - W_o^{1-m})\{\exp(-v(1-m)t)\}]^{1/(1-m)} \qquad (2)$$

where:

W_o = the mass or volume at time t=0.

The upper limit to growth is given by:

$$S = \lim_{t\to\infty} W_t = (\frac{n}{v})^{1/(1-m)} \qquad (3)$$

Thus equation (2) may be simplified by substituting S from (3), and letting $k=v(1-m)$ and $b=1-S^{m-1}W_o^{1-m}$:

$$W_t = S[1-b\{\exp(-kt)\}]^{1/(1-m)} \qquad (4)$$

Equation (4) gives rise to a family of growth curves, the shapes of which depend on the value of m. For example, m=2 yields the logistic equation, while m=0 results in a monomolecular relationship. In all cases, the growth rate $(\frac{dWt}{dt})$ declines over time, and the size of the individual or population has a finite upper bound, S (Pienaar and Turnbull 1973).

In order to apply this basic growth equation to the specific case of understory development in thinned pine plantations, the following working hypotheses were formulated. First, it was proposed that understory growth follows the basic Von Bertalanffy relationship; i.e., that growth rate starts out high and declines over time. Second, it was proposed that the total biomass (W_t) of the understory approaches an upper limit S over time. For a particular stand, S should be a function of the quality of the site and the amount of growing space on the site. For this study, site quality should be primarily determined by the moisture, light, and nutrient relationships on the site, and may be characterized by such measurements as slope, aspect, slope position, overstory site index, and soil type. The amount of growing space on the site for understory vegetation should be a function of the competition for light, moisture, and nutrients from the understory itself (self-decelerating growth) and from the upper strata, primarily the canopy.

The basic objective here was to develop logical equations for predicting understory forage production in the 0 to 2 m stratum (PRODUC) as a function of time since thinning (TH), age of the stand at thinning (TP), overstory basal area (BATOT), and site quality, initially expressed by overstory site index (SI) (Table 2). If PRODUC represents understory growth rate, and t = TH years after thinning, then (4) can be differentiated with respect to time to give:

$$\mathrm{PRODUC} = \frac{dW}{d\mathrm{TH}} = \frac{S}{(1-m)}\,[1-b\{\exp(-k\mathrm{TH})\}]^{m/(1-m)}bk\{\exp(-k\mathrm{TH})\} \tag{5}$$

Since $b = 1-S^{m-1}W_o^{\,1-m}$, this gives:

Table 2. Notation and description of variables used in study of overstory-understory relationships in loblolly pine plantations in the Virginia Piedmont.

Variable	Description	Units
ASPECT	Aspect measured at plot center	Degrees azimuth
BACO	Basal area of dominants and codominants	m^2/ha
BACOI	Basal area of dominants, codominants, and intermediates	m^2/ha
BAMID	Basal area of midstory (BATOT-BACOI)	m^2/ha
BATOT	Basal area of all overstory trees	m^2/ha
C_p	C_p evaluation of prediction error	---
CAL	Gross energy content of forage	cal/g
CANCOV	Canopy cover measured at plot center	percent
CAR_e	Energy based carrying capacity	deer/ha
CAR_p	Protein based carrying capacity	deer/ha
COSAS	Cosine of (ASPECT - 45°)	---
CPROT	Crude protein content of forage	percent
DAYS	Time elapsed since sampling began	days
DEN1	Foliage density at 0.5 m	percent
DEN2	Foliage density at 1.0 m	percent
DEN3	Foliage density at 1.5 m	percent
DEN4	Foliage density at 2.0 m	percent
DMD	Dry matter digestibility of forage	percent
E_p	Average residual from validation set	---
FAF	Functional availability factor	---
IMPVAL	Importance value	percent
MSLOF	Validation mean square lack of fit	---
MQA_e	Energy based minimum qualitative ability of habitat to support deer	---
MQA_p	Protein based minimum qualitative ability of habitat to support deer	---
NCO	Number of dominants and codominants	number/ha
NCOI	Number of dominants, codominants, and intermediates	number/ha
NMID	Number of midstory trees	number/ha
NTOT	Total number of overstory trees	number/ha
PDM	Dry matter of forage material	percent
PIEL	Pielou's spatial pattern index	---
PRODUC	Total forage production, 0 to 2 m	kg/ha
PRODUC1	Forage production, 0 to 1 m	kg/ha
PRODUC2	Forage production, 1 to 2 m	kg/ha
$R^2{}_c$	Coefficient of determination, corrected for pure error	---
RELABUND	Relative abundance	percent
RELCOV	Relative cover	percent
RELDEN	Relative density	percent

Table 2. Notation and description of variables used in study of overstory-understory relationships in loblolly pine plantations in the Virginia Piedmont (continued).

Variable	Description	Units
RELDOM	Relative dominance	percent
RELFREQ	Relative frequency	percent
RUVOL	Volume of forage material occurring in deer rumen for each species	percent
SI	Site index for loblolly pine	m at age 25 years
SLOPE	Slope measured at plot center	percent
SRANK	Slope position ranked by production	1-6 rank scale
SSE	Model residual sum of squares	---
SSLOF	Model lack of fit sum of squares	---
SSPE	Pure error sum of squares	---
SSPR	Validation residual sum of squares	---
SST	Total sum of squares	---
STEMS	Total number of understory trees stems	number/ha
STEMS1	Number of understory tree stems, 1 m	number/ha
STEMS2	Number of understory tree stems, 1 m to 5 m	number/ha
TH	Time since thinning (as of summer 1978)	years
TP	Age of stand at most recent thinning	years
UI	Utilization index for forage species	---

$$PRODUC = \frac{S}{(1-m)} [1-(1-S^{m-1}W_o{}^{1-m})\{exp(-kTH\}]^{m/(1-m)} (1-S^{m-1}W_o{}^{1-m})$$
$$k\{exp(-kTH)\} \qquad (6)$$

The understory biomass (unknown) at time TH = 0 is W_o, and thus represents understory biomass just prior to thinning (Fig. 2). W_o may be represented as a function of TP by the relationship:

$$W_{o_{TP}} = P[1-c\{exp(-hTP)\}]^{1/(1-m)} \qquad (7)$$

where:

P = the upper growth limit for W_o,

$c = 1-P^{m-1}W_{oo}{}^{1-m}$,

h = a constant similar to k in (6), and

W_{oo} = the initial biomass in the stand at planting.

Substituting (7) into (6) gives:

$$PRODUC = \frac{S}{(1-m)} [1-(1-S^{m-1}P^{1-m}(1-P^{m-1}W_{oo}{}^{1-m})\{exp(-hTP)\})$$
$$\{exp(-kTH)\}]^{m/(1-m)}[1-S^{m-1}P^{1-m}(1-(1-P^{m-1}W_{oo}{}^{1-m})\{exp(-hTP)\})]$$
$$k\{exp(-kTH)\} \qquad (8)$$

For $m=0$ (monomolecular growth) and assuming $W_{oo} = 0$, this simplifies to:

$$PRODUC = [S-P+P\{exp(-hTP)\}]k\{exp(-kTH)\} \qquad (9)$$

Initially assume S is a function (of unspecified form) of BATOT and SI. Because there was no information on pre-thinning basal areas, any differences in initial understory biomass were assumed to be related to site quality alone; thus P was assumed to be a function of SI.

The monomolecular form (9) was employed in most attempts to develop prediction equations, because of its relative simplicity and because, in

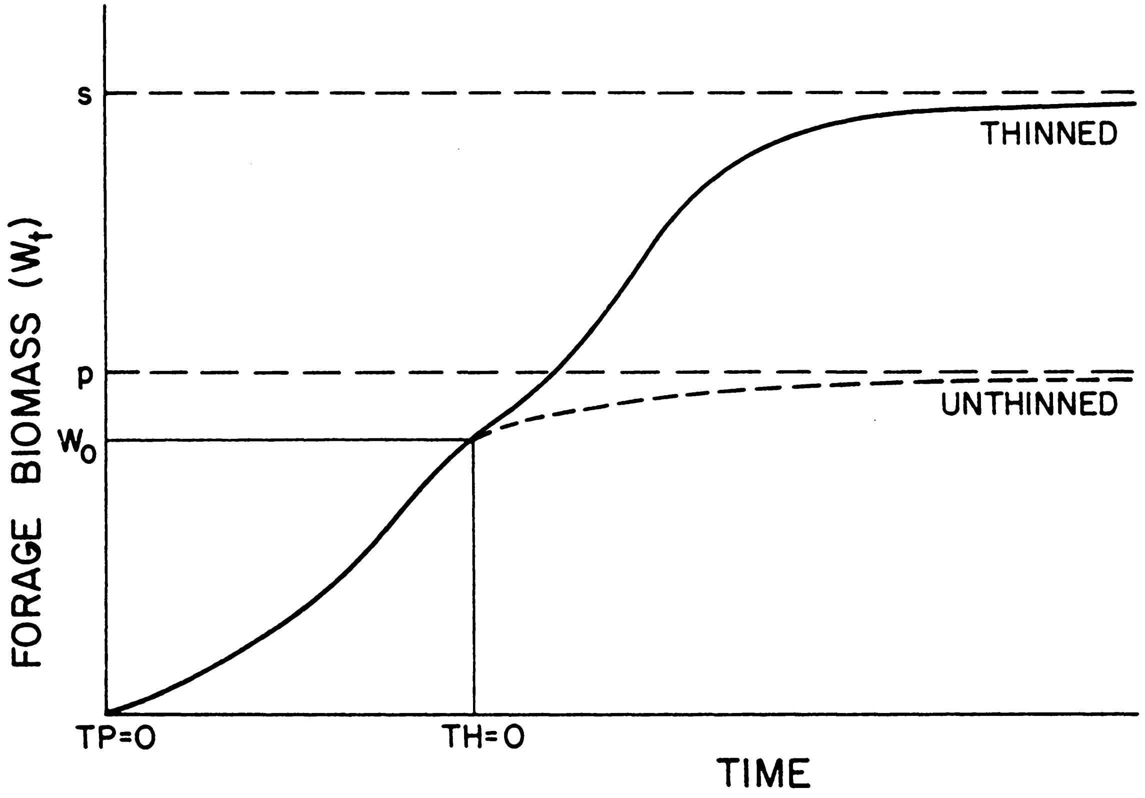

Figure 2. Hypothesized relationship between time since thinning, time since planting, and understory production in loblolly pine plantations in the Virginia Piedmont.

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[a] TH and TP represent time since thinning and age of the stand at thinning, respectively. P and S represent the upper limits to understory growth following planting and thinning, respectively. W_0 is the initial understory biomass at time TH = 0.

the investigator's opinion, it could adequately approximate the basic growth relationships involved. Several variations on the basic model expressed in (9) were developed. Assuming that BATOT and SI affect the upper growth limit S in a linear fashion, (9) gives:

$$\text{PRODUC} = [a\text{SI} - b\text{BATOT} - c\text{SI} + c\text{SI}\{\exp(-h\text{TP})\}]k\{\exp(-k\text{TH})\} \qquad (10)$$

If SI and BATOT interact, (1) may be rewritten as:

$$\text{PRODUC} = [a\text{SI} - b\text{BATOT} - c\text{SI} + d\text{SI}*\text{BATOT} + c\text{SI}\{\exp(-h\text{TP})\}] \; k\{\exp(-k\text{TH})\} \qquad (11)$$

Basal area may act not only as an upper limit to production, but may act over time to dampen growth, yielding:

$$\text{PRODUC} = [a\text{SI} - b\text{BATOT} - c\text{SI} + c\text{SI}\{\exp(-h\text{TP})\}]k\{\exp(-k\text{BATOT}*\text{TH})\} \qquad (12)$$

Parameter estimation for the theoretical models. Initially only SI and BATOT were used as expressions of site quality and overstory structure, respectively. In all but the simplest cases, models of the forms in equations 10 to 12 were nonlinear in the parameters (a,b,c,d,h,k). The modified Gauss-Newton and Marquardt procedures (Barr et al. 1976) were used to obtain estimates iteratively. Starting values were obtained by splitting complex equations into additive parts, each of which could be estimated using log-linear models. When this approach gave non-convergent estimates, grid search procedures (Barr et al. 1976) were used to obtain regions of parameter space for which estimates would converge.

Empirical approaches to prediction equations. The above, while founded on biological growth theory, had the disadvantage of confining the model building procedure to specific model forms. Further, these procedures assumed that the model contained all of the necessary predictor variables; hence, they were inappropriate for screening variables in an exploratory fashion. Thus, the problem was also approached in the absence of *a priori* models. The data were examined using linear and rank correlations (Barr et al. 1976) and scatterplots of the dependent variable versus several likely predictor variables. Predictor variables included: time since thinning (TH), age of the stand at thinning (TP), overstory basal area (BATOT), overstory density (NTOT), overstory spatial pattern (PIEL), slope (SLOPE), aspect, slope position, and site index (SI). A modification of Smith and Burkhart's (1976) ranking procedure was used to place slope position on a 1 to 6 ordinal scale (SRANK) according to a hypothetical production gradient (Appendix XXI). Aspect was related to an insolation gradient by a cosine transformation (COSAS) described by Stage (1976). Stepwise regression procedures (Barr et al. 1976) were used to screen variables from simple linear, log-linear, quadratic, and inverse models, involving subsets of the above variables.

Methods for comparing prediction equations. Once the parameters for the models described above were estimated, the resulting prediction equations were compared with respect to how well they fit the sample data, and how well they predicted. A goodness of fit statistics was computed by modifying the R^2 statistic (Draper and Smith 1966) as:

$$R_c^2 = \frac{SSR}{SST - SSPE} \tag{13}$$

where:

SSR = the sum of squares due to the model,

SST = the corrected total sum of squares of PRODUC, and

SSPE = the pure error sum of squares, based on the variation within each of the 29 overstory plots, i.e., on repeated measurements for PRODUC on each point in predictor space (Draper and Smith 1966).

The model residual sum of squares (SSE) could be partitioned into parts: lack of fit (SSLOF) and SSPE, where:

$$SSLOF = SSE - SSPE \tag{14}$$

The C_p statistic (Gorman and Toman 1966) is considered to be a measure of the variance of the predicted values from a model, and was computed as:

$$C_p = k + \frac{(s^2 - \hat{\sigma}^2)}{\hat{\sigma}^2} (p-k) \tag{15}$$

where:

k = the number of parameters being estimated,

s^2 = the residual mean square from the model,

$\hat{\sigma}^2$ = the estimate of the variance of PRODUC based on SSPE, and

p = the number of points in prediction space (29 overstory plots).

In addition to these statistics, the residuals from the respective models were examined using scatterplots for trends over the sampling period and over the ranges of the predicted and predictor variables, including variables not in the model which might be candidates for inclusion as predictors.

A more rigorous test of a prediction equation is its performance in a data set independent of that used to estimate the model's parameters (Snee 1977). To that end, the 29 overstory plots were stratified into six groups according to three major factors thought to control much of the variability in PRODUC: soil type, SRANK, and CANCOV. A random sample of ten plots, proportional to the number of plots in each group, was selected as a validation set. The remaining 19 plots were used to estimate the parameters for each candidate model. These estimates were used in conjunction with the predictor variables of the validation set to obtain predicted values for PRODUC. A prediction sum of squares (SSPR) was computed as:

$$\mathrm{SSPR} = \sum_{i=1}^{N_2} (Y_i - \hat{Y}_i)^2 \tag{16}$$

where:

Y_i = the observed values for PRODUC in the validation set,

$\hat{Y}_i$ = the predicted values for PRODUC based on the independently derived estimates, and

N_2 = the size of the validation set (ten plots times 20 replicates per plot).

Two model comparison statistics were based on the validation set residuals. These were a lack of fit mean square (MSLOF) and an average prediction residual (E_p), computed as:

$$\mathrm{MSLOF} = \frac{\mathrm{SSPR - SSPE2}}{p-k} \tag{17}$$

where:

SSPR, k, and p are defined above, and

SSPE_2 = the pure error sum of squares in the validation set.

$$E_p = \sum_{i=1}^{N_2} \frac{(Y_i - \hat{Y}_i)}{N_2} \tag{18}$$

where:

Y_i, $\hat{Y}_i$, and N_2 are defined above.

Ordination Procedures

Ordination techniques can be used to parsimoniously represent vegetation structure and composition data by artificially constructed axes. These axes represent "vegetatively derived gradients," which can sometimes be interpreted by their correlations with known physical gradients (Pielou 1977, Isebrands and Crow 1975). Principal component (Isebrands and Crow 1975) and polar (Bray and Curtis 1957) ordinations were used to develop vegetative gradients, based on sample data collected in the overstory, relevé, and production plots. Relative dominance (RELDOM), density (RELDEN), and frequency (RELFREQ) (Mueller-Dombois and Ellenberg 1974) were used as input into the ordination procedures. For the overstory plots RELDOM and RELDEN for each species were computed as:

$$\text{RELDOM}_i = \frac{\text{Basal area (m}^2\text{/ha) for the i}^{\text{th}}\text{ species}}{\text{Basal area for all species on the plot}} \times 100 \text{ percent} \quad (19)$$

$$\text{RELDEN}_i = \frac{\text{Density (stems/ha) for the i}^{\text{th}}\text{ species}}{\text{Density for all species on the plot}} \times 100 \text{ percent} \quad (20)$$

Importance values (IMPVAL) were calculated from the overstory data as:

$$\text{IMPVAL}_i = 1/2\ (\text{RELDOM}_i + \text{RELDEN}_i) \quad (21)$$

Importance values were calculated by strata for the relevé data using cover as an expression of dominance, and abundance (Table 1) as an expression of density and frequency:

$$\text{IMPVAL}_i = 1/2\ (\text{RELDOM}_i + \text{RELABUND}_i) \quad (22)$$

where:

$$\text{RELDOM}_i = \frac{\text{Cover of the } i^{th} \text{ species, midpoint of intervals (Table 1)}}{\text{Cover of all species on the plot}} \times 100 \text{ percent} \quad (23)$$

$$\text{RELABUND}_i = \frac{\text{Abundance value (Table 1) for } i^{th} \text{ species}}{\text{Abundance value of all species on the plot}} \quad (24)$$

Relative dominance, density, and frequency for the forage production plots were computed by strata on each 400 m^2 plot as:

$$\text{RELDOM}_i = \frac{\text{Production of the } i^{th} \text{ species (kg/ha)}}{\text{Production of all species on the plot}} \quad (25)$$

$$\text{RELDEN}_i \text{ (tree species only)} = \frac{\text{Stems/ha for the } i^{th} \text{ species}}{\text{Stems for all species on the plot}} \times 100 \text{ percent} \quad (26)$$

$$\text{RELFREQ}_i = \frac{\text{Number of occurrences in 1 } m^2 \text{ plots for } i^{th} \text{ species}}{\text{Number of occurrences for all species}} \times 100 \text{ percent} \quad (27)$$

Importance values for the tree species were computed as:

$$\text{IMPVAL}_i = 1/3(\text{RELDOM}_i + \text{RELFREQ}_i + \text{RELDEN}_i) \quad (28)$$

and for non-tree species as:

$$\text{IMPVAL}_i = 1/2(\text{RELDOM}_i + \text{RELFREQ}_i) \quad (29)$$

The ORDIFLEX procedure (Gauch 1977) was used to perform principal component and polar ordinations on the transformed data. Species which occurred in fewer than two plots were deleted from the analyses to reduce the number of zero values in the data matrix. Plot scores, representing the positions of overstory plots in species space, and species scores, representing the positions of species in sample space, were computed and graphically displayed. In an effort to add biological meaning to these scores, the plot scores for each of the first three PCA axes and two polar axes were compared with overstory variables measured on the plots using linear and rank correlation procedures (Barr et al. 1976). To assist in comparing the ordination results with the forage production models, PCA and polar scores were also correlated with mean PRODUC values on each plot. Variables which correlated at the 0.10 significance level with plot scores were retained as being possibly related to the vegetatively derived axes. In addition, there is a direct relationship between the PCA structure of sample ordination and that of species ordination, such that scores for one may be obtained from the other by a linear transformation (Pielou 1977:339). Thus, any biological interpretations placed on the PCA plot scores would be equally applicable to the species scores. The same is not true for polar ordination, because the axes for sample and species ordinations are derived independently of one another (Bray and Curtis 1957).

Analysis of Nutrient Information

General linear model procedures (Barr et al. 1976) were used to analyze the variability in gross energy (CAL), percent dry matter digestibility (DMD) and percent crude protein (CPROT) according to species groups and plant parts (leaves, twigs, or fruit). Certain species and plant part groupings for CAL, DMD, and CPROT were also analyzed with respect to their relationships to average stand characteristics using correlation procedures.

Calculation of Forage Based Carrying Capacity for White-Tailed Deer

A weighted averaging technique (Forsythe 1978:28-30) was applied to the production data to calculate "functionally available" forage produced for deer in the summer season. A utilization index (UI) for each species group was computed as:

$$UI_i = \frac{RUVOL_i \ PDM_i}{PRODUC_i} \tag{30}$$

where:

$RUVOL_i$ = percent occurrence by volume in deer rumen for the summer season for the i^{th} species (Harlow and Hooper 1971),

PDM_i = the average percent dry matter of the i^{th} species (Crawford et al., 1975, Miller 1958), and

$PRODUC_i$ = the production (kg/ha) in the 0 to 2 m stratum for the i^{th} forage species.

Forage items were ranked according to UI, and a functional availability factor (FAF) for each species was computed as:

$$FAF_i = [(UI_i/UI_n) + (i/n)]0.5 \qquad i=1,2,.....n \tag{31}$$

where:

n = the number of food items in the summer diet (Harlow and Hooper 1971),

i = the rank of the i^{th} food item,

UI_i = the utilization index of the i^{th} ranked food item, and

UI_n = the utilization index of the n^{th} (highest) ranked food item.

Ranks were introduced in the equation "to temper any extreme effects in the FAF calculations caused by relying exclusively on the sensitive (and sometimes questionable) utilization indices" (Forsythe 1978:

29). Total functionally available nutrient supply (TFAF) was calculated as:

$$\mathrm{TFAF} = 0.40 \left[\sum_{i=1}^{n} \mathrm{FAF}_i \ \mathrm{PRODUC}_i \ \mathrm{NUT}_i \right] \qquad (32)$$

where:

0.40 = the average maximum browse utilization that a forage plant can tolerate without impeding future production (Lay 1965),

FAF_i, PRODUC_i, and n are as defined above, and

NUT_i = the nutrient concentration of the i^{th} species for digestible energy (kcal CAL times percent DMD) or percent crude protein.

Available nutrient levels were compared to daily maintenance requirements for white-tailed does in summer (Silver et al. 1969; Ullrey et al. 1969, 1970; Moen 1973; Robbins et al. 1974). Minimum qualitative ability of the vegetation to meet the daily requirements of a doe in summer based on energy (MQA_e) and protein (MQA_p) requirements were computed as:

$$\mathrm{MQA}_e = \mathrm{DI}_e/\mathrm{DMR}_e \qquad (33)$$

$$\mathrm{MQA}_p = \mathrm{DI}_p/\mathrm{DMR}_p \qquad (34)$$

where:

DI_e = daily ingestion of energy, and

DI_p = daily ingestion of protein, computed as:

DI_e = (0.176)(20.83) x weighted (by UI) average digestible energy, and (35)

DI_p = (0.176)(20.83) x weighted (by UI) average CPROT, (36)

where:

20.83 kg = the approximate average metabolic body weight (MBW) for does in the summer season (Moen 1973, Carlile 1978, Forsythe 1978),

0.176 = the approximate average daily intake rate (kg/kg MBW) for lactating does in summer (Moen 1973, Forsythe 1978),

DMR_e = daily metabolic requirements for energy (kcal/day), and

DMR_p = daily metabolic requirements for protein (g/day).

For values of MQA_e or MQA_p less than one, the habitat was considered to have insufficient nutrient concentrations in the forage plants to support one doe, regardless of total forage production. For MQA_e and MQA_p both greater or equal to one, seasonal carrying capacities (deer/ha) based on energy (CAR_e) and protein (CAR_p) were calculated as:

$$CAR_e = \frac{TFAF_e}{(107)DMR_e} \qquad (37)$$

$$CAR_p = \frac{TFAF_p}{(107)DMR_p} \qquad (38)$$

where:

$TFAF_e$ = the total functionally available levels for energy (kcal/ha),

$TFAF_p$ = the total functionally available levels for protein (kg/ha),

107 days = the length of the summer season (Harlow and Hooper 1971), and

DMR_e and DMR_p are defined above.

Energy and protein based carrying capacities were evaluated for individual stands and for the study area as a whole. Carrying capacities were also compared with average stand characteristics using correlation procedures.

RESULTS AND DISCUSSION

Overstory Structure and Understory Forage Production

The overstory plots exhibited a wide range in structural and site characteristics, with basal areas (BATOT) ranging from 18.8 to 43.5 m^2/ha, canopy coverages (CANCOV) ranging from 51.6 to 90.9 percent, and site indices (SI) ranging from 14.2 to 23.8 m (base age 25 years). Understory forage production (PRODUC) was extremely variable, with 400 m^2 plot means ranging from 154 to 1690 kg/ha; individual 1 m^2 plot measurements of PRODUC ranged from 0 to 2545.8 kg/ha. Linear correlation analyses indicated apparent relationships between PRODUC and certain overstory characteristics, in particular time since thinning (TH), age of the stand at thinning (TP), transformed aspect (COSAS), ranked slope position (SRANK), BATOT, and CANCOV (Table 3). Rank correlations were in general agreement with the linear correlations, and are not presented.

Prediction Equations for Forage Production

As discussed earlier, two approaches to building prediction equations were taken. Initially BATOT, SI, TH and TP were included as variables in theoretically derived nonlinear models. Residual plots from these models indicated trends with variables not included in the models, including quadratic terms in TH, TP, and BATOT, and linear and quadratic terms in SRANK, CANCOV, SLOPE, and COSAS. Stepwise selection procedures (Barr et al. 1976) were applied to empirical linear models, which included linear, quadratic, and logarithmic terms for TH, TP, SLOPE, COSAS, SRANK, SI, BATOT, CANCOV, and PIEL, and inverse terms for BATOT and CANCOV. The best five empirical and best three theoretically derived

Table 3. Correlations of understory forage production and key overstory structural variables for loblolly pine plantations in the Virginia Piedmont.[a]

	PRODUC	TH	TP	SLOPE	COSAS	SRANK	SI	BATOT	CANCOV	PIEL
PRODUC	---	-0.34** (1)	-0.26** (1)	0.07^{+} (1)	0.20** (1)	0.11** (1)	-0.02 (1)	-0.29** (1)	-0.34** (1)	0.06 (1)
TH	-0.34** (1)	--- ---	0.23** (2)	-0.55** (2)	-0.29** (2)	0.35** (2)	0.47** (2)	0.54** (2)	0.54** (2)	-0.10* (2)
TP	-0.26** (1)	0.23** (2)	--- ---	0.11** (2)	-0.02 (2)	-0.14** (2)	0.23** (2)	0.39** (2)	0.27** (2)	0.09* (2)
SLOPE	0.07 (1)	-0.55** (2)	0.11** (2)	--- ---	0.25** (2)	-0.66** (2)	-0.19** (2)	-0.20** (2)	-0.30** (2)	-0.03 (2)
COSAS	0.20** (1)	-0.29** (2)	-0.02 (2)	0.25** (2)	--- ---	-0.12** (2)	-0.10* (2)	-0.08^{+} (2)	-0.32** (2)	0.06 (2)
SRANK	0.11** (1)	0.35** (2)	-0.14** (2)	-0.66** (2)	-0.12** (2)	--- ---	0.35** (2)	0.12** (2)	0.32** (2)	-0.06 (2)
SI	-0.02 (1)	0.47** (2)	0.23** (2)	-0.19** (2)	0.10* (2)	0.35** (2)	--- ---	0.54** (2)	0.40** (2)	-0.30** (2)
BATOT	-0.29** (1)	0.54** (2)	0.39** (2)	-0.20** (2)	-0.08^{+} (2)	0.12** (2)	0.54** (2)	--- ---	0.57** (2)	-0.05 (2)
CANCOV	-0.34 (1)	0.54 (2)	0.27 (2)	-0.30 (2)	-0.32 (2)	0.32 (2)	0.40 (2)	0.57 (2)	--- ---	-0.11 (2)
PIEL	0.06 (1)	-0.10* (2)	0.09* (2)	-0.03 (2)	0.06 (2)	-0.06 (2)	-0.30** (2)	-0.05 (2)	-0.11** (2)	--- ---

[a] Variable symbols are defined in Table 2. Sample size: (1) N=564; (2) N=581.

+ Correlation coefficient significant, p<.10.

* Correlation coefficient significant, p<.05.

** Correlation coefficient significant, p<.01.

models (in terms of R_c^2, C_p, MSLOF, and E_p) are presented in Table 4 (models 1 to 5 and 6 to 8, respectively).

All of the empirical models except model 5 were comparable in terms of R_c^2 and C_p; however, model 1 was clearly superior in terms of validation statistics (MSLOF and E_p). The theoretically derived models performed more poorly in terms of R_c^2 and C_p than did the empirical models. However, they had lower MSLOF than any of the empirical models except model 1, and E_p closer to zero than models 4 and 5, indicating superior prediction ability. Model 8 was an attempt to include variables determined by stepwise procedures to be important in a theoretically based model. These variables included CANCOV in addition to BATOT, and SRANK instead of SI (contrasted to models 6 and 7). This model gave higher R_c^2 and lower C_p values than models 6 or 7, but predicted more poorly in the validation set.

Based on goodness of fit and prediction statistics (Table 4), model 1 was selected as a tentative prediction model for understory forage production (Table 5). Plots of residuals from this model versus predictor variables in the model, and versus candidate predictors, revealed no apparent trends, suggesting model adequacy. Further refinement of the model by stratification according to soil types or number of thinnings (two stands were thinned twice) was not practical, because of low numbers of plots in these potential strata. However, examination of residual plots revealed no apparent trends with respect to either soil type or number of thinnings.

In order to evaluate the performance of the model over a wide range

Table 4. Comparison of selected prediction equations for understory forage production in loblolly pine plantations in the Virginia Piedmont.[a]

Model	R_c^2	C_p	MSLOF	E_p
1. $\hat{Y} = b_0 + b_1\ \text{CANCOV} + b_2\ \text{SRANK}^2 + b_3\ (1/\text{BATOT}) + b_4\text{SRANK*CANCOV} + b_5\ \text{SRANK*BATOT}$	0.73	11.65	4750	1.99
2. $\hat{Y} = b_0 + b_1\ \text{CANCOV} + b_2\ \text{SRANK}^2 + b_3\ \text{BATOT}^2 + b_4\ \text{SRANK*CANCOV}$	0.66	12.60	7925	-1.92
3. $\hat{Y} = b_0 + b_1\ \text{CANCOV} + b_2\ \text{SRANK}^2 + b_3\ \text{BATOT} + b_4\ \text{BATOT}^2 + b_5\ \text{SRANK*CANCOV}$	0.71	12.30	9578	-3.65
4. $\hat{Y} = b_0 + b_1\ \text{CANCOV} + b_2\ \text{SRANK} + b_3\ \text{SRANK}^2 + b_4\ \text{BATOT} + b_5 + \text{BATOT}^2 + b_6\ \text{SRANK*CANCOV}$	0.76	11.90	10897	-5.77
5. $\hat{Y} = b_0 + b_1\ \text{CANCOV} + b_2\ (1/\text{BATOT}) + b_3\ \text{SRANK} + b_4\ \text{SRANK*CANCOV}$	0.46	17.70	10603	13.20
6. $\hat{Y} = -\text{bkBATOT}\{\exp(-\text{kTH})\} + \text{akSI}\{\exp(-\text{kTH} - \text{hTP})\}$	0.43	18.14	6599	-3.98
7. $\hat{Y} = [-\text{bBATOT} + \text{cSI}\{\exp(-\text{hTP})\} + \text{dSI*BATOT}]\text{k}\{\exp(-\text{kTH})\}$	0.44	17.92	6755	-4.58
8. $Y = [\text{cSRANK}\{\exp(-\text{hTP})\} + \text{dSRANK*BATOT} + \text{fSRANK*CANCOV} - \text{gCANCOV}]\ \text{k}\{\exp(-\text{kTH})\}$	0.48	17.21	7870	5.67

[a] $\hat{Y}$ = Predicted forage production for 0 to 2m stratum, g/m^2(=kg/ha÷10); other variable symbols are defined in Table 2.

Table 5. Coefficients of tentative prediction equation for forage production in loblolly pine plantations in the Virginia Piedmont.[a]

Parameter	Estimate	Standard Error	95% Confidence Interval
b_0	-149.96	34.34	(-217.27,-82.65)
b_1	2.16	0.40	(1.38,2.94)
b_2	9.89	0.76	(8.40,11.37)
b_3	3699.3	428.83	(2858.79,4539.81)
b_4	-1.48	0.13	(-1.73,-1.23)
b_5	1.41	0.20	(1.02,1.80)

[a] Predicted value for forage production in g/m^2 (=production in kg/ha÷10). Based on model 1 (Table 4):

$$\hat{Y} = b_0 + b_1 \text{ CANCOV} + b_2\text{SRANK}^2 + b_3(1/\text{BATOT}) + b_4 \text{ SRANK*CANCOV} + b_5 \text{ SRANK*BATOT}.$$

Variables in equation defined in Table 2.

of predictor variables, predicted values for forage production were computed for selected values of BATOT and CANCOV, and for all values of SRANK (Table 6). BATOT values were selected to cover the range of basal areas which might be encountered in thinned stands. CANCOV values were selected to correspond with BATOT values; even at low BATOT values, CANCOV would seldom be below 50 percent, while for BATOT of 40 to 50 m^2/ha, CANCOV would likely approach 100 percent. Predicted values for these combinations of values were generally reasonable except at very low values for BATOT (less than 10 m^2/ha), at which point the inverse term in BATOT became quite large. However, basal areas this small would be quite unusual. Predicted values for a wide range of BATOT (10 to 50 m^2/ha) are biologically reasonable. On certain slope positions (SRANK = 3, 4, or 5) and with high BATOT (greater than 40 m^2/ha), the equation gives negative predictions. However, these predictions (-40 to -150 kg/ha) were easily within one standard deviation of sampling error of being equal to zero. Furthermore, as basal area increases beyond 40 m^2/ha, the equation predicts approximately constant, low forage production levels. These predictions are biologically reasonable, and are consistent with observations made in stands with very closed canopies.

Biological significance of the forage production models. As hypothesized, all models predicted decreasing forage production with increasing basal areas. Forage production was negatively correlated with time since thinning, age of the stand at thinning, and canopy cover (Table 3). Because of multicollinearities among TH, TP, and CANCOV, it was redundant to predict PRODUC using a model including all of these

Table 6. Extrapolation behavior of the tentative model for predicting forage production in loblolly pine plantations in the Virginia Piedmont.[a]

BATOT (m^2/ha)	5	10	20	30	40	50
CANCOV (percent)	50	50	50	70	90	100
SRANK	Predicted forage production (g/m^2=kg/ha÷10)					
1	633	278	107	72	69	71
2	547	247	90	40	21	23
3	585	236	93	28	-7	-6
4	587	245	116	35	-15	-16
5	608	274	158	62	-4	-5
6	650	322	222	109	27	25

[a] Model 1 in Table 4: $\hat{Y} = b_0 + b_1$ CANCOV $+ b_2$ SRANK^2 $+ b_3$ (1/BATOT) $- b_4$ SRANK*CANCOV $+ b_5$ SRANK*BATOT.
Variables in equation defined in Table 2.

variables. Thus,, TH and TP were eliminated early in the variable selection process. Canopy cover (CANCOV) entered into model 1 (Table 4) with a positive term, but negatively in interaction with slope position (SRANK). Clearly, the general trend for vegetation development following thinning was for high forage production followed by decreasing production, due to increasing overstory competition for light, moisture, and nutrients. The relationship was complicated by the fact that on more favorable sites (higher SRANK), overstory basal areas and canopy coverages were higher (Table 3). Therefore, SRANK interacted with both BATOT and CANCOV in determining forage production. This can be seen more clearly by examining predicted values for model 1 (Table 6). Forage production increased between poor slope position (SRANK = 1) and favorable slope position (SRANK = 6), but on intermediate slopes the increase in overstory competition probably outweighed innate site quality in determining forage production.

Site index (SI) appeared to be a poor predictor of forage production, and was eliminated early in selecting variables for the empirical models. While SI may be a good indicator of site potential for loblolly pine production, it appears to be a poor index of potential for understory forage production. It is likely that forage plants are sensitive to changes in moisture, light, and nutrients that would scarcely influence tree growth. Further, forage production as measured here is an integration of the responses of many species to spatially and temporally varying environments, as opposed to the single-species response evaluated by overstory site index. The influence of SI on PRODUC in the prediction equations was probably also tempered by the relatively high positive correlations of SI with both BATOT and CANCOV (Table 3).

Midstory basal (BAMID) did not appear to be strongly related to PRODUC. In only a few stands did BAMID contribute significantly to any canopy coverage, and in no case did BAMID appear to be a major factor limiting PRODUC. In contrast to the situation reported in natural loblolly stands (Blair and Enghardt 1976) it appears that the midstory layer in old-field stands will seldom develop to the point where it suppresses forage production in the lower strata.

Overstory spatial pattern as measured by PIEL appeared to have no strong relationship to PRODUC. In most plots PIEL was not significantly different from 1, indicating a random pattern (Pielou 1959), and in no case was there significant overstory aggregation. The poor relationship between PIEL and PRODUC is understandable, in light of the tendency of artificially thinned plantations toward random or regular spatial patterns, coupled with the low degree of variability among stands in PIEL.

Empirical versus theoretical prediction models. There was no clear distinction between theory and empiricism in constructing adequate prediction models for PRODUC. Biology and common sense were both required in screening variables for inclusion in the empirical models, even before statistical screening began. Conversely, the results of the correlation analyses and stepwise procedures suggested modifications in the theoretical models. The three best theoretical models had predictive ability comparable to the empirically derived prediction models (Table 4). Nonetheless, these analyses illustrate several difficulties in using nonlinear theoretical models to explore data sets of this kind. First, neither the model form nor the predictor variables could be reliably specified beforehand. This was partly due to inherent uncertainty about the biological relationships involved, and partly due to difficulties with the sample data, especially multicollinearities among the predictor variables. The nonlinear models were extremely difficult to work with in any exploratory fashion. Introduction of new variables or substitution of one variable for another often completely changed the model form, or resulted in a model for which the parameter estimates would not converge. Further, unlike linear models, the addition of parameters to the model did not necessarily improve goodness of fit, and often resulted in decidedly poorer predictions. The theoretical models hinged on growth hypotheses, and thus TH and TP were central to these models; however, TH and TP were not particularly good predictors. They were strongly correlated with several better predictors, including BATOT, CANCOV, and SRANK (Table 3).

Model 1 (Tables 5 and 6) appeared to be a good prediction model, and had biologically reasonable parameters and good extrapolation properties. This model was also based on three easily measured predictor variables, i.e., BATOT, CANCOV, and SRANK. However, the model should be used with caution in attempting to predict understory production, due to limitations of the sample data used to construct the model. Perhaps the most serious limitation of the data is the design, in which spatially separated plots with different thinning and planting histories were used to establish temporal changes in forage production. It would be more desirable to remeasure plots through the course of stand histories, in order to better establish the dynamics of forage production with overstory structure, and the relationship of site quality to these dynamics. This approach would also be more consistent with the growth models, in that changes in forage production would be directly measured, rather than inferred from differences among "similar" plots located along artificially constructed time scales.

Ordinations

Principal component (PCA) and polar ordinations gave similar results, both in terms of plot and species scores, and in the correlations of plot scores with plot variables. Because of the direct relationship between plot and species scores in PCA (Pielou 1977) and because the ORDIFLEX procedure (Gauch 1977) provides three axes for PCA and only two for polar ordination, only PCA results are presented here. In order to more clearly represent the PCA results, plot and species scores were plotted in three dimensional PCA space, and cluster analysis (Barr et al. 1976) was used to reduce the individual scores to centroids of clusters in PCA space. In addition, variables significantly ($p<0.10$) correlated with plot scores were represented along the axes, to aid in their interpretation. Individual plots and species comprising the score clusters illustrated in the figures are presented in accompanying tables. All species used in the ordinations are presented for the shrub and tree strata, while only those species occurring in more than 15 percent of the plots or having importance values greater than 5 percent, are presented for the herb stratum. Details on the species and plot scores, including correlation coefficients between plot scores and plot variables, are provided in the Appendices.

For all ordinations, the major factors correlated with PCA scores were TH, TP, BATOT, CANCOV, SRANK, SI, and PRODUC. There appeared to be no distinct groupings beyond the imposed clusters among either plots or species in PCA space, suggesting that species composition varied along continua, rather than with distinct environmental breaks.

Herb Stratum

On drier sites (lower SI and SRANK) species composition appeared to shift from successional species (*Eupatorium* spp., *Daucus carota*, *Senecio* spp., *Fragaria virginiana*) and low to mid-shade-tolerant tree species (*Prunus serotina*, *Robinia pseudoacacia*) with low canopy coverages, toward a higher prevalence of tree species (*Juniperus virginiana*, *Quercus falcata*, *Q. velutina*, *Pinus taeda*) and ericaceous ground cover (*Vaccinium stamineum*) in closed canopied stands (Figs. 3-6, Tables 7-10). However, even in some very closed stands, successional species including *Aster* spp., *Solidago* spp., and *Eupatorium hyssopifolium* were frequent. Moister sites with open canopies had higher forage production, and typically an abundance of *Lonicera japonica*, *Rhus radicans*, and *Cornus florida*. Increasing crown coverage on these sites appeared to be related to a decrease in intolerants, and an increased prevalence of species such as *Acer rubrum*, *Campsis radicans*, and *Polystichum acrostichoides*. Once again, there was no completely consistent pattern of species distribution along the PCA gradients. Some species such as *Lonicera japonica* were essentially ubiquitous. Total forage production, much of it contributed by honeysuckle, appeared to be more closely related to

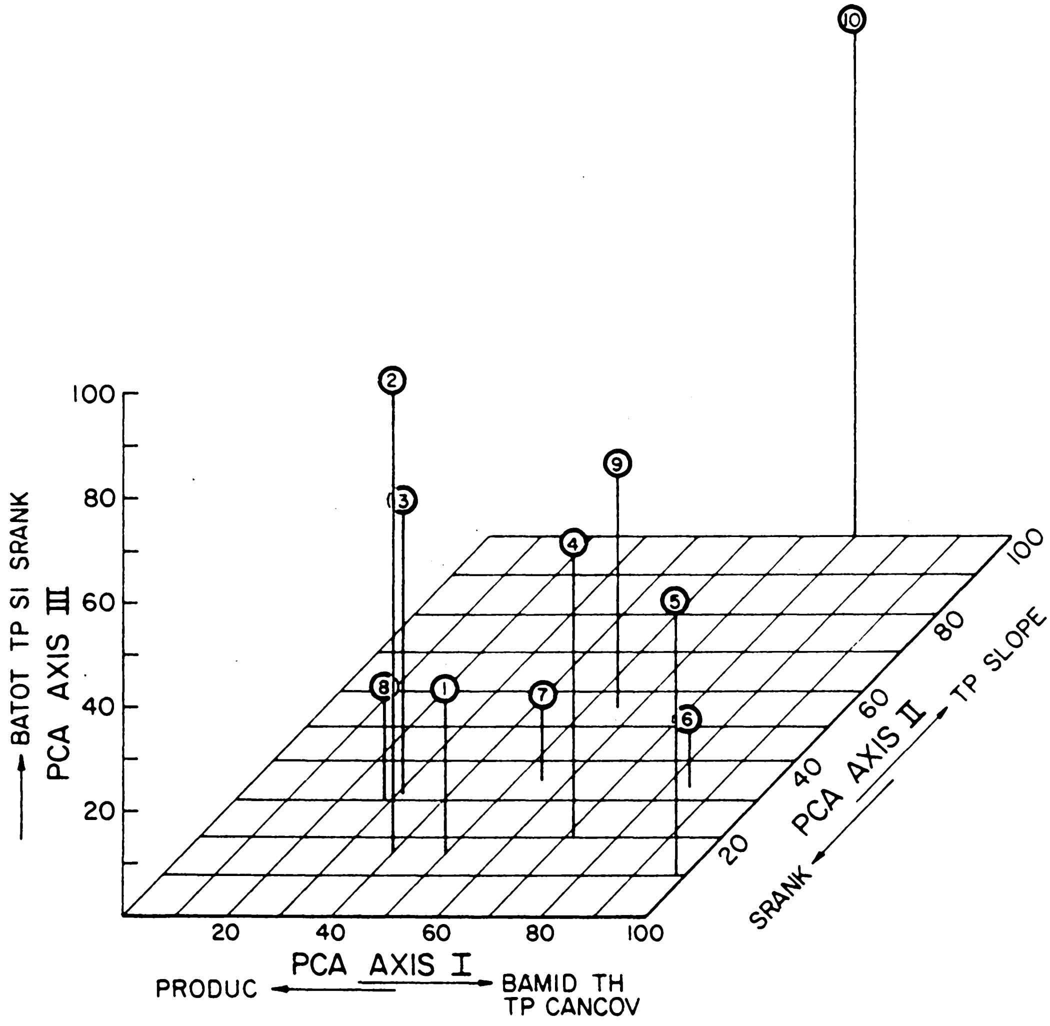

Figure 3. Principal component (PCA) plot score clusters for herb stratum releve data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:

Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]

Circled numbers are centroids of clusters in scaled PCA space (Table 7). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 7. Principal component (PCA) plot score clusters for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	5	28	3	6	10	17	24	23	22
	2		29	7	8	16	18	26	25	
	4			11	9	21	19	27		
				13	12		20			
				14						
				15						

[a] Cluster numbers depicted are centroids of clusters in PCA space (Fig. 3). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

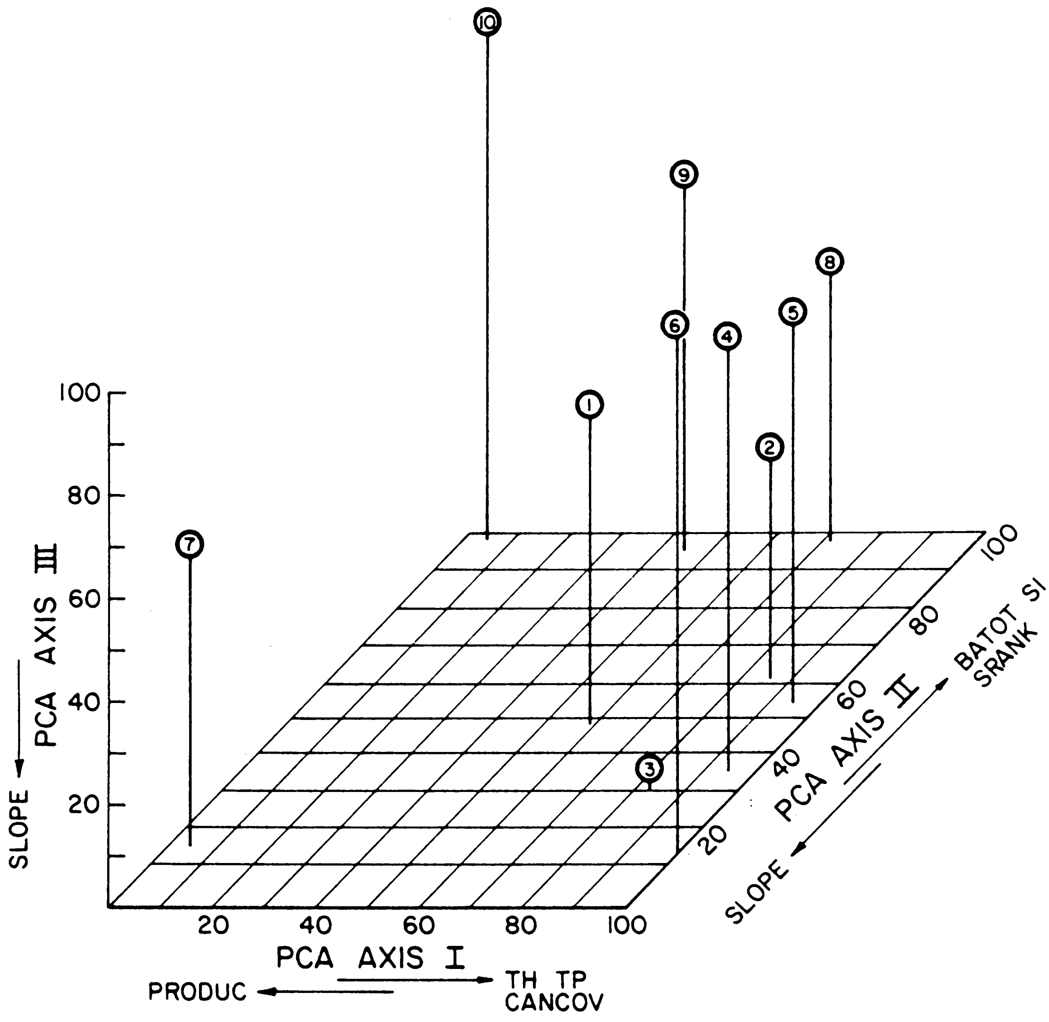

Figure 4. Principal component (PCA) plot score clusters for herb stratum production data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum)/100]
Circled numbers are centroids of clusters in scaled PCA space (Table 8). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 8. Principal component (PCA) plot score clusters for herb stratum production data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	14	18	3	8	9	24	4	5	29
	2	16		6	11		26	15	28	
	13	17		7	12		27	22		
	19	20		10						
	23	21								
	25									

[a] Cluster numbers depicted are centroids of clusters in PCA space (Fig. 4). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

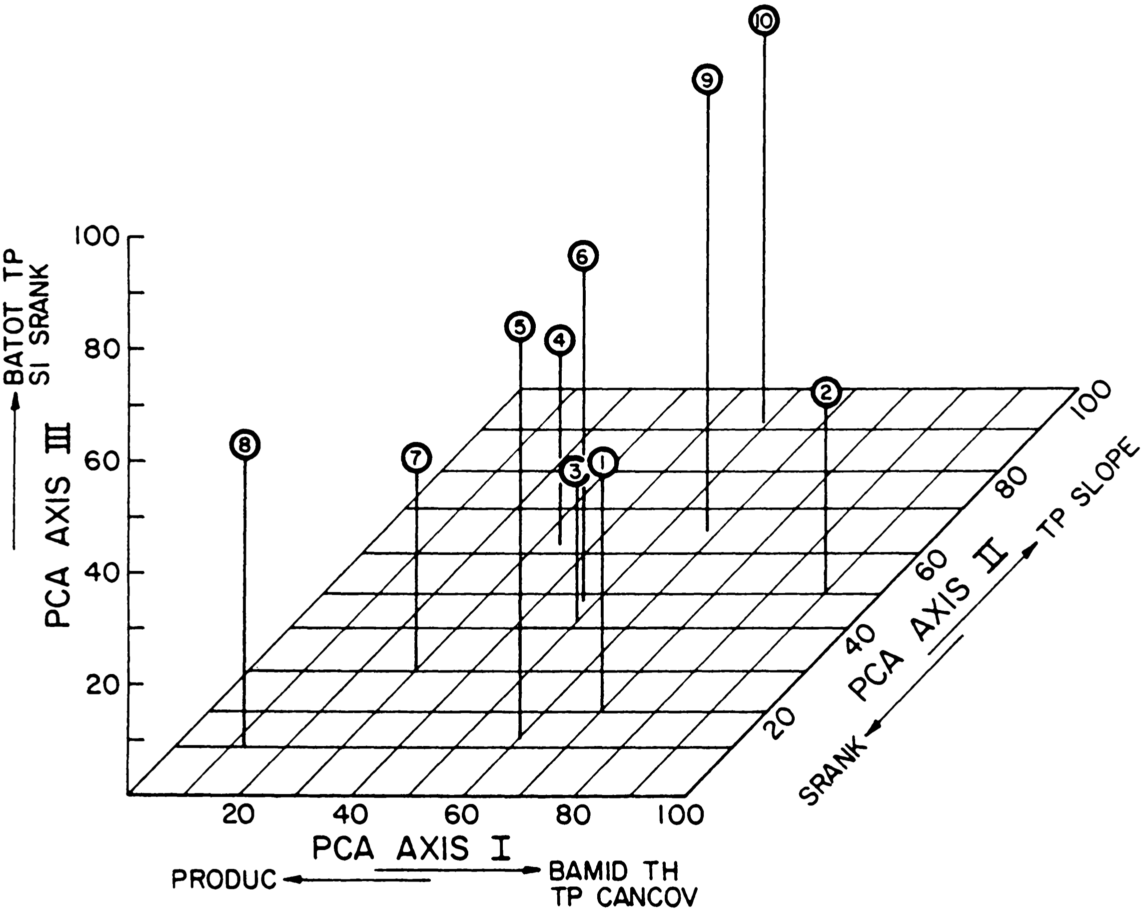

Figure 5. Principal component (PCA) species score clusters for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 9). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 9. Principal component (PCA) species score clusters for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

Species Score Clusters 1	2	3	4	5
Amelanchier arborea *Asclepias* sp. *Chrysopsis mariana* *Desmodium paniculatum* *Desmodium* sp. *Diospyros virginiana* *Eupatorium hyssopifolium* *Euphorbia corollata* *Ilex opaca* *Juniperus virginiana* *Lespedeza intermedia* *Lespedeza repens* Lichens *Nyssa sylvatica* *Panicum miliaceum* *Parthenocissus quinquefolia* *Pinus taeda* *Potentilla* sp. *Rubus flagellaris* *Smilax glauca* *Ulmus alata* *Vaccinium vacillans*	*Chimaphila maculata* *Pinus virginiana* *Quercus velutina* *Solidago* sp. *Vaccinium stamineum*	*Euonymus americanus* *Eupatorium album* *Ilex verticillata* *Quercus stellata* *Rhus copallinum* *Rubus argutus*	*Carya tomentosa* *Chrysanthemum leuchanthemum* *Convolvulus* sp. *Crataegus* sp. *Desmodium viridiflorum* *Galium circaezens* *Sericocarpos asteroides* *Smilax rotundifolia*	*Apocynum cannibinum* *Campsis radicans* *Danthonia spicata* *Liquidambar styraciflua* *Lycopodium complanatum* *Polystichum acrostichoides* *Prunus serotina* *Quercus falcata* *Quercus phellos* *Rhus radicans* *Sassafras albidum* *Trifolium* sp.

Table 9. Principal component (PCA) species score clusters for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont (continued).[a]

Species Score Clusters				
6	7	8	9	10
Apocynum sp. *Carya glabra* *Cercis canadensis* *Fragaria virginiana* *Panicum commutatum* *Panicum hians* *Quercus alba* *Quercus rubra* *Vitis* sp.	*Achillea millefolium* *Liriodendron tulipifera* *Solidago juncea* *Symphoricarpos orbiculatus* *Viburnum prunifolium* *Vitis aestivalis*	*Carpinus caroliniana* *Hypericum perforatum* *Lonicera japonica* *Solanum carolinense*	*Acer rubrum* *Fagus grandifolia* *Fraxinus pennsylvanica* Mosses *Robinia pseudoacacia*	*Albizzia julibrissin* *Andropogon scoparius* *Cornus florida* *Oxydendrum arboreum* *Quercus coccinea*

[a] Clusters depicted are centroids of clusters in PCA space (Fig. 5). Species listed had occurrences among plots >15% or importance value in any plot >5%. Complete species listings for each cluster are provided in Appendix.

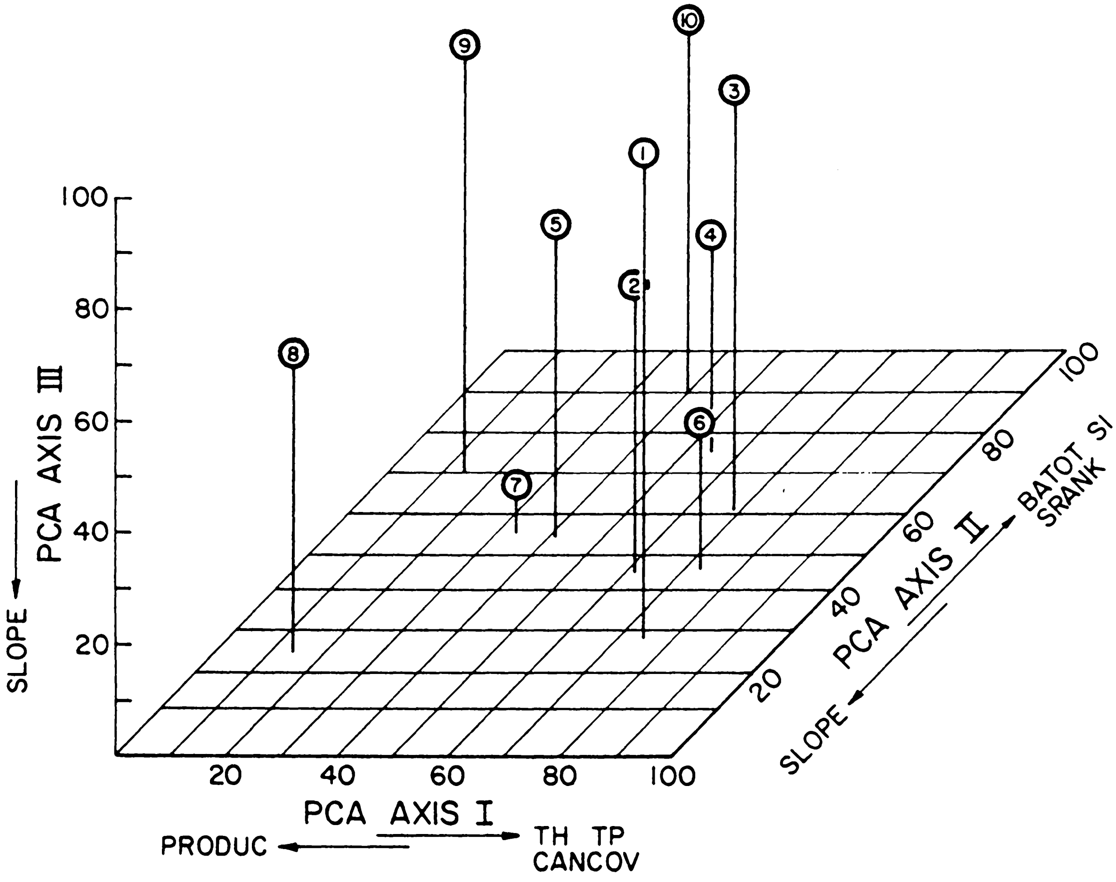

Figure 6. Principal component (PCA) species score clusters for herb stratum production data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 10). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 10. Principal component (PCA) species score clusters for herb stratum production data in loblolly pine plantations in the Virginia Piedmont.[a]

Species Score Clusters				
1	2	3	4	5
Aster sp. *Chimaphila maculata* *Desmodium laevigatum* *Desmodium paniculatum* *Diospyros virginiana* *Fagus grandifolia* *Juniperus virginiana* Lichens *Quercus falcata* *Quercus* sp. *Pinus taeda* *Rubus* sp. *Ulmus alata*	*Apocynum* sp. *Convolvulus* sp. *Eupatorium* sp. *Eupatorium hyssopifolium* *Pinus virginiana* *Quercus alba* *Nyssa sylvatica* *Smilax glauca*	*Desmodium* sp. *Desmodium viridiflorum* *Lespedeza* sp. *Liquidambar styraciflua* Mosses	*Acer rubrum* *Amelanchier arborea* *Campsis radicans* *Carya tomentosa* *Euonymus americanus* *Lycopodium complanatum* *Polystichum acrostichoides* *Rubus flagellaris* *Vaccinium vacillans*	*Fraxinus pennsylvanica* *Gramineae* spp. *Sassafras albidum*

Table 10. Principal component (PCA) species score clusters for herb stratum production data in loblolly pine plantations in the Virginia Piedmont (continued).[a]

Species Score Clusters				
6	7	8	9	10
Euphorbia corollata *Lespedeza repens* *Quercus coccinea* *Quercus velutina* *Oxydendrum arboreum* *Vaccinium stamineum*	*Potentilla* sp. *Rhus copallinum* *Rubus argutus* *Smilax rotundifolia* *Solidago* sp.	*Cercis canadensis* *Daucus carota* *Eupatorium album* *Fragaria virginiana* *Galium* sp. *Lespedeza* sp. *Prunus serotina* *Senecio* sp. *Symphoricarpos orbiculatus* *Viburnum prunifolium*	*Albizzia julibrissin* *Carpinus caroliniana* *Cornus florida* *Liriodendron tulipifera* *Lonicera japonica* *Panicum* sp. *Parthenocissus quinquefolia* *Rhus radicans* *Vitis* sp.	*Robinia pseudoacacia* *Carya glabra*

[a] Clusters depicted are centroids of clusters in PCA space (Fig. 6). Species listed had occurrences among plots >15%, or importance value in any plot >5%. Complete species listings for each cluster are provided in Appendix.

these gradients than was species composition. However, it also appeared that the greatest species diversity occurred on favorable sites some time before crown closure, when both successional and mid-tolerant species occurred in relatively high abundance.

Shrub Stratum

Shrub stratum species on drier, open canopied sites typically included *Oxydendrum arboreum, Rhus copallium,* and *Smilax* spp. (Figs. 7-10, Tables 11-14). Drier sites with more crown closure were typified by species such as *Pinus taeda, P. virginiana, Juniperus virginiana, Vaccinium* spp., and *Ulmus alata.* On moister, open canopied sites *Lonicera japonica* and *Rhus radicans* were especially abundant. With increasing crown closure, species composition appeared to shift toward low to mid-tolerant trees such as *Acer rubrum, Fagus grandifolia,* and *Fraxinus pennsylvanica.* Besides the evident relationship of species abundance to crown closure, there also was an apparent relationship between overstory spatial pattern (PIEL) and the third PCA axis (Fig. 9). It is not clear from the species clusters whether this relationship is biologically significant. It may reflect the negative correlation between PIEL and SI (Table 3); SI was also correlated with axis 3. This negative correlation may be due to poor or patchy site conditions resulting in a tendency toward aggregated spatial patterns in the trees (higher values for PIEL).

Tree Stratum

The tree stratum in open canopied stands on drier sites was comprised mainly of planted *Pinus taeda,* with some invading *P. virginiana*

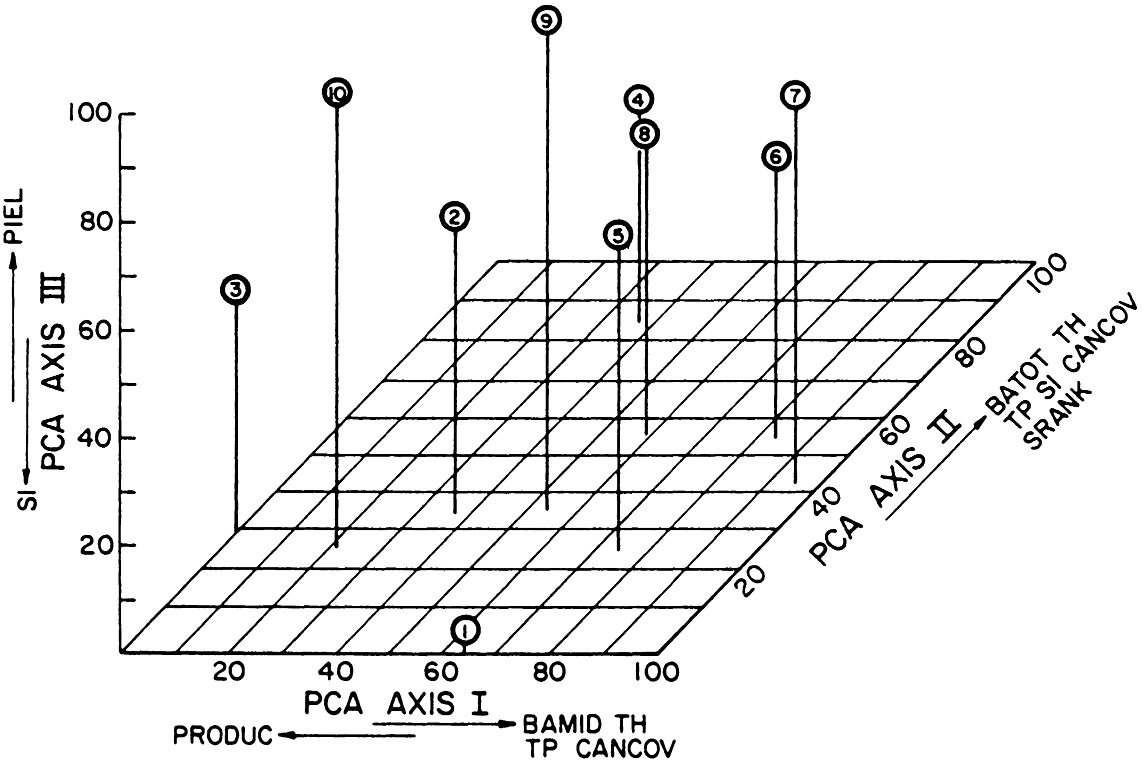

Figure 7. Principal component (PCA) plot score clusters for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 11). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 11. Principal component (PCA) plot score clusters for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	2	28	5	3	4	7	13	18	27
		24		23	16	6	8	17	20	
		26				11	9	19	25	
		29					10	21		
							12	22		
							14			
							15			

[a] Cluster numbers depicted are centroids of clusters in PCA space (Fig. 7). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

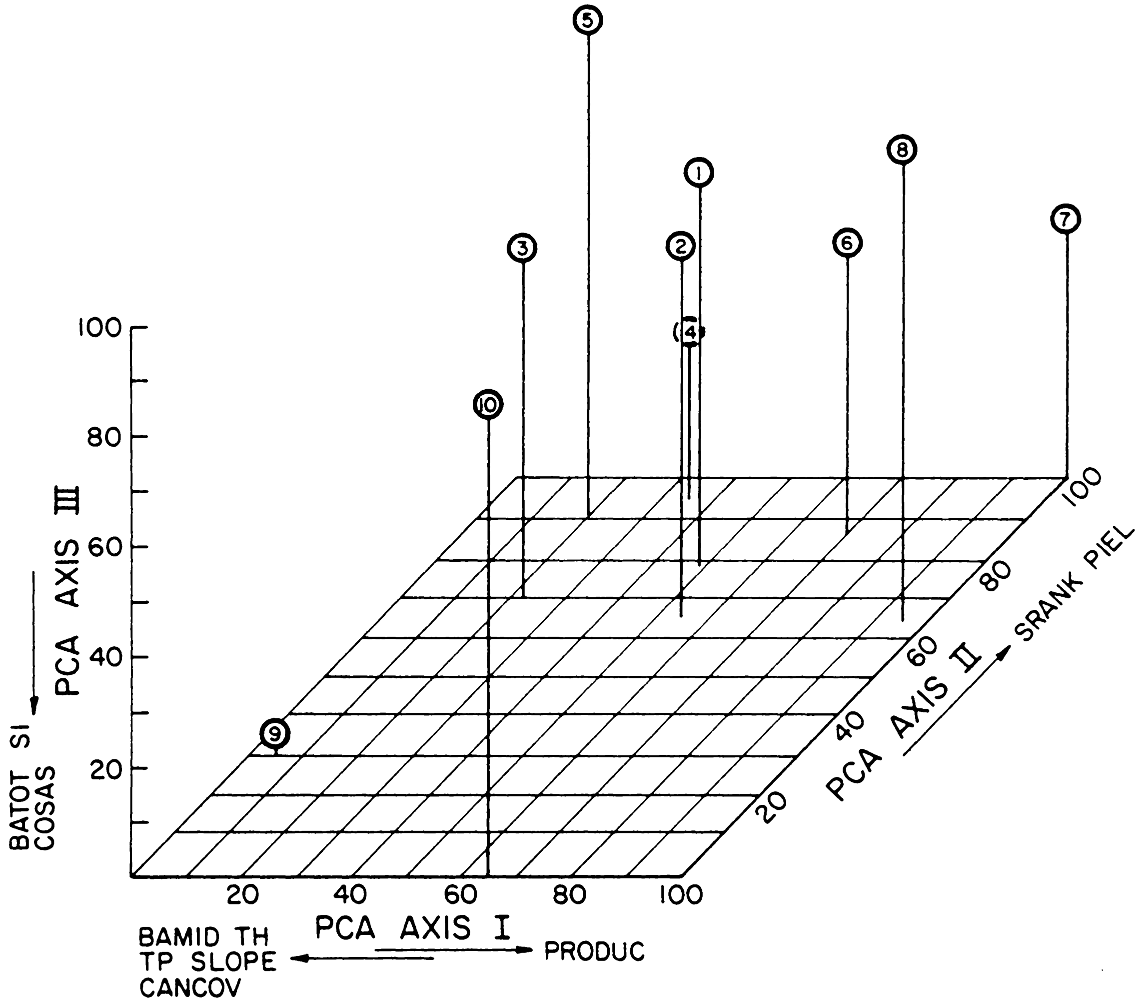

Figure 8. Principal component (PCA) plot score clusters for low shrub stratum (1' to <2m) production data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum)/100]
Circled numbers are centroids of clusters in scaled PCA space (Table 12). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 12. Principal component (PCA) plot score clusters for low shrub stratum (1 to <2 m) production data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	2	3	13	6	23	26	27	11	16
	4	15	7		9	28	29			18
	5	17	8		12					
	21	19	10							
	24	22	14							
		25								

[a] Cluster numbers depicted are centroids of clusters in PCA space (Fig. 8). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

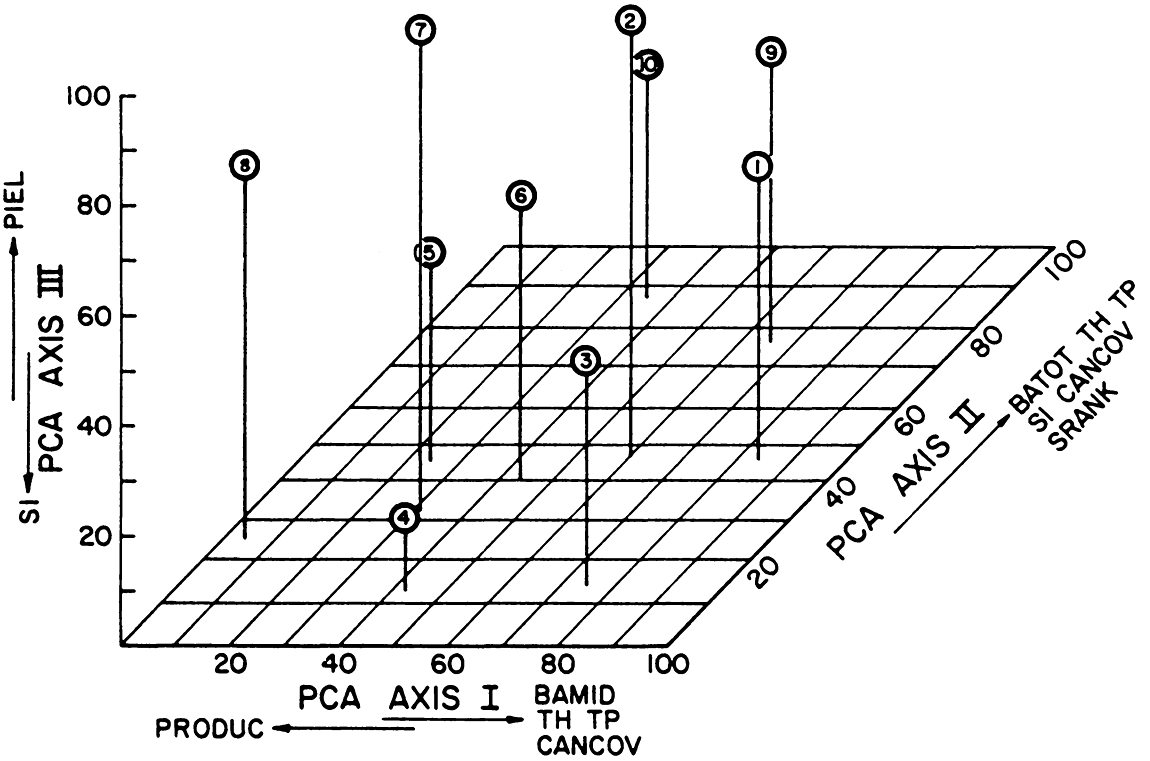

Figure 9. Principal component (PCA) species score clusters for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 13). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 13. Principal component (PCA) species score clusters for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

Species Score Clusters				
1	2	3	4	5
Ilex opaca *Lespedeza bicolor* *Liquidambar styraciflua* *Nyssa sylvatica* *Pinus taeda* *Ulmus alata*	*Amelanchier arborea* *Diospyros virginiana* *Pinus virginiana* *Vaccinium stamineum*	*Juniperus virginiana* *Quercus falcata*	*Cornus florida* *Prunus serotina* *Quercus coccinea* *Rubus argutus* *Sassafras albidum* *Smilax glauca*	*Carpinus caroliniana* *Eupatorium purpureum* *Rhus radicans* *Verbesina alternifolia* *Vitis* sp.
6	7	8	9	10
Campsis radicans *Carya glabra* *Cercis canadensis* *Ilex verticillata*	*Liriodendron tulipifera* *Oxydendrum arboreum* *Parthenocissus quinquefolia* *Rhus copallium* *Smilax rotundifolia* *Solidago* sp. *Viburnum acerifolium* *Viburnum prunifolium*	*Lonicera japonica* *Vitis aestivalis*	*Acer rubrum* *Fagus grandifolium* *Fraxinus pennsylvanica* *Quercus velutina*	*Albizzia julibrissin* *Apocynum* sp. *Carya tomentosa* *Corylus americana* *Lindera benzoin* *Platanus occidentalis* *Quercus alba* *Quercus rubra* *Robinia pseudoacacia*

[a] Numbers depicted are centroids of clusters in PCA space (Fig. 9).

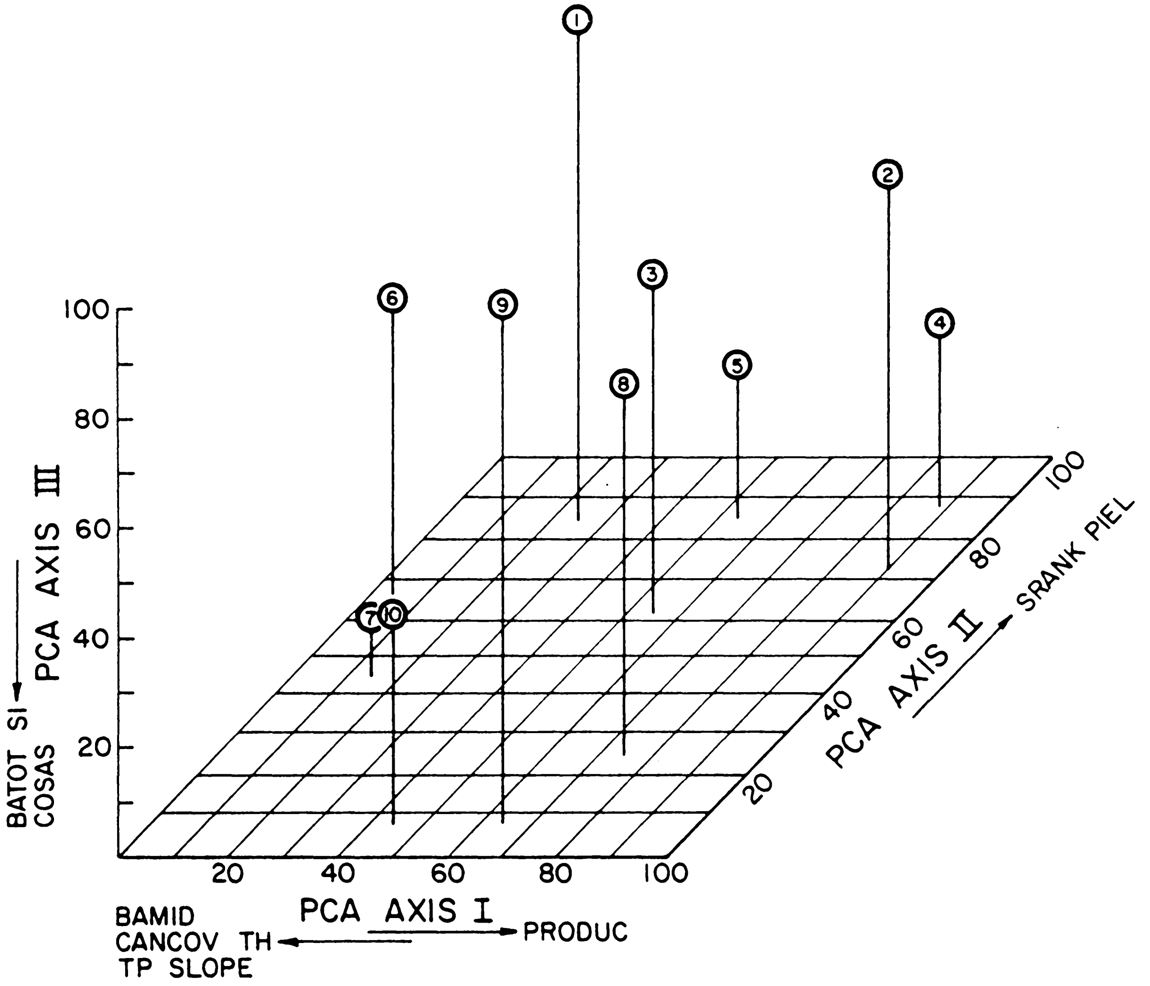

Figure 10. Principal component (PCA) species score clusters for low shrub stratum (1 to <2m) production data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 14). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 14. Principal component (PCA) species score clusters for low shrub stratum (1 - <2 m) production data in loblolly pine plantations in the Virginia Piedmont.[a]

Species Score Clusters				
1	2	3	4	5
Juniperus virginiana Lichens *Pinus taeda* *Pinus virginiana* *Vaccinium arboreum* *Vaccinium stamineum* *Ulmus alata*	*Cornus florida* *Cercis canadensis* *Diospyros virginiana* *Lonicera japonica* *Parthenocissus quinquefolia* *Viburnum prunifolium*	*Carpinus caroliniana* *Platanus occidentalis* *Quercus alba* *Quercus coccinea* *Robinia pseudoacacia*	*Albizzia julibrissin* *Fraxinus pennsylvanica* *Verbesina alternifolia* *Vitis* sp.	*Campsis radicans* *Rhus radicans*
6	7	8	9	10
Acer rubrum *Liquidambar styraciflua* *Quercus falcata*	*Fagus grandifolia* *Nyssa sylvatica* *Quercus velutina*	*Liriodendron tulipifera* *Prunus serotina*	*Oxydendrum arboreum* *Rhus copallinum* *Smilax glauca*	*Smilax rotundifolia*

[a] Numbers depicted are centroids of clusters in PCA space (Fig. 10).

and *Diospyros virginiana* (Figs. 11-14, Tables 15-18). With increasing crown closure, the latter two species plus *Juniperus virginiana* became more prevalent. On moister sites with open to partially closed canopies, *Lonicera japonica, Rhus radicans,* and *Acer rubrum* were abundant in the tree stratum. On a few older stands on moister sites and having closed crowns, *Acer rubrum* and *Liriodendron tulipifera* were abundant as intermediates or in some cases as codominants.

Relationship of Ordinations to Environmental Gradients

As discussed earlier, there were no obvious discontinuities in any of the ordinations. Site conditions including soil type are probably responsible for much of the variability in species composition. However, only plots 28 and 29 appeared to be distinguishable in the PCA's, based on soil types. These latter plots occurred on Altavista alluvial soils, and had substantially different moisture regimes than the other plots. However, even these plots were not sharply separated from the others in the ordinations, but appeared as part of a continuum. The relative continuity and lack of zonation among plots suggests that species distributions were more related to continuous gradients in factors such as light and moisture, than to any sharp environmental differences. This hypothesis is further supported by the correlations of PCA scores with factors such as BATOT, CANCOV, and SRANK, which are indirectly related to light and moisture gradients. The lack of distinct environmental differences is probably to be expected in this area, because of similarities among parent materials and soils underlying the study plots. As discussed in the previous section, it is very difficult to separate the

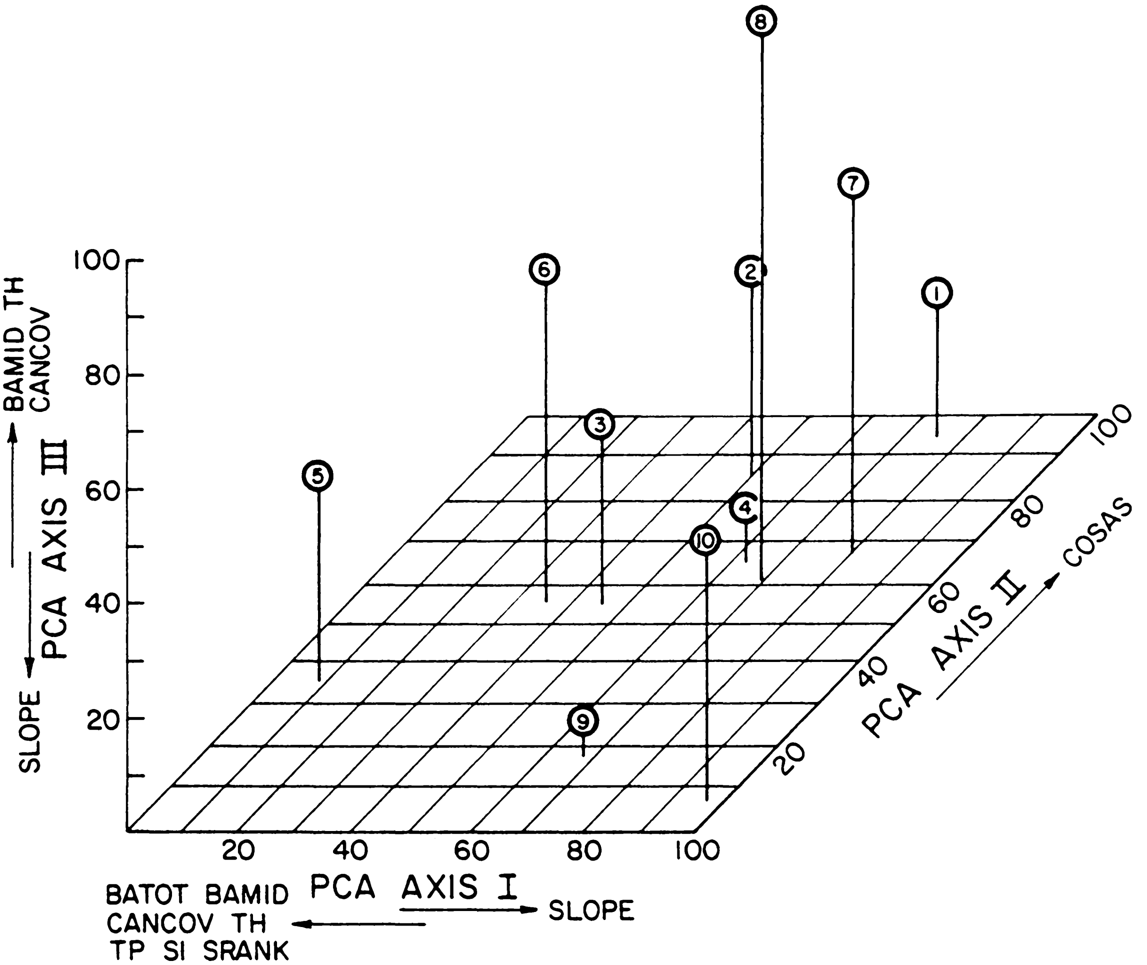

Figure 11. Principal component (PCA) plot score clusters for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 15). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 15. Principal component (PCA) plot score clusters for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	7	12	25	4	8	6	9	3	18
	2	23	14	27	5	11	16	10	19	24
	26	28	17		15	13			20	
	29		21							
			22							

[a] Numbers depicted are centroids of clusters in PCA space (Fig. 11). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

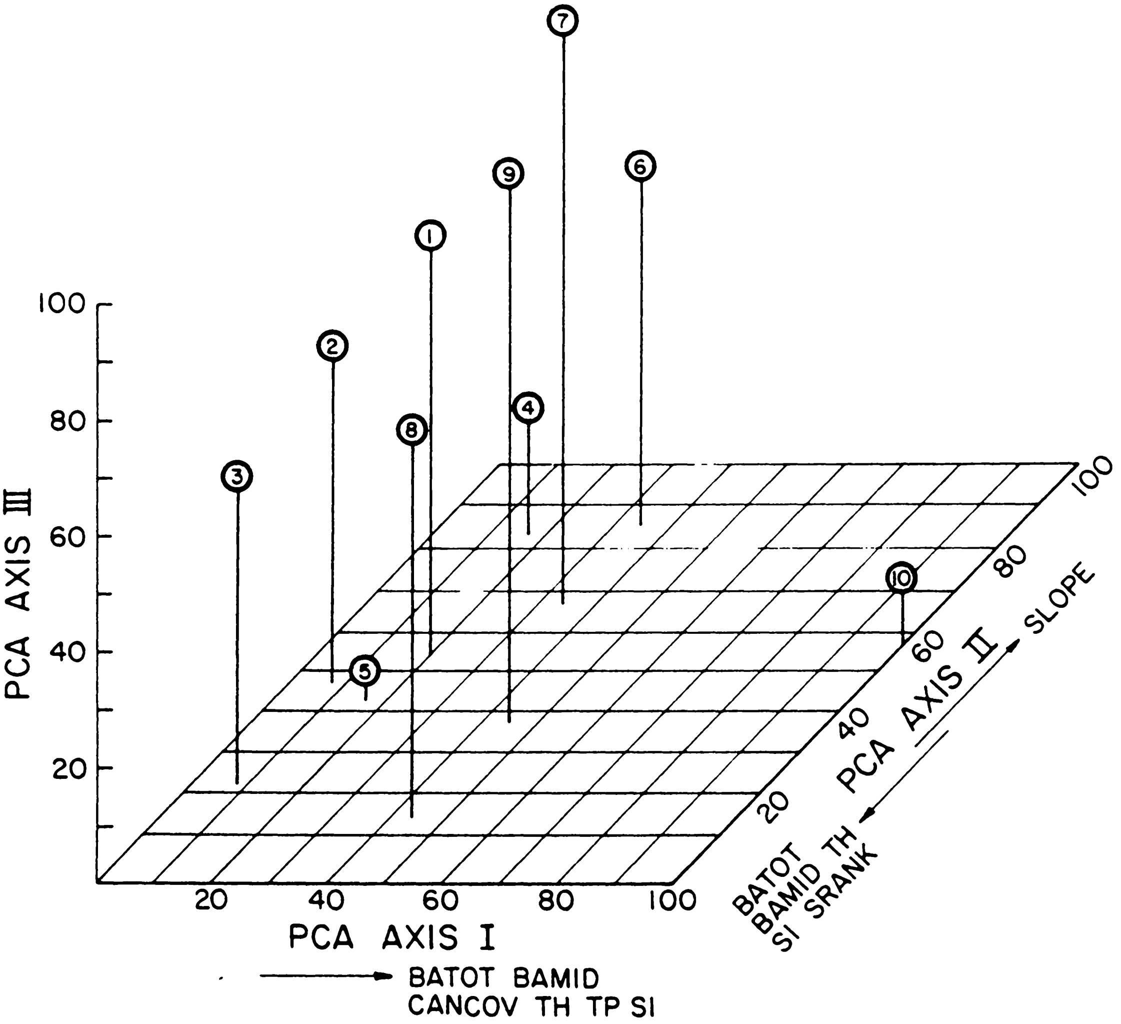

Figure 12. Principal component (PCA) plot score clusters for overstory data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum) /100]
Circled numbers are centroids of clusters in scaled PCA space (Table 16). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 16. Principal component (PCA) plot score clusters for overstory data in loblolly pine plantations in the Virginia Piedmont.[a]

	Plot Score Clusters									
	1	2	3	4	5	6	7	8	9	10
Plots	1	2	9	18	24	3	21	8	12	5
	4	10	16			19	22	11	13	
	6					20			14	
	7					25			15	
	17									
	23									
	26									
	27									
	28									
	29									

[a] Numbers depicted are centroids of clusters in PCA space (Fig. 12). Plot details including individual PCA scores and correlations with plot variables are provided in Appendix.

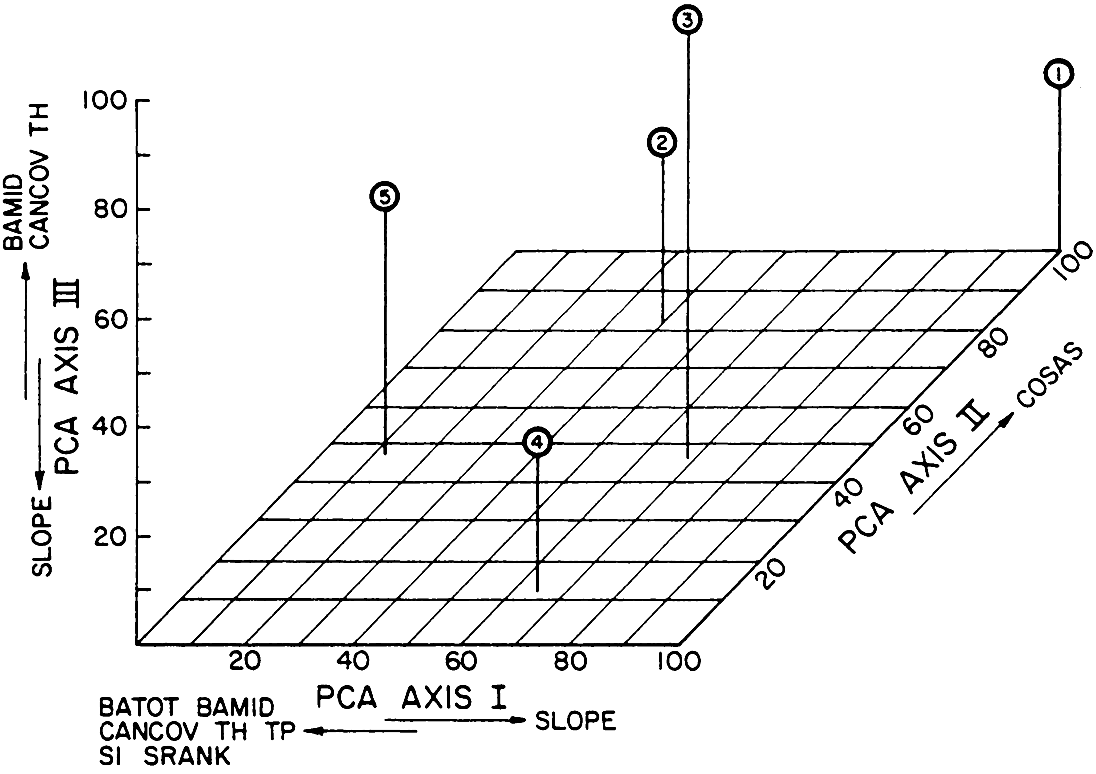

Figure 13. Principal component (PCA) species score clusters for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/ (maximum - minimum) /100
Circled numbers are centroids of clusters in scaled PCA space (Table 17). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 17. Principal component (PCA) species score clusters for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

Species score clusters				
1	2	3	4	5
Pinus taeda	*Fraxinus pennsylvanica* *Rhus radicans*	*Juniperus virginiana* *Nyssa sylvatica* *Quercus coccinea*	*Diospyros virginiana* *Oxydendrum arboreum* *Pinus virginiana*	*Acer rubrum* *Cornus florida* *Liquidambar styraciflua* *Lonicera japonica* *Robinia pseudoacacia* *Ulmus alata*

[a] Numbers depicted are centroids of clusters of PCA space (Fig. 13).

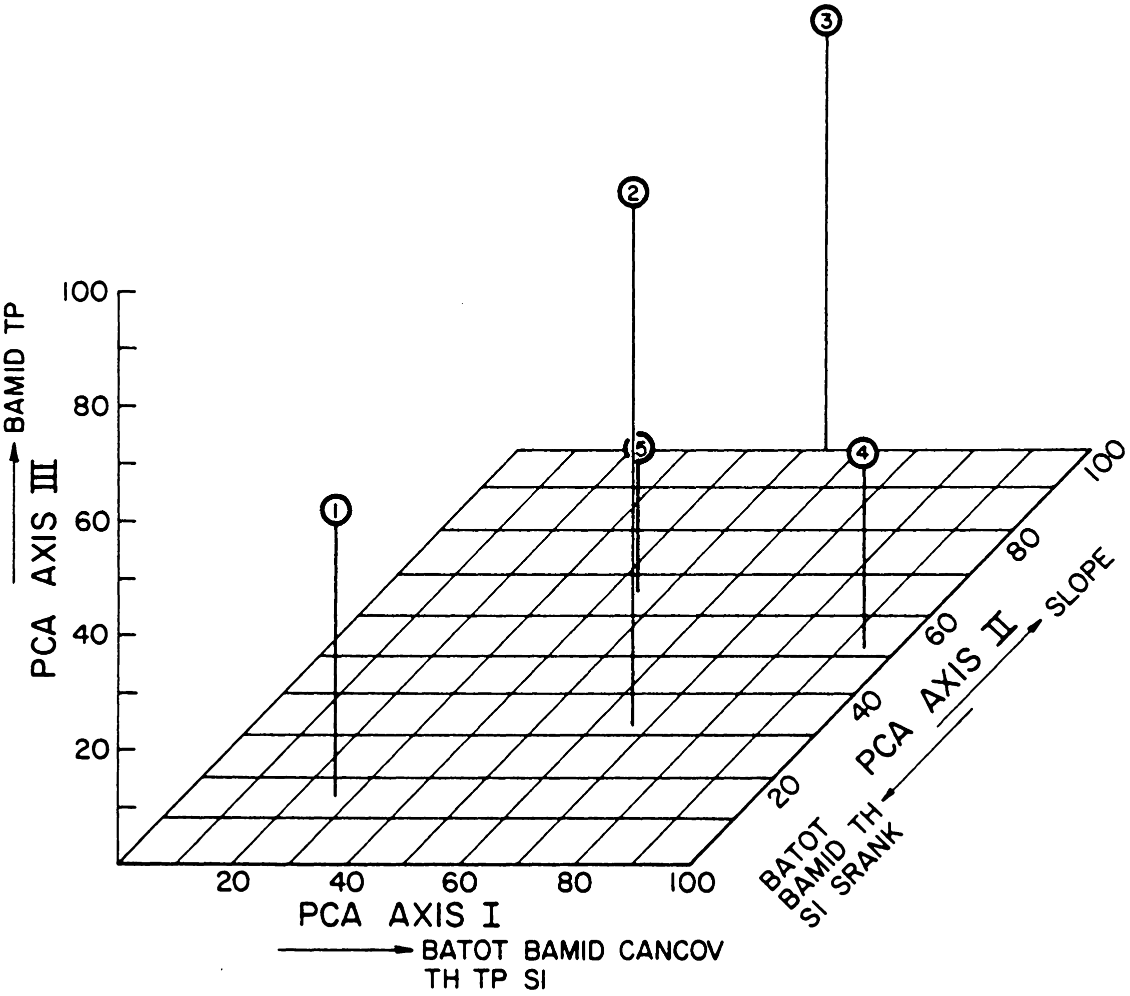

Figure 14. Principal component (PCA) species score clusters for overstory data in loblolly pine plantations in the Virginia Piedmont.[a]

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[a] Units are scaled PCA scores (Gauch 1977) where:
Scaled score = (original PCA score - minimum score)/[(maximum - minimum)/100]
Circled numbers are centroids of clusters in scaled PCA space (Table 18). Arrows indicate directions of increase in variables correlated with PCA scores. Variable symbols are defined in Table 2.

Table 18. Principal component (PCA) species score clusters for overstory data in loblolly pine plantations in the Virginia Piedmont.[a]

Species Score Clusters				
1	2	3	4	5
Juniperus virginiana	*Acer rubrum*	*Diospyros virginiana*	*Liriodendron tulipifera*	*Carpinus caroliniana*
Nyssa sylvatica	*Cornus florida*	*Pinus virginiana*	*Platanus occidentalis*	*Fraxinus pennsylvanica*
Pinus taeda	*Liquidambar styraciflua*			*Prunus serotina*
Quercus coccinea	*Robinia pseudoacacia*			

[a] Numbers depicted are centroids of clusters in PCA space (Fig. 14).

influence of site (as expressed largely by SRANK) from the influences of BATOT and CANCOV, in attempting to predict the response of the lower strata. As a generalization, it appears that the greatest diversity in understory species occurred following thinning but before crown closure, when successional species were abundant and low to mid-tolerant tree species were also well established. The forage production models and the correlations of forage production with the PCA scores, indicate that production peaked earlier than this and was often comprised of a few dominating species, particularly *Lonicera japonica*.

Forage Nutrient Analyses

Mean gross energy (CAL) for all forage material was 4643 cal/g. There were significant differences in CAL among the 19 species examined, and among plant parts (leaves, twigs, and fruit) (Table 19), with mean CAL values ranging from 3593 cal/g for *Rhus radicans* leaves to 5979.6 cal/g for *Rhus radicans* fruit (Appendix XIX). There were no significant differences in CAL among stands (Table 20). Mean dry matter digestibility (DMD) for all forage material was 38.3 percent. DMD varied significantly among the 24 species examined and among structural categories (Table 21), ranging from 16.6 percent for *Quercus* spp. twigs to 58.1 percent for *Rhus radicans* fruit (Appendix XX). There were significant differences in DMD among stands for *Lonicera japonica* leaves and twigs, *Vaccinium* spp. leaves, and *Rubus* spp. leaves (Table 22). DMD for *Lonicera japonica* leaves was negatively correlated with time elapsed since sampling began (DAYS) and PIEL. DMD in *Vaccinium* spp. twigs was positively correlated with CANCOV and PIEL. DMD in *Lonicera japonica* twigs

Table 19. Analysis of variance for forage gross energy concentration (CAL) pooled across stands in loblolly pine plantations in the Virginia Piedmont.[a]

Source	df	Type III Sum of Squares[b]	F
Species	18	2649275	2.17*
Plant part[c]	2	2578494	18.98*
Species X plant part	14	4628827	4.87**
Error	36	2445423	--

*Significant, $p<.05$.

**Significant, $p<.01$.

[a] Dependent variable is cal/g.

[b] Hypothesis tests adjusted for differing cell sizes (Barr et al. 1976).

[c] Leaves, twigs, and fruit.

Table 20. Analysis of variance for forage gross energy concentration (CAL) of *Lonicera japonica* leaves separated by stands in loblolly pine plantations in the Virginia Piedmont.[a]

Source	df	Sum of Squares	F
Stands	11	2363797.7	0.46
Error	22	102108883.5	--

[a] Dependent variable is cal/g.

Table 21. Analysis of variance for forage dry matter digestibility (DMD) pooled across stands in loblolly pine plantations in the Virginia Piedmont.[a]

Source	df	Type III Sum of Squares[b]	F
Species	22	13484	12.32**
Plant part[c]	2	1052	10.58**
Species X plant part	12	3039	5.09**
Error	89	4429	--

**Significant, p<.01.

[a] Dependent variable is percent DMD.

[b] Hypothesis tests adjusted for differing cell sizes (Barr et al. 1976).

[c] Leaves, twigs, and fruit.

Table 22. Analysis of variance for forage dry matter digestibility (DMD) separated by stands in loblolly pine plantations in the Virginia Piedmont.[a]

Species	Plant part[b]	Sum of Squares Due to Stands	df	Error Sum of Squares	df	F
Lonicera japonica	leaves	634.43	8	146.23	23	12.47**
Lonicera japonica	twigs	557.40	9	193.33	20	6.41**
Vaccinium spp.	leaves	286.19	5	281.00	15	3.06*
Vaccinium spp.	twigs	110.79	3	695.33	13	0.69
Rubus spp.	leaves	448.19	6	365.71	15	3.06*

*Significant, $p<.05$.

**Significant, $p<.01$.

[a] Dependent variable is percent DMD.

[b] Leaves, twigs, and fruit.

was positively, and in *Rubus* spp. leaves negatively, correlated with PIEL (Table 23). Crude protein (CPROT) concentration averaged 8.4 percent, and varied significantly among the 19 species examined and with plant part (Table 24), ranging from 2.2 percent for *Cornus florida* leaves to 23.2 percent for legume twigs (Appendix XX). CPROT did not vary significantly among stands (Table 25).

It is difficult to make biological inferences regarding the variability of CAL, DMD, and CPROT among stands, because of high sample variances and low numbers of replicates per stand. The trends between DMD and stand structural and site characteristics (Table 23) were weak or contradictory. The lack of significant variability among stands for CAL and CPROT suggests that there is little evidence of trends due to overstory characteristics. Most variability in nutrient parameters appeared to be due to species and plant parts, suggesting that the species breakdown of forage production is an important factor in determining the total amounts of available energy (kcal/ha) and protein (kg/ha) for any particular stand.

Forage Based Carrying Capacity for Deer

The mean qualitative abilities of the pine habitat to meet daily energy (MQA_e) and protein (MQA_p) requirements for deer were determined to be 1.0 and 3.7, respectively (Table 26). Stand values for MQA_e ranged from 0.9 to 1.1 while MQA_p ranged from 3.4 to 4.8. These data suggest that daily energy requirements are marginally or inadequately met by the habitat, while daily protein requirements are adequately met (minimum MQA_e or MQA_p equal to one). Estimates for energy based

Table 23. Correlation of forage dry matter digestibility (DMD) with stand variables in loblolly pine plantations in the Virginia Piedmont.[a]

Stand Variables					
DAYS	CANCOV	BATOT	SRANK	PIEL	n
-0.40*	0.28	-0.27	-0.02	-0.63**	32
0.18	0.12	0.12	0.02	0.53**	30
0.32	0.38+	-0.24	-0.27	0.23*	21
0.03	0.04	0.11	-0.26	-0.60*	22

+Significant, $p<.10$.

*Significant, $p<.05$.

**Significant, $p<.01$.

[a] Pearson product-moment correlation coefficient between DMD and stand variables. Variables defined in Table 2.

Table 24. Analysis of variance for forage crude protein (CPROT) pooled across stands in loblolly pine plantations in the Virginia Piedmont.[a]

Source	df	Type III Sum of Squares[b]	F
Species	18	734	46.79**
Plant part[c]	2	1050	602.14**
Species X plant part	13	245	21.68**
Error	66	57.6	--

**Significant, p .01.

[a] Dependent variable is percent CPROT.

[b] Hypothesis tests adjusted for differing cell sizes (Barr et al. 1976).

[c] Leaves, twigs, and fruit.

Table 25. Analysis of variance for forage crude protein concentration (CPROT) separated by stand in loblolly pine plantations in the Virginia Piedmont.[a]

Species	Plant Part[b]	Sum of Squares Due to Stands	df	Error Sum of Squares	df	F
Lonicera japonica	leaves	126.30	12	4.32	2	4.88
Lonicera japonica	twigs	8.59	12	0.63	2	2.26
Vaccinium spp.	leaves	55.55	11	0.97	1	5.23
Vaccinium spp.	twigs	3.52	11	0.24	1	1.32

[a] Dependent variable is percent CPROT.

[b] Leaves, twigs, and fruit.

Table 26. Energy and protein based mean qualitative ability (MQA_e and MQA_p) and carrying capacity (CAR_e and CAR_p) of stands for white-tailed does in summer in loblolly pine plantations in the Virginia Piedmont.

Stand[a]	MQA_e[b]	MQA_p	CAR_e (deer/ha)	CAR_p (deer/ha)
1-13-43	0.9	4.8	0.10	0.38
1-17-37	1.0	3.6	0.04	0.16
1-19-31	1.0	3.9	0.04	0.16
1-26-52	1.0	3.4	0.03	0.11
1-26-58	1.0	3.6	0.03	0.12
1-28-47	1.0	3.9	0.03	0.12
2-3-25	0.9	3.8	0.03	0.14
2-3-34	0.9	3.5	0.11	0.29
2-6-10	1.0	3.7	0.15	0.53
2-14-5	1.1	3.6	0.04	0.20
2-18-24	1.0	3.8	0.10	0.41
2-26-50	1.0	3.7	0.10	0.30
2-26-52	1.0	3.6	0.10	0.28
2-28-7	1.0	4.5	0.19	0.97
All stands	1.0	3.7	0.09	0.34

[a] First number of code signifies forest (1=Cumberland, 2=Buckingham-Appomattox). Remainder of code corresponds to Virginia Division of Forestry management unit and stand codes, respectively. Details of stand descriptions in Appendix.

[b] Minimum value to support deer = 1 for MQA_e and MQA_p.

carrying capacity (CAR_p) averaged 0.34 deer/ha, and ranged from 0.11 to 0.97 deer/ha. MQA_e was positively correlated with PIEL, while MQA_p was negatively correlated with TP. CAR_e was positively correlated with PRODUC and COSAS and negatively correlated with TH, BATOT, and CANCOV. CAR_p was positively correlated with PRODUC and COSAS and negatively correlated with TH, CANCOV, and SRANK (Table 27).

Forsythe (1978:68-71 and pers. comm.) and Carlile (1978) calculated carrying capacities for low production oak sites in the Ridge and Valley Province of Virginia. Their values for MQA_e and MQA_p ranged from 1.0 to 1.1 and 2.8 to 3.5, respectively, and for CAR_e and CAR_p ranged from 0 to 0.05 and 0.19 to 0.23, respectively. All three studies indicated that energy, not protein, appears to be the critical nutritive parameter in the respective habitats. Nutrient concentrations (CAL, DMD, and CPROT) and values for MQA_e were comparable among the studies, while values for MQA_p were somewhat higher in this study. Carrying capacities were generally much higher for this study, mainly due to the lower mean productions for Forsythe's and Carlile's studies of 198 kg/ha and 366 kg/ha compared to 610 kg/ha for this study. Comparable carrying capacity estimates are not available for other loblolly pine plantations in the Piedmont. Forage production values of 138 to 413 kg/ha were reported for an all-aged natural stand of loblolly and shortleaf pine in Louisiana (Blair and Brunett 1976). Wolters and Schmidtling (1975) reported forage productions in a 12-year-old converted site mixed pine plantation in coastal Mississippi of 246 to 1043 kg/ha. Neither of these pine ecosystems are directly comparable to those in this study; however, they

Table 27. Correlation analysis[a] of forage based habitat quality for deer with average stand characteristics[b] in loblolly pine plantations in the Virginia Piedmont.

	PRODUC	TH	TP	SLOPE	COSAS	SRANK	SI	BATOT	CANCOV	PIEL
MQA_e[c]	0.02	0.32	0.19	0.12	0.10	-0.14	0.14	0.17	0.02	0.53*
MQA_p	0.35	-0.19	-0.45^{+}	-0.30	0.10	0.32	0.12	0.10	-0.34	-0.21
CAR_e	0.91**	-0.70**	-0.41	0.30	0.61*	-0.01	-0.20	-0.48^{+}	-0.64	0.01
CAR_p	0.94**	-0.52^{+}	-0.42	0.01	0.61*	0.23	-0.08	-0.35	-0.56*	0.05

$^{+}$Significant, p<.10.

*Significant, p<.05.

**Significant, p<.01.

[a] Pearson product-moment correlation (n=14).

[b] Variables described in Table 2.

[c] Measures of forage based habitat quality (Tables 2, 26).

indicate the wide range of forage production possible in pine stands subject to differing site conditions and cultural treatments.

CAR_e and CAR_p were both highly correlated with PRODUC, suggesting that forage based carrying capacity can be determined by referring only to forage production, once basic levels of CAL, DMD, and CPROT have been established for an area. There was little indication of trends in nutrient concentrations with changes in overstory characteristics; any relationship of CAR_e and CAR_p with such characteristics appeared to be due to their relationship to PRODUC.

Use of these results for predicting deer production in the loblolly pine habitat should be made with caution. Sampling variances in the estimates used to compute MQA_e, MQA_p, CAR_e, and CAR_p were quite high, particularly those associated with production values. In addition, much of the information used in deriving these indices, including forage preferences, ingestion rates, and metabolic requirements, were obtained from the literature, and may not be wholly applicable in this locality. Forage utilization indices (UI) depended heavily on Harlow and Hooper's (1971) regional rumen analysis, which does not include many of the species (such as *Rhus radicans*) found in abundance in this area, that may be important to deer. Further, deer may be able to discriminate nutrient levels among forage plants, enabling them to consume a more nutritious diet than that indicated by combined forage analyses and regionally based utilization indices (Blair and Epps 1969, Wallmo et al. 1977). Perhaps the most serious limitation to the use of these results in estimating carrying capacities, is that forage constitutes only one portion of the habitat needs of white-tailed deer (Zeedyk 1969). Other aspects of habitat such as interspersion of food, cover, and water need to be considered. Vertical stratification of vegetative cover for four strata to 2 m height (DEN1, DEN2, DEN3, DEN4) was estimated in this study. These estimates were extremely variable within plots, and were only weakly correlated with plot overstory characteristics. The utility of such estimates is further limited by the paucity of information relating cover to specific physiological needs of deer. In addition, factors besides habitat such as population dispersion and human activity may significantly affect populations, and even override habitat considerations. The values presented here represent a relative measure of potential production, based on forage needs alone. These values likely underestimate potential deer production, because several of the plant species that occurred on these study areas in relatively high abundance and which had high nutritional value were not included in the computation of carrying capacity estimates.

SUMMARY AND CONCLUSIONS

Understory forage production, species composition, and nutrient concentrations were studied in relation to overstory structure and site characteristics in thinned loblolly pine stands in the central Piedmont of Virginia. Attempts were made to use growth models based on biological hypotheses to predict understory production from overstory and site variables. The results, however, showed that an empirical model using overstory basal area, crown coverage, and slope position as predictors was somewhat superior. Forage production was highest (up to 1690 kg/ha) in stands on moister sites that had low basal areas (20 m^2/ha) and canopy coverages (50 to 60 percent). Higher basal areas and canopy coverages resulted in lower understory production. The lowest understory production (minimum of 154 kg/ha) occurred on drier sites which had high basal areas (35 to 40 m^2/ha) and closed canopies (90 percent coverage).

Vegetation ordination techniques were used to analyze species composition along overstory structural and site gradients. Species composition appeared to be less closely related than production to these gradients, with many species occurring in stands of widely different characteristics. Species composition among plots appeared to vary continuously, with little evidence of discrete patterns. The greatest diversity of understory species appeared to occur during the period following thinning but before crown closure, when low and mid shade-tolerant species were mixed with successional species. Understory production peaked somewhat earlier than this, and was comprised mainly of a few dominant species, the most important being *Lonicera japonica.*

There were no clear trends in forage nutrient concentrations with respect to overstory characteristics. Nutrients varied mainly according to species and plant part. Thus, the total availability of nutrients in the habitat was a function of total production and species composition. This was substantiated by the high correlations between forage based carrying capacity for white-tailed deer and understory production. Based on these estimated carrying capacities, the pine habitat studied could likely support the forage needs of deer during the summer season. Comparison of these results with those of similar studies in the Ridge and Valley Province of Virginia indicate that approximately twice as many deer based on energy needs, and 70 percent more based on protein needs, could be supported by the Piedmont study area.

Directions for Future Research

This study represented a pilot effort to establish understory-overstory relationships in pine plantations of the Virginia Piedmont. To improve understanding of these relationships, and their utility in the management of pine stands for wildlife needs, further efforts are needed. In this study, several overstory and site characteristics appeared to be fairly closely related to understory production and species composition dynamics. These factors need to be studied more intensively, preferably using planned manipulations of the overstory to observe understory response. The establishment of permanent plots followed by repeated measurements would greatly enhance predictive relationships, and would enable a better understanding of the dynamics of time, basal area, canopy cover, and site quality with understory production and species composition. Data from such improved studies would result in prediction equations which could be used by managers to determine thinning schedules and intensities for optimizing a given set of timber and wildlife objectives.

A clear weakness of the carrying capacity estimates was their reliance on forage preference values based on regional rumen studies. Improved local food preference studies are needed to determine more precisely the forage species that should be included in carrying capacity estimates. Better information is needed on local seasonal metabolic requirements for deer, including variations in food intake rates. Finally, and perhaps most importantly, studies are needed to determine the movements and population dynamics of deer in the Piedmont, in order to establish whether the pine habitat is or could be an integral part of their habitat. Such aspects as plantation size, shape, and interspersion with other forest types may be discovered to be at least as important as internal stand characteristics.

Much emphasis was placed on white-tailed deer needs in this study, to the exclusion of other wildlife species. This was as much due to the paucity of information on other wildlife species needs, as it was due to the economic and esthetic importance of deer. Many of the results reported here are general in nature, and could be applied to the forage needs of other species, if those needs were known. It is important to remember that this study remains essentially a study of vegetation dynamics, and not one of wildlife populations. Inferences about wildlife populations drawn from such studies are indirect at best and likely weak. The interface between wildlife habitat and wildlife population dynamics remains, in this author's opinion, one of the weakest areas in ecology. Perhaps it is this interface, rather than specific studies in either habitat or population dynamics, that should serve as the focus for future habitat-population research efforts.

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APPENDICES

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont.

	Stand[a]								
	1-13-42						1-17-37		
Variable	Plot 1			Plot 2			Plot 3		
TH (years)[b]	2.75			2.75			1.75		
TP (years)	22.5			22.5			34.5		
SLOPE (percent)	10.0			10.0			9.0		
ASPECT (degrees)	185			40			295		
SRANK (rank)	2			1			2		
SI (m at 25 yrs)	18.4			18.4			15.9		
BATOT (m^2/ha)	29.84			27.06			24.54		
BACO (m^2/ha)	28.67			26.06			23.04		
BACOI (m^2/ha)	29.05			26.06			23.50		
BAMID (m^2/ha)	0.79			1.00			1.04		
NTOT (trees/ha)	900			775			850		
NCO (trees/ha)	825			700			575		
NCOI (trees/ha)	850			700			625		
NMID (trees/ha)	50			75			225		
CANOV (percent)	62.24			54.95			70.83		
	$\bar{x}$	SD	n[c]	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	7.58	14.94	20	16.72	24.91	20	7.58	10.60	20
DEN 2 (percent)	5.69	13.64	20	9.71	23.44	20	3.89	7.90	20
DEN 3 (percent)	7.00	15.13	20	8.43	21.00	20	0.88	3.79	20
DEN 4 (percent)	7.00	15.13	20	7.73	21.00	20	2.16	6.56	20
PIEL	0.66	0.05	20	0.75	0.05	20	0.90	0.05	20
STEMS (stems/ha)	11500	12680	20	13000	23200	20	23500	21100	20
STEM 1 (stems/ha)	11500	12680	20	13000	23200	20	23000	21000	20
STEM 2 (stems/ha)	0	--	--	0	--	--	500	2200	20
PRODUC (kg/ha)	154.37	92.69	20	794.29	365.79	20	308.78	156	20
PRODUC 1 (kg/ha)	143.38	95.98	20	692.84	334.69	20	282.0	149.8	20
PRODUC 2 (kg/ha)	10.98	3.88	20	101.46	245.20	20	26.72	49.19	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	1-19-31						1-26-52		
Variable	Plot 4			Plot 5			Plot 6		
TH (years)	11.75			11.75			8.5		
TP (years)	29.5			29.5			26.75		
SLOPE (percent)	5.0			2.0			8.0		
ASPECT (degrees)	90			60			300		
SRANK (rank)	4			6			4		
SI (m at 25 yrs)	21.46			23.8			17.2		
BATOT (m^2/ha)	39.93			43.50			23.91		
BACO (m^2/ha)	35.13			37.19			22.06		
BACOI (m^2/ha)	37.44			42.07			22.06		
BAMID (m^2/ha)	2.49			1.43			1.85		
NTOT (trees/ha)	1225			1150			700		
NCO (trees/ha)	500			350			475		
NCOI (trees/ha)	700			650			475		
NMID (trees/ha)	525			500			225		
CANOV (percent)	75.00			90.89			76.3		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	16.26	15.12	20	8.41	14.15	20	2.81	7.12	20
DEN 2 (percent)	10.99	10.49	20	13.26	22.41	20	2.40	6.37	20
DEN 3 (percent)	9.03	9.87	20	12.26	16.86	20	2.97	5.41	20
DEN 4 (percent)	9.18	9.04	20	10.08	16.38	20	2.56	5.36	20
PIEL	0.71	0.05	20	0.65	0.05	20	0.59*	0.05	20
STEMS (stems/ha)	54500	36900	20	29500	34500	20	20500	16000	20
STEM 1 (stems/ha)	43500	31800	20	27000	32600	20	19500	14700	20
STEM 2 (stems/ha)	11000	12100	20	2500	5500	20	1000	3100	20
PRODUC (kg/ha)	721.24	256.27	20	352.84	131.68	20	283.31	325.83	19
PRODUC 1 (kg/ha)	560.23	236.5	20	264.26	127.33	20	207.90	281.42	19
PRODUC 2 (kg/ha)	160.83	90.85	20	96.80	107.16	20	71.45	100.50	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	1-26-52								
Variable	Plot 7			Plot 8			Plot 9		
TH (years)	8.5			8.5			8.5		
TP (years)	26.75			26.75			26.75		
SLOPE (percent)	13.0			6.0			1.0		
ASPECT (degrees)	320			320			290		
SRANK (rank)	2			2			3		
SI (m at 25 yrs)	20.2			19.2			18.3		
BATOT (m^2/ha)	33.11			34.84			24.20		
BACO (m^2/ha)	32.15			31.11			22.02		
BACOI (m^2/ha)	32.37			31.11			22.83		
BAMID (m^2/ha)	0.74			3.73			1.37		
NTOT (trees/ha)	800			1275			675		
NCO (trees/ha)	525			500			400		
NCOI (trees/ha)	550			500			425		
NMID (trees/ha)	250			775			250		
CANOV (percent)	72.40			88.80			60.15		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	10.01	17.24	19	7.46	14.62	20	4.50	6.13	20
DEN 2 (percent)	10.08	17.00	19	7.18	15.49	20	5.38	14.05	20
DEN 3 (percent)	8.08	17.32	19	11.34	16.35	20	0.66	1.68	20
DEN 4 (percent)	7.09	16.60	19	6.9	14.35	20	0.63	1.68	20
PIEL	0.69	0.05	20	0.81	0.05	20	0.92	0.05	20
STEMS (stems/ha)	16500	13900	20	29000	22500	20	50500	72600	20
STEM 1 (stems/ha)	15000	13600	20	26000	21900	20	49500	71000	20
STEM 2 (stems/ha)	1500	3700	20	3000	4700	20	1000	3100	20
PRODUC (kg/ha)	262.23	270.69	20	302.30	190.46	20	424.79	542.62	19
PRODUC 1 (kg/ha)	169.10	155.88	20	140.67	119.81	20	347.70	436.2	19
PRODUC 2 (kg/ha)	93.09	168.91	20	161.63	158.80	20	90.69	188.80	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	- - 1-26-52 -			- - - - - - 1-26-58 - - - - - - -					
Variable	Plot 10			Plot 11			Plot 12		
TH (years)	8.5			8.5			8.5		
TP (years)	26.75			29.75			29.75		
SLOPE (percent)	5.0			8.0			1.0		
ASPECT (degrees)	170			340			230		
SRANK (rank)	2			2			5		
SI (m at 25 yrs)	20.5			21.3			19.8		
BATOT (m^2/ha)	21.52			40.24			24.97		
BACO (m^2/ha)	19.63			30.85			18.87		
BACOI (m^2/ha)	19.63			36.31			19.60		
BAMID (m^2/ha)	1.89			3.93			5.37		
NTOT (trees/ha)	475			1025			2200		
NCO (trees/ha)	250			375			275		
NCOI (trees/ha)	250			600			350		
NMID (trees/ha)	225			425			1850		
CANOV (percent)	73.70			66.93			72.14		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	10.09	22.67	20	8.09	15.78	20	7.11	11.01	20
DEN 2 (percent)	9.02	22.75	20	8.81	14.38	20	8.69	9.63	20
DEN 3 (percent)	12.34	25.48	20	7.22	14.72	20	5.21	6.46	20
DEN 4 (percent)	12.10	23.28	20	13.0	15.24	20	5.98	6.31	20
PIEL	0.59*	0.05	20	0.71	0.05	20	0.99	0.05	20
STEMS (stems/ha)	33500	31200	20	22000	28000	20	51000	39900	20
STEM 1 (stems/ha)	28000	25700	20	18500	25800	20	44000	38000	20
STEM 2 (stems/ha)	5500	2000	20	3500	6700	20	7000	9200	20
PRODUC (kg/ha)	412.90	260.72	20	428.02	308.66	20	488.22	437.71	20
PRODUC 1 (kg/ha)	209.48	169.62	20	239.90	209.92	19	280.47	246.48	20
PRODUC 2 (kg/ha)	203.38	230.04	20	183.88	165.03	20	207.68	280.25	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	1-28-47								
Variable	Plot 13			Plot 14			Plot 15		
TH (years)	7.0			7.0			7.0		
TP (years)	30.25			30.25			30.25		
SLOPE (percent)	4.0			5.0			5.0		
ASPECT (degrees)	75			15			30		
SRANK (rank)	6			4			2		
SI (m at 25 yrs)	18.2			19.9			18.7		
BATOT (m^2/ha)	30.92			28.62			40.09		
BACO (m^2/ha)	27.47			22.98			25.78		
BACOI (m^2/ha)	28.71			24.26			28.14		
BAMID (m^2/ha)	2.21			4.36			11.95		
NTOT (trees/ha)	1175			1125			1250		
NCO (trees/ha)	425			250			225		
NCOI (trees/ha)	500			325			350		
NMID (trees/ha)	675			800			900		
CANOV (percent)	75.26			63.54			83.07		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	10.78	18.78	20	4.71	12.45	20	9.38	19.13	20
DEN 2 (percent)	5.79	13.85	20	6.59	12.85	20	6.55	16.24	20
DEN 3 (percent)	6.05	13.82	20	3.79	9.61	20	6.58	16.23	20
DEN 4 (percent)	5.27	13.90	20	3.30	7.23	20	4.62	14.08	20
PIEL	0.69	0.05	20	0.54*	0.05	20	0.62	0.05	20
STEMS (stems/ha)	11000	7900	20	20500	20800	20	27000	34700	20
STEM 1 (stems/ha)	7000	6600	20	19500	21100	20	26500	34500	20
STEM 2 (stems/ha)	4000	6000	20	1000	3100	20	500	2200	20
PRODUC (kg/ha)	562.52	357.29	20	268.26	201.81	20	349.22	176.31	20
PRODUC 1 (kg/ha)	387.78	144.76	20	171.03	138.3	20	295.74	147.09	20
PRODUC 2 (kg/ha)	174.30	277.20	20	97.19	134.1	20	53.48	88.37	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	2-3-25			2-3-34					
Variable	Plot 16			Plot 17			Plot 18		
TH (years)	10.5			1.25			1.25		
TP (years)	20.75			28.0			28.0		
SLOPE (percent)	3.0			14.0			17.0		
ASPECT (degrees)	110			45			160		
SRANK (rank)	3			2			2		
SI (m at 25 yrs)	17.2			20.0			17.5		
BATOT (m^2/ha)	25.28			19.88			20.95		
BACO (m^2/ha)	23.58			18.87			19.85		
BACOI (m^2/ha)	23.58			19.71			19.85		
BAMID (m^2/ha)	1.70			0.17			1.10		
NTOT (trees/ha)	900			525			750		
NCO (trees/ha)	575			450			500		
NCOI (trees/ha)	575			500			500		
NMID (trees/ha)	325			25			250		
CANOV (percent)	64.06			67.18			67.97		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	5.63	10.08	19	10.87	14.16	20	11.09	20.17	20
DEN 2 (percent)	2.23	4.21	19	4.01	7.75	20	1.74	2.80	20
DEN 3 (percent)	2.62	5.35	19	4.24	14.12	20	0.98	3.81	20
DEN 4 (percent)	1.79	4.09	19	2.59	9.18	20	1.43	6.37	20
PIEL	0.62	0.05	20	0.57*	0.05	20	0.86	0.05	20
STEMS (stems/ha)	7000	9800	20	34500	22400	20	20000	17500	20
STEM 1 (stems/ha)	7000	9800	20	33000	22000	20	19500	16700	20
STEM 2 (stems/ha)	0	--	--	1500	4900	20	500	2200	20
PRODUC (kg/ha)	477.67	408.98	20	782.27	278.60	20	723.99	429.0	20
PRODUC 1 (kg/ha)	363.99	282.11	20	707.80	252.80	20	684.70	406.81	20
PRODUC 2 (kg/ha)	113.61	205.8	20	74.35	112.58	20	39.19	72.70	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	2-6-10						2-14-5		
Variable	Plot 19			Plot 20			Plot 21		
TH (years)	3.75			3.75			9.25		
TP (years)	26.5			26.5			32.0		
SLOPE (percent)	9.0			16.0			8.0		
ASPECT (degrees)	300			240			100		
SRANK (rank)	1			1			2		
SI (m at 25 yrs)	16.4			16.3			19.0		
BATOT (m^2/ha)	18.76			29.07			32.40		
BACO (m^2/ha)	17.16			27.29			30.16		
BACOI (m^2/ha)	17.66			27.85			31.59		
BAMID (m^2/ha)	1.10			1.22			0.81		
NTOT (trees/ha)	700			950			775		
NCO (trees/ha)	425			650			300		
NCOI (trees/ha)	450			675			350		
NMID (trees/ha)	250			275			425		
CANOV (percent)	51.56			64.06			70.05		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	25.36	23.05	20	14.86	15.27	20	6.44	10.47	20
DEN 2 (percent)	12.53	20.82	20	4.93	9.58	20	7.00	13.97	20
DEN 3 (percent)	12.58	18.80	20	3.83	9.69	20	5.25	13.97	20
DEN 4 (percent)	9.47	21.00	20	3.67	9.73	20	4.78	14.04	20
PIEL	0.65	0.05	19	0.93	0.05	20	1.13	0.05	20
STEMS (stems/ha)	108500	82100	20	88000	45700	20	34000	37200	20
STEM 1 (stems/ha)	99500	82700	20	86000	44100	20	27000	28300	20
STEM 2 (stems/ha)	9000	12500	20	2000	4100	20	7000	12200	20
PRODUC (kg/ha)	1249.05	365.94	19	683.62	317.85	19	435.64	293.04	20
PRODUC 1 (kg/ha)	1029.27	350.81	19	601.80	305.53	19	273.53	180.00	20
PRODUC 2 (kg/ha)	233.14	227.54	20	78.38	145.27	20	162.10	188.40	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	2-18-24						2-26-50		
Variable	Plot 22			Plot 23			Plot 24		
TH (years)	4.0			4.0			2.0		
TP (years)	35.25			35.25			26.25		
SLOPE (percent)	16.0			15.0			11.0		
ASPECT (degrees)	190			120			160		
SRANK (rank)	2			1			1		
SI (m at 25 yrs)	20.0			20.7			19.9		
BATOT (m^2/ha)	32.78			31.65			28.64		
BACO (m^2/ha)	29.81			26.61			26.99		
BACOI (m^2/ha)	30.19			26.89			27.21		
BAMID (m^2/ha)	2.59			4.76			1.43		
NTOT (trees/ha)	825			600			800		
NCO (trees/ha)	325			325			500		
NCOI (trees/ha)	350			350			525		
NMID (trees/ha)	475			250			275		
CANOV (percent)	57.29			67.45			64.84		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	24.44	28.94	20	16.45	18.40	20	10.38	19.98	19
DEN 2 (percent)	14.99	22.70	20	10.31	13.85	20	5.09	14.42	19
DEN 3 (percent)	13.94	22.00	20	5.94	10.27	20	3.58	14.17	19
DEN 4 (percent)	15.26	21.53	20	7.37	12.35	20	3.53	14.18	19
PIEL	0.82	0.05	20	0.57*	0.05	20	0.82	0.05	19
STEMS (stems/ha)	39500	31000	20	28000	29300	20	32100	31000	19
STEM 1 (stems/ha)	35000	25700	20	23000	28100	20	31000	29600	19
STEM 2 (stems/ha)	4500	10000	20	5000	10000	20	1100	4600	19
PRODUC (kg/ha)	678.94	399.72	19	857.25	461.93	20	899.48	535.93	18
PRODUC 1 (kg/ha)	489.42	320.0	19	663.99	427.81	20	871.37	545.44	18
PRODUC 2 (kg/ha)	188.20	210.01	19	193.25	352.27	20	27.69	64.00	19

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

	Stand								
	2-26-50			2-26-52					
Variable	Plot 25			Plot 26			Plot 27		
TH (years)	2.0			2.25			2.25		
TP (years)	26.25			22.0			22.0		
SLOPE (percent)	7.0			1.2			16.0		
ASPECT (degrees)	260			90			115		
SRANK (rank)	1			2			2		
SI (m at 25 yrs)	14.2			18.2			17.9		
BATOT (m^2/ha)	29.09			20.52			25.44		
BACO (m^2/ha)	27.11			17.54			22.97		
BACOI (m^2/ha)	28.16			17.92			24.16		
BAMID (m^2/ha)	0.93			2.60			1.28		
NTOT (trees/ha)	1250			850			1150		
NCO (trees/ha)	800			375			825		
NCOI (trees/ha)	975			400			925		
NMID (trees/ha)	275			450			225		
CANOV (percent)	66.15			63.54			66.67		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	6.14	10.78	20	10.76	15.61	20	7.24	11.66	22
DEN 2 (percent	5.61	16.14	20	5.28	7.25	20	9.68	16.58	22
DEN 3 (percent	4.51	11.20	20	1.94	2.77	20	15.07	29.59	22
DEN 4 (percent)	4.63	10.56	20	3.10	7.17	20	10.66	22.65	22
PIEL	0.89	0.05	20	0.81	0.05	20	0.65	0.05	21
STEMS (stems/ha)	59000	37300	20	42000	54800	20	15000	11900	22
STEM 1 (stems/ha)	57500	35700	20	39000	50600	20	14500	1400	22
STEM 2 (stems/ha)	1500	4900	20	3000	92000	20	500	2100	22
PRODUC (kg/ha)	372.78	307.14	20	1067.38	419.13	19	544.53	333.44	21
PRODUC 1 (kg/ha)	342.19	264.96	20	885.24	296.21	19	390.70	257.71	21
PRODUC 2 (kg/ha)	30.50	71.75	20	173.74	245.83	20	148.04	206.09	21

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Variable	Stand 2-28-7 Plot 28			Plot 29		
TH (years)	2.25			2.25		
TP (years)	22.0			20.0		
SLOPE (percent)	1.0			2.0		
ASPECT (degrees)	195			45		
SRANK (rank)	6			6		
SI (m at 25 yrs)	20.2			18.2		
BATOT (m^2/ha)	27.36			21.35		
BACO (m^2/ha)	26.21			21.35		
BACOI (m^2/ha)	27.08			21.35		
BAMID (m^2/ha)	0.28			0		
NTOT (trees/ha)	625			500		
NCO (trees/ha)	600			500		
NCOI (trees/ha)	625			500		
NMID (trees/ha)	0			0		
CANOV (percent)	68.75			57.81		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n
DEN 1 (percent)	19.49	26.83	20	21.18	21.69	20
DEN 2 (percent)	3.25	5.33	20	9.63	6.56	20
DEN 3 (percent)	1.71	4.00	20	5.18	6.99	20
DEN 4 (percent)	1.24	2.55	20	4.29	7.74	20
PIEL	0.76	0.05	20	0.86	0.05	20
STEMS (stems/ha)	3500	7500	20	32000	39200	20
STEM 1 (stems/ha)	3500	7500	20	27000	38900	20
STEM 2 (stems/ha)	0	--	--	5000	7600	20
PRODUC (kg/ha)	1408.25	357.59	16	1689.62	405.16	20
PRODUC 1 (kg/ha)	1370.08	347.08	16	1426.25	300.43	18
PRODUC 2 (kg/ha)	54.55	87.14	20	246.97	223.46	20

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Variable	Mean	SD	N	Range
TH (years)	5.58	3.37	29	1.25- 11.75
TP (years)	27.27	4.19	29	20.0 - 35.25
SLOPE (percent)	8.5	5.3	29	1.0 - 19.0
ASPECT (degrees)	168.5	100.9	29	15.0 -340
SRANK (rank)	2.7	1.6	29	1 - 6
SI (m at 25 yrs)	18.9	1.9	29	14.2 - 23.8
BATOT (m^2/ha)	28.6	6.5	29	18.76- 43.50
BACO (m^2/ha)	25.45	5.08	29	17.16- 37.10
BACOI (m^2/ha)	26.42	5.87	29	17.66- 42.07
BAMID (m^2/ha)	2.21	2.29	29	0 - 11.95
NTOT (trees/ha)	925.1	337.3	29	475 -2200
NCO (trees/ha)	477.0	167.3	29	225 -825
NCOI (trees/ha)	537.6	177.5	29	250 -975
NMID (trees/ha)	387.5	359.0	29	0 -1850
CANOV (percent)	68.40	8.85	29	51.56- 90.89
DEN 1 (percent)	11.1	17.7	579	0 -100
DEN 2 (percent)	7.3	14.5	579	0 -100
DEN 3 (percent)	6.4	14.6	579	0 -100
DEN 4 (percent)	5.9	13.7	579	0 -100
PIEL	0.75*	0.002	579	0.54- 1.13
STEMS (stems/ha)	32900	40700	581	0 - 350000
STEM 1 (stems/ha)	30100	38700	581	0 - 350000
STEM 2 (stems/ha)	2800	7700	581	0 - 90000
PRODUC (kg/ha)	609.7	483.3	564	0 - 2545.8
PRODUC 1 (kg/ha)	489.2	430.6	564	0 - 2223.4
PRODUC 2 (kg/ha)	120.7	186.6	580	0 - 1258.9

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a Stand codes according to Virginia Division of Forestry.

Appendix I. Overstory and understory structure summary statistics for 400 m^2 plots in loblolly pine plantations in the Virginia Piedmont. (continued).

b Variables defined in Table 1.

c For understory variables mean is based on n = 20 replicated per 400 m^2 plot. For overstory except PIEL assumed measured exactly on each plot. For PIEL based on n = 20 random point-to-plant distances per plot.

* PIEL significantly different than $\bar{1}$, $p < 0.05$.

Appendix II. Principal Component (PCA) ordination scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

	Cluster	Plot Mean	PCA Axis			Total Percent
			I	II	III	
Percent Eigenvalue			10.7	7.3	6.4	24.4
		Plot				
	1	1	57.960	9.244	61.158	
		4	49.144	30.180	60.110	
		2	44.656	10.971	41.760	
		Mean	50.586	16.798	54.343	
		Plot				
	2	5	42.709	16.350	92.921	
	3	28	0.000	0.000	59.464	
		29	20.298	7.678	55.737	
		Mean	10.149	3.839	57.601	
		Plot				
	4	3	70.256	16.318	50.361	
		7	66.049	22.053	56.752	
		13	67.398	18.583	56.434	
		15	68.180	19.549	57.619	
		11	78.110	20.130	55.072	
		14	81.137	23.608	57.661	
		Mean	71.855	20.040	55.650	
		Plot				
	5	6	100.000	12.306	40.241	
		9	94.013	16.707	48.046	
		8	96.114	10.111	56.058	
		12	99.743	1.107	56.729	
		Mean	97.468	10.058	50.269	

Appendix II. Principal Component (PCA) ordination scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Plot Mean	PCA Axis I	 II	 III
	Plot			
6	10	89.971	23.523	9.485
	16	86.468	36.368	9.506
	21	80.665	40.843	8.381
	Mean	85.702	33.578	9.124
	Plot			
7	17	52.582	31.827	22.388
	19	44.644	32.604	14.148
	18	61.171	36.195	0.000
	20	65.350	32.375	28.280
	Mean	55.937	33.250	16.204
	Plot			
8	24	28.305	45.062	24.365
	26	24.909	28.087	17.759
	27	34.819	22.957	15.617
	Mean	29.345	32.036	19.247
	Plot			
9	23	58.427	52.570	61.140
	25	53.183	60.472	31.038
	Mean	55.805	56.521	46.089
	Plot			
10	22	68.744	100.00	100.00

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[a] $$\text{Scaled score} = \frac{\text{Original PCA Score} - \text{Minimum Score}}{(\text{Maximum} - \text{Minimum})/100}$$

Appendix III. PCA ordination species scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	80.254	10.019	42.732
	Solidago rugosa	74.627	11.540	45.062
	Diospyros virginiana	79.245	17.794	49.618
	Nyssa sylvatica	83.104	20.555	39.446
	Eupatorium hyssopifolium	86.604	26.077	44.943
	Juniperus virginiana	73.216	23.935	54.107
	Desmodium paniculatum	71.134	31.134	50.669
	Vaccinium vacillans	76.422	31.587	45.711
	Lespedeza intermedia	81.752	29.680	50.227
	Ulmus alata	83.888	7.383	60.789
	Lichen	90.811	1.490	56.265
	Desmodium sp.	99.428	19.396	55.082
	Amelanchier arborea	62.353	25.744	26.109
	Rubus flagellaris	63.572	27.303	31.455
	Panicum boscii	70.189	18.422	30.622
	Panicum miliaceum	62.819	15.190	19.201
	Euphorbia corollata	80.760	17.326	25.496
	Ilex opaca	78.303	24.148	28.920
	Panicum depauperatum	69.557	33.714	23.578
	Smilax glauca	70.934	35.695	31.808
	Asclepaias sp.	63.654	25.413	40.424
	Desmodium marindilandicum	61.276	19.396	43.503
	Hieracium sp.	70.931	23.037	43.476
	Chimaphila umbellata	60.657	30.097	47.007
	Lespedeza repens	60.697	34.516	49.585
	Triodia flava	52.412	30.647	43.174
	Parthenocissus quinquefolia	53.004	28.080	52.204
	Ascelepias tuberosa	50.338	27.816	54.141
	Potentilla sp.	47.021	24.673	54.224
	Prunella vulgaris	58.110	18.754	50.736
	Chrysopsis mariana	52.489	17.348	57.916
	Solidago nemoralis	47.296	16.694	46.128
	Mean	68.834	22.735	43.682
2	*Pinus virginiana*	85.559	41.134	16.965
	Vaccinium stamineum	94.128	52.206	27.938
	Chimaphila maculata	100.00	31.395	36.140
	Quercus velutina	93.057	37.667	46.774

Appendix III. PCA ordination species scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
2	*Solidago* sp.	88.625	33.892	45.793
	Mean	92.274	39.259	34.722
3	*Andropogon* sp.	44.720	47.029	23.493
	Rubus argutus	45.733	39.741	22.659
	Ascyrum hypericoides	43.545	39.189	21.217
	Viburnum acerifolium	46.062	41.427	17.725
	Ilex verticillata	38.564	38.480	21.945
	Castanea pumila	47.744	36.275	37.168
	Smilax bona-nox	47.510	38.376	31.082
	Euonymus americanus	40.595	40.462	32.128
	Corylus americana	59.655	42.813	29.752
	Eupatorium vaseyi	54.701	42.878	25.854
	Eupatorium album	58.207	53.014	24.820
	Lespedeza hirta	52.829	45.238	14.049
	Quercus stellata	58.520	34.440	16.660
	Gentiana villosa	60.971	43.273	19.938
	Rhus copallinum	57.995	39.298	0.000
	Mean	50.491	41.462	22.562
4	*Carya tomentosa*	48.958	60.642	45.452
	Gramineae (spp.)	44.390	71.149	52.256
	Seriococarpos asteroides	48.398	71.916	46.793
	Crataegus spp.	55.455	82.697	41.074
	Chrysanthemum leucanthemum	25.576	56.238	22.423
	Galium circaezens	24.839	46.611	14.043
	Convolvulus sp.	36.866	67.822	40.244
	Desmodium viridiflorum	29.886	71.726	37.632
	Danthonia sp.	30.293	54.627	34.925
	Smilax rotundifolia	38.726	63.430	30.092
	Lespedeza cuneata	23.926	51.788	42.641
	Oxalis stricta	33.878	47.509	31.184
	Mean	36.766	62.430	36.563
5	*Liquidambar styracifluc*	61.949	7.691	81.094
	Aster sp.	73.201	2.446	72.903
	Quercus phellos	69.041	0.000	70.261
	Lycopodium complanatum	75.467	5.245	77.601
	Prunus serotina	71.235	6.463	56.639
	Desmodium ciliare	68.029	14.341	54.672
	Ilex decidua	64.049	9.458	65.837
	Mitchella repens	71.218	8.140	64.227
	Eupatorium rotundifolium	71.173	12.181	65.444

Appendix III. PCA ordination species scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
5	*Quercus falcata*	80.771	16.066	66.354
	Danthonia spicata	83.444	24.783	72.448
	Campsis radicans	47.896	25.262	74.466
	Poa compressa	58.426	29.306	68.156
	Polystichum acrostichoides	65.315	27.864	83.304
	Allium sp.	53.561	4.467	70.105
	Sassafras albidum	54.886	6.629	67.071
	Smilax hispida	57.499	4.904	74.065
	Apocynum cannabinum	45.244	0.699	77.222
	Rhus radicans	36.092	11.116	61.954
	Trifolium sp.	45.285	5.646	63.755
	Lespedeza virginica	46.857	8.251	61.210
	Lindera benzoin	36.031	17.410	82.752
	Smilacina racemosa	38.089	25.496	82.324
	Bromus ciliatus	26.576	11.463	85.169
	Mean	58.389	11.889	70.793
6	*Cercis candensis*	33.144	33.023	56.232
	Athyrium filix-femina	34.956	27.672	65.274
	Fragaria virginiana	39.106	32.293	68.626
	Panicum hians	34.993	28.478	73.745
	Quercus rubra	49.226	48.524	61.983
	Vitis spp.	50.605	44.982	71.146
	Potentilla simplex	33.196	51.327	61.717
	Viola sp.	38.373	45.594	45.090
	Carex complanata	46.920	49.202	50.075
	Apocynum sp.	65.149	52.685	42.748
	Panicum commutatum	68.754	40.214	43.081
	Carya glabra	68.975	46.961	68.274
	Quercus alba	80.985	42.987	61.895
	Mean	49.568	41.842	59.222
7	*Lirodendron tulipifera*	29.699	18.585	46.157
	Senecio sp.	31.993	21.341	47.929
	Panicum sphaerocarpon	34.511	16.549	42.905
	Achillea millefolium	32.265	36.993	35.193
	Rosa carolina	32.107	33.501	32.775
	Solidago juncea	35.415	30.681	24.281
	Eupatorium saltuense	32.933	28.698	26.073
	Asplenium platyneuron	28.365	27.362	30.738
	Rudbeckia hirta	26.157	28.187	29.881
	Symphoricarpos orbiculatus	25.975	24.850	32.042

Appendix III. PCA ordination species scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
7	*Erigeron* sp.	13.507	40.090	48.892
	Juglans nigra	11.370	36.339	48.743
	Viburnum prunifolium	18.629	34.169	31.556
	Vitis aestivalis	23.292	37.898	39.300
	Clematis sp.	23.681	40.879	33.561
	Mean	26.660	30.408	36.668
8	*Carpinus caroliniana*	11.060	24.181	56.427
	Solanum carolinese	22.109	18.870	56.057
	Pycnamthemum flexuosum	18.634	10.889	56.549
	Celtis occidentalis	17.491	19.124	37.751
	Cirsium muticum	8.165	23.399	44.543
	Hypericum perforatum	13.873	13.824	48.303
	Anemone quinquefolia	10.719	4.110	56.408
	Geum sp.	14.546	7.489	54.845
	Daucus sp.	6.683	13.325	58.130
	Lonicera japonica	0.000	14.078	48.643
	Boehmeria cylindrica	13.904	3.275	65.158
	Galium triflorum	13.904	3.275	65.158
	Impatiens biflora	10.875	1.312	65.893
	Panicum sp.	23.817	8.075	66.177
	Scutellaria integrifolia	16.865	5.246	77.566
	Mean	13.510	11.365	57.174
9	*Acer rubrum*	44.535	62.907	70.893
	Fraxinus pennsylvanica	51.455	56.368	84.651
	Robinia pseudoacacia	58.986	57.792	76.256
	Castanea dentata	55.516	74.114	83.632
	Moss	58.417	66.832	83.992
	Eupatorium rugosum	45.952	71.191	100.000
	Fagus grandifolia	89.784	62.917	83.743
	Mean	57.806	64.589	83.310
10	*Cornus florida*	53.591	92.343	68.448
	Andropogon scoparius	42.150	95.225	65.688
	Antennaria sp.	43.619	100.000	70.951
	Oxydendrum arboreum	44.880	96.125	54.188
	Quercus coccinea	67.095	92.193	68.481
	Albizzia julibrissin	42.461	88.541	82.000
	Juncus tenuis	43.054	91.142	75.782
	Galium sp.	52.254	96.037	89.350
	Vicia caroliniana	51.452	92.065	86.908

Appendix III. PCA ordination species scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
10	Mean	48.951	93.741	73.533

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a $$\text{Scaled score} = \frac{\text{Original PCA Score - Minimum Score}}{(\text{Maximum - Minimum})/100}$$

Appendix IV. Correlations of plot variables and ordination scores for herb stratum relevé data in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	-0.72930**	0.01410	-0.12483	-0.63990**	0.22069	-0.22956
BATOT	0.09248	0.07476	0.61688**	0.10099	0.03300	0.61133**
BAMID	0.31921+	-0.02389	0.26865	0.44863*	0.09559	0.26238
TH	0.57614**	-0.17592	0.24930	0.54080**	-0.10518	0.23870
TP	0.44605*	0.43800*	0.35745+	0.48473**	0.22159	0.33239+
SI	-0.6209	-0.08983	0.49080*	-0.03646	-0.05419	0.52125**
COSAS	-0.22111	0.19672	0.06869	-0.21472	0.07741	0.04413
SLOPE	-0.20279	0.49328	-0.28818	-0.25843	0.50451**	-0.27523
SRANK	-0.10650	-0.46732	0.43045*	0.14399	-0.54478**	0.35244+
CANCOV	0.27334	-0.29472	0.26779	0.30722	-0.24489	0.17492
PIEL	0.05325	0.07351	-0.11055	0.02217	-0.04975	-0.13350

\+ Significant, $p < .10$

* Significant, $p < .05$

** Significant, $p < .01$

Appendix V. Principal component (PCA) ordination scores for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

	Cluster	Plot Mean	PCA Axis I	 II	 III	Total Percent
Percent Eigenvalue			11.45	9.87	8.23	29.55
		Plot				
	1	1	63.117	0.000	0.000	
	2	2	36.547	26.445	40.502	
		29	32.840	42.192	45.230	
		24	38.423	34.780	69.322	
		26	43.424	34.765	56.806	
		Mean	37.809	34.545	52.965	
		Plot				
	3	28	0.000	32.050	45.671	
	4	5	37.260	100.000	40.487	
		23	37.704	70.858	43.849	
		Mean	37.482	85.429	42.168	
		Plot				
	5	3	71.558	32.494	54.306	
		16	78.216	21.433	55.466	
		Mean	74.887	26.963	54.886	
		Plot				
	6	4	74.396	52.468	52.572	
		11	82.197	45.165	52.307	
		6	93.288	62.570	54.049	
		Mean	83.293	53.401	52.976	
		Plot				
	7	7	96.568	44.361	52.364	
		10	98.528	42.313	54.970	
		14	93.584	41.611	49.256	
		15	85.860	36.861	59.211	
		8	94.141	37.988	68.657	
		12	92.216	41.126	65.579	
		9	100.000	40.195	62.938	
		Mean	94.414	40.636	58.996	

Appendix V. Principal component (PCA) ordination scores for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Plot Mean	PCA Axis		
		I	II	III
	Plot			
8	13	61.223	48.464	59.135
	19	57.082	40.966	58.830
	17	57.253	49.319	45.653
	21	58.600	65.348	65.064
	22	53.407	59.256	59.935
	Mean	57.513	52.671	57.723
	Plot			
9	18	57.181	30.945	100.000
	20	55.364	41.356	88.460
	25	47.238	29.075	82.726
	Mean	53.261	33.792	90.395
	Plot			
10	27	21.126	23.770	85.559

[a] $$\text{Scaled score} = \frac{\text{Original PCA Score - Minimum Score}}{(\text{Maximum - Minimum})/100}$$

Appendix VI. Principal component (PCA) ordination species scores for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	82.261	45.749	55.236
	Ilex opaca	77.035	42.306	51.483
	Nyssa sylvatica	81.217	34.475	56.121
	Lespedeza bicolor	66.991	40.397	64.181
	Liquidambar styraciflua	96.717	47.484	45.587
	Ulmus alata	100.000	52.534	50.698
	Mean	84.037	43.824	53.884
2	*Pinus virginiana*	62.474	55.844	81.509
	Vaccinium stamineum	70.935	43.633	86.341
	Amelanchier arborea	59.769	32.688	81.099
	Diospyros virginiana	50.328	40.989	80.444
	Mean	60.876	43.289	82.348
3	*Juniperus virginiana*	66.176	0.000	45.236
	Quercus falcata	81.912	25.793	31.685
	Mean	74.044	12.897	38.461
4	*Prunus serotina*	20.678	7.158	21.486
	Rubus argutus	20.508	16.574	2.592
	Cornus florida	47.885	9.891	7.483
	Sassafras albidum	52.907	8.876	0.000
	Smilax glauca	59.128	3.232	15.877
	Quercus coccinea	61.373	26.248	10.287
	Mean	43.747	11.996	9.621
5	*Carpinus caroliniana*	36.438	44.573	42.178
	Vitis sp.	29.460	51.015	32.242
	Rhus radicans	20.607	51.124	45.210
	Eupatorium purpureum	13.744	37.284	36.686
	Verbesina alternifolia	14.736	35.436	40.148
	Mean	22.997	43.887	39.293
6	*Cercis canadensis*	34.549	38.058	54.724
	Carya glubra	37.051	22.624	51.550
	Campsis radicans	60.777	45.106	51.202

Appendix VI. Principal component (PCA) ordination species scores for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
6	*Ilex verticillata*	48.966	52.370	52.263
	Mean	45.336	39.539	52.435
7	*Liriodendron tulipifera*	28.451	32.680	82.534
	Smilax rotundifolia	37.997	36.114	85.644
	Parthenocissus quinquefolia	31.517	32.016	70.799
	Viburnum prunifolium	17.589	46.860	72.948
	Oxydendrum arboreum	43.720	25.733	96.096
	Viburnum acerifolium	42.756	35.131	98.916
	Rhus copallinum	31.007	19.982	100.000
	Solidago sp.	34.826	25.316	97.688
	Mean	33.483	31.729	88.078
8	*Lonicera japonica*	0.000	28.661	65.683
	Vitis aestivalis	11.578	25.820	65.785
	Mean	5.789	27.241	65.734
9	*Acer rubrum*	64.778	100.000	66.121
	Fraxinus pennsylvanica	58.541	76.498	41.952
	Quercus velutina	68.527	65.812	42.150
	Fagus grandifolia	61.431	66.196	59.996
	Mean	63.319	77.126	52.555
10	*Platanus occidentalis*	43.054	86.332	38.133
	Quercus alba	42.903	98.899	39.250
	Carya tomentosa	30.263	92.643	33.381
	Quercus rubra	29.755	99.546	32.205
	Corylus americana	24.795	89.625	40.289
	Lindera benzoin	32.607	79.370	30.796
	Robinia pseudoacacia	40.565	75.251	55.689
	Albizzia julibrissin	30.952	67.429	52.135
	Apocynum sp.	26.154	59.465	51.996
	Mean	33.450	83.173	41.542

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a $$\text{Scaled score} = \frac{\text{Original PCA Score - Minimum Score}}{\text{(Maximum - Minimum)/100}}$$

Appendix VII. Correlations of plot variables and plot scores for shrub stratum relevé data in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	-0.65419**	-0.01442	0.01784	-0.68325**	-0.02266	0.03251
BATOT	0.09601	0.40618*	-0.15857	0.07882	0.30985+	-0.08768
BAMID	0.36903*	0.08154	0.03273	0.36043+	0.24021	0.16925
TH	0.60322**	0.46327*	-0.11125	0.54080**	0.48336**	-0.11960
TP	0.31964+	0.55761**	0.10295	0.34945+	0.61878**	0.01904
SI	0.01482	0.54974**	-0.38502*	0.08203	0.53578**	-0.44735*
COSAS	-0.22663	-0.02112	0.00101	-0.21422	0.14273	-0.16566
SLOPE	-0.25635	-0.09736	0.26121	-0.29327	-0.08771	-0.19642
SRANK	-0.07125	0.30506+	-0.23894	0.18220	0.24068	-0.27473
CANCOV	0.27574	0.42465	0.04873	0.33949+	0.36758*	0.04262
PIEL	-0.06989	-0.06483	0.42430*	-0.10197	-0.18867	0.52759**

+ Significant, $p < .10$.
* Significant, $p < .05$.
** Significant, $p < .01$.

Appendix VIII. Principal component (PCA) ordination scores for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

		Plot	PCA Axis			Total
	Cluster	Mean	I	II	III	Percent
Percent Eigenvalue			17.54	13.00	12.32	42.86
		Plot				
	1	1	82.380	91.891	23.490	
		2	82.380	91.891	23.490	
		29	71.773	100.000	28.364	
		26	66.476	89.514	5.809	
		Mean	75.752	93.324	20.288	
		Plot				
	2	7	64.676	84.525	35.697	
		28	46.880	78.592	37.259	
		23	39.583	94.504	28.909	
		Mean	50.380	85.873	33.955	
		Plot				
	3	12	44.010	59.257	33.328	
		14	43.315	54.951	42.401	
		17	52.818	38.394	32.489	
		21	46.958	63.562	17.455	
		22	33.129	65.219	19.880	
		Mean	44.046	56.277	29.111	
		Plot				
	4	25	55.508	71.388	4.718	
		27	67.167	58.626	3.798	
		Mean	61.338	65.007	4.258	
		Plot				
	5	4	17.195	40.892	22.882	
		5	10.819	49.818	31.584	
		15	0.000	22.438	51.951	
		Mean	9.338	37.716	35.472	
		Plot				
	6	8	34.231	43.856	58.751	
		11	38.587	43.140	51.528	
		13	28.780	72.902	52.576	
		Mean	33.866	53.300	54.285	

Appendix VIII. Principal component (PCA) ordination scores for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Plot Mean	PCA Axis I	PCA Axis II	PCA Axis III
	Plot			
7	6	76.697	74.492	48.559
	16	87.285	59.671	74.814
	Mean	81.991	67.082	61.687
	Plot			
8	9	67.003	51.695	100.000
	10	67.810	68.736	93.129
	Mean	67.407	60.216	96.565
	Plot			
9	3	71.202	20.583	0.000
	20	67.974	31.601	6.513
	19	67.069	0.694	2.680
	Mean	68.749	17.626	3.064
	Plot			
10	18	100.000	0.000	54.026
	24	94.570	14.857	32.442
	Mean	97.285	7.428	43.234

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a $$\text{Scaled score} = \frac{\text{Original PCA Score - Minimum Score}}{\text{(Maximum - Minumin)/100}}$$

Appendix IX. Principal component (PCA) ordination species scores for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	100.000	100.000	30.104
2	*Fraxinus pennsylvanica*	41.759	79.706	15.541
	Rhus radicans	37.069	84.515	46.627
	Mean	39.414	82.111	31.084
3	*Nyssa sylvatica*	55.296	59.295	100.000
	Juniperus virginiana	81.781	43.493	85.740
	Quercus coccinea	79.919	30.832	61.306
	Mean	72.332	44.540	82.349
4	*Pinus virginiana*	57.498	25.531	0.000
	Diospyros virginiana	61.189	0.000	43.271
	Oxydendrum arboreum	77.102	9.762	37.060
	Mean	65.263	11.764	26.777
5	*Acer rubrum*	2.811	62.739	69.951
	Liquidambar styraciflua	0.000	44.620	59.073
	Ulmus alata	13.052	44.656	58.382
	Liriodendron tulipifera	7.028	31.447	17.238
	Cornus florida	16.592	56.921	39.998
	Robinia pseudoacacia	15.670	62.121	40.448
	Lonicera japonica	33.761	40.791	37.931
	Mean	12.702	49.042	46.146

[a] $\text{Scaled score} = \dfrac{\text{Original PCA Score} - \text{Minimum Score}}{(\text{Maximum} - \text{Minimum})/100}$

Appendix X. Correlations of plot variables and plot scores for tree stratum relevé data in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	0.16702	0.08433	-0.26388	0.14337	0.02611	-0.2655
BATOT	-0.72232**	-0.01502	0.00994	-0.63899**	0.00985	0.05370
BAMID	-0.58696**	-0.16969	0.19993	-0.50166**	-0.15375	0.31071
TH	-0.47549**	0.02238	0.49738**	-0.43692**	0.06416	0.39291**
TP	-0.49534**	-0.30183	-0.05594	-0.58323**	-0.27603	0.07346
SI	-0.50411**	0.12527	0.26381	-0.56344**	0.09436	0.28455
COSAS	-0.01726	0.30758	0.00096	-0.06386	0.21179	-0.09172
SLOPE	0.32180+	-0.08375	-0.47356**	0.30418	-0.08451	-0.46158*
SRANK	-0.3397+	0.26672	0.22353	-0.29517	0.18495	0.40279
CANOV	-0.56336**	-0.11862	0.25439	-0.45115*	-0.15572	0.35530+
PIEL	0.11454	-0.10510	-0.22028	0.12218	-0.11775	-0.25176

\+ Significant, $p < .10$.

* Significant, $p < .05$.

** Significant, $p < .01$.

Appendix XI. Principal component (PCA) ordination scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont.[a]

	Cluster	Plot Mean	PCA Axis I	II	III	Total Percent
Percent Eigenvalue			13.05	7.41	7.04	27.50
		Plot				
	1	1	68.662	62.111	70.883	
		13	65.434	71.639	64.026	
		2	46.741	51.559	66.380	
		23	51.153	63.746	63.379	
		19	51.358	54.033	48.585	
		25	62.027	40.314	51.588	
		Mean	57.562	57.234	60.807	
		Plot				
	2	14	87.076	65.860	53.868	
		21	84.981	72.167	50.152	
		20	75.435	56.087	53.721	
		16	95.425	50.586	35.980	
		17	78.135	60.649	29.566	
		Mean	84.210	61.070	44.657	
		Plot				
	3	18	81.795	33.824	0.000	
	4	3	94.610	33.437	94.931	
		7	86.259	47.023	88.177	
		6	100.000	29.701	78.362	
		10	98.053	29.140	74.859	
		Mean	94.731	34.825	84.082	
		Plot				
	5	8	99.917	62.624	82.126	
		11	82.807	51.397	70.625	
		13	94.374	54.112	72.678	
		Mean	92.366	56.044	75.143	
		Plot				
	6	9	99.609	14.275	99.516	
	7	24	10.824	31.260	55.955	
		26	0.000	10.030	66.246	
		27	5.966	0.000	50.980	
		Mean	5.597	13.763	57.727	

Appendix XI. Principal component (PCA) ordination scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Plot Mean	PCA Axis I	 II	 III
	Plot			
8	4	66.686	99.361	50.627
	15	67.863	99.474	51.482
	22	74.671	95.612	53.339
	Mean	69.740	98.149	51.816
	Plot			
9	5	49.655	89.316	63.570
	28	37.779	100.000	83.078
	Mean	43.717	94.658	73.324
	Plot			
10	29	3.891	98.959	100.000

a Scaled score = $\frac{\text{Original PCA Score - Minimum Score}}{\text{(Maximum - Minimum)/100}}$

Appendix XII. Principal component (PCA) ordination species scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	87.551	21.081	94.914
	Lichen	86.483	22.190	99.016
	Quercus sp.	81.305	31.947	100.000
	Fagus grandifolia	79.285	29.827	93.135
	Desmodium laevigatum	73.043	14.909	85.054
	Pinus sp.	65.827	18.150	81.029
	Fungi	63.209	19.228	92.986
	Juniperus virginiana	79.170	39.063	81.738
	Diospyros virginiana	73.031	45.297	87.047
	Aster sp.	63.064	39.259	79.568
	Ilex americana	67.446	33.439	78.997
	Desmodium paniculatum	68.600	35.851	88.408
	Ulmus alata	69.797	35.270	83.485
	Rubus sp.	58.800	38.389	91.471
	Chimaphila maculata	90.374	11.580	75.830
	Quercus falcata	100.000	18.587	72.770
	Mean	75.437	28.379	86.591
2	*Pinus virginiana*	55.127	30.706	45.889
	Antennaria sp.	47.516	45.355	41.663
	Convolvulus sp.	53.912	40.500	45.448
	Nyssa sylvatica	74.085	46.933	45.807
	Smilax glauca	70.616	47.284	36.025
	Ilex verticillata	63.935	46.068	51.208
	Viburnum acerifolium	65.254	41.509	48.124
	Eupatorium sp.	61.157	44.477	46.260
	Apocynum sp.	67.186	49.259	66.118
	Chimaphila umbellata	64.312	52.796	49.370
	Quercus alba	71.091	58.793	54.215
	Eupatorium hyssopifolium	74.232	31.948	66.304
	Mean	64.035	44.636	49.703
3	*Liquidambar styraciflua*	76.595	62.328	73.221
	Moss	77.853	57.206	75.389
	Desmodium viridiflorum	70.418	51.138	79.177
	Ilex decidua	69.478	57.740	79.574

Appendix XII. Principal component (PCA) ordination species scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
3	Desmodium sp.	61.666	67.958	75.843
	Lespedeza sp.	56.248	74.504	70.623
	Mean	68.710	61.812	75.638
4	Acer rubrum	52.644	75.035	21.155
	Euonymus americanus	50.590	77.209	23.031
	Crataegus sp.	56.047	64.899	16.433
	Asclepias sp.	60.126	70.281	40.547
	Quercus phellos	55.529	69.402	30.850
	Rubus flagellaris	65.018	63.877	32.565
	Vaccinium vacillans	66.034	68.156	33.963
	Amelanchier arborea	42.603	76.448	38.336
	Campsis radicans	52.594	92.229	44.436
	Quercus ruba	53.588	86.598	40.522
	Carya tomentosa	47.680	73.757	49.437
	Castanea dentata	55.503	79.592	47.136
	Lycopodium complanatum	54.810	83.528	51.450
	Polystichum acrostichoides	51.848	82.054	52.187
	Vaccinium arboreum	60.740	73.020	51.113
	Mean	55.024	75.739	38.211
5	Fraxinum pennsylvanica	42.120	61.456	60.423
	Sassafras albidum	51.806	59.951	61.499
	Viola sp.	47.945	53.283	58.367
	Corylus americana	54.397	61.212	48.923
	Hypericum perforatum	41.581	46.295	57.824
	Gramineae spp.	30.455	53.172	60.238
	Solanum carolinense	32.720	54.638	34.107
	Mean	43.003	55.715	54.483
6	Euphorbia corollata	60.802	39.034	30.361
	Lespedeza repens	70.545	31.643	23.594
	Oxydendrum arboreum	64.955	55.840	18.925
	Quercus coccinea	74.333	54.812	20.324
	Quercus velutina	87.746	49.753	35.664
	Vaccinium stamineum	84.428	48.268	16.222
	Mean	73.802	46.559	24.182
7	Potentilla sp.	50.630	44.235	10.167
	Seriococarpus asteroides	57.124	37.070	7.136
	Rhus copallinum	64.021	46.887	0.000

Appendix XII. Principal component (PCA) ordination species scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
7	*Smilax rotundifolia*	52.125	26.335	2.956
	Solidago sp.	62.566	19.820	9.928
	Rubus argutus	36.616	35.589	9.663
	Mean	53.847	34.989	6.642
8	*Prunus serotina*	19.980	0.000	53.946
	Achillea millefolium	2.538	9.647	48.362
	Mentha aquatica	1.757	6.989	50.423
	Celtis occidentalis	9.983	12.059	51.258
	Symphoricarpos orbiculatus	11.923	9.355	49.063
	Cercis canadensis	15.372	18.516	62.757
	Juglans nigra	11.543	20.327	57.843
	Fragaria virginiana	9.324	18.568	53.003
	Viburnum prunifolium	6.434	20.099	49.824
	Galium sp.	0.000	25.760	53.725
	Clematis sp.	11.179	34.389	60.035
	Cirsium sp.	5.871	36.507	65.387
	Trifolium sp.	13.501	40.531	54.377
	Daucus carota	13.933	41.147	47.941
	Lespedeza intermedia	23.563	40.987	48.387
	Polypodiaceae sp.	25.849	36.683	46.715
	Senecio sp.	31.218	12.348	46.803
	Eupatorium album	30.564	19.439	53.200
	Euphorbia sp.	43.204	17.170	59.214
	Mean	15.144	22.133	53.277
9	*Liriodendron tulipifera*	14.231	84.949	74.069
	Panicum sp.	24.563	75.785	81.964
	Rhus radicans	32.043	79.095	78.624
	Rubus occidentalis	19.384	85.861	92.025
	Verbesina alternifolia	19.239	87.553	92.452
	Vitis sp.	6.743	73.444	90.862
	Cornus florida	0.022	77.583	58.877
	Lonicera japonica	8.522	61.804	54.479
	Parthenocissus quinquefolia	3.152	61.396	57.728
	Carpinus caroliniana	4.904	53.824	75.427
	Lespedeza cuneata	13.452	54.438	70.656
	Albizzia julibrissin	21.833	60.046	86.010
	Geum sp.	10.365	59.877	85.384
	Mean	13.727	70.435	76.812

Appendix XII. Principal component (PCA) ordination species scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
10	*Robinia pseudoacacia*	35.320	100.000	69.912
	Impatiens sp.	35.521	85.748	72.122
	Carya glabra	45.738	87.489	57.720
	Lindera benzoin	39.316	83.595	60.262
	Mean	38.974	89.208	65.004

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a $$\text{Species score} = \frac{\text{Original PCA Score - Minimum Score}}{\text{(Maximum - Minimum)/100}}$$

Appendix XIII. Correlations of plot variables and plot scores for herb stratum production plots in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	-0.67549**	0.23944	0.00903	-0.65419**	0.12217	-0.23842
BATOT	0.11660	0.52244**	0.05271	-0.1478	0.50640**	-0.00591
BAMID	0.15702	0.24531	-0.06329	0.20645	0.04582	-0.06430
TH	0.51440**	0.21901	0.15189	0.46024*	0.21905	0.09274
TP	0.44428*	0.20192	-0.11067	0.36479+	0.30073	-0.14072
SI	-0.02849	0.40634*	0.08405	-0.04336	0.40916*	0.10987
COSAS	-0.16628	-0.01017	0.22145	-0.17503	0.02342	0.19080
SLOPE	-.25685	-0.38216*	-0.41821*	-0.22458	-0.35479+	-0.35751+
SRANK	-0.05370	0.44980*	0.30164	0.14815	0.34750	0.31268+
CANOV	0.28343	0.20586	0.07802	0.31338+	0.17246	0.10815
PIEL	0.02871	-0.04008	0.13346	-0.00443	-0.04384	0.19951

+ Significant, p < .10

* Significant, p < .05

** Significant, p < .01

Appendix XIV. Principal component (PCA) ordination scores for low shrub (1-2 m) stratum production plots in loblolly pine plantations in the Virginia Piedmont.

	Cluster	Plot Mean	PCA Axis I	II	III	Total Percent
Percent Eigenvalue	- - - - - - - - - - -	-	12.19	9.56	8.86	30.61
		Plot				
	1	1	51.521	79.597	74.616	
		21	39.800	79.194	77.838	
		4	40.083	74.910	59.772	
		5	44.082	76.155	59.772	
		24	62.034	83.547	79.478	
		Mean	47.504	78.681	70.295	
		Plot				
	2	2	65.872	66.095	67.460	
		22	65.262	67.780	59.603	
		15	45.291	66.180	70.430	
		25	50.570	64.846	72.159	
		19	56.754	67.926	75.088	
		17	46.907	51.298	63.137	
		Mean	55.110	64.021	67.980	
		Plot				
	3	3	21.483	64.693	65.554	
		7	25.806	69.312	61.222	
		8	28.961	73.818	65.224	
		10	20.437	78.820	65.742	
		14	14.006	64.957	55.980	
		Mean	22.139	70.320	62.744	
		Plot				
	4	13	33.385	95.505	26.998	
	5	6	25.489	84.152	82.826	
		9	20.977	96.272	98.152	
		20	29.111	92.003	94.709	
		12	0.000	95.734	91.353	
		Mean	18.894	92.040	91.760	
		Plot				
	6	23	71.872	78.696	50.669	
		28	68.390	86.403	48.456	
		Mean	70.131	82.549	49.563	

Appendix XIV. Principal component (PCA) ordination scores for low shrub (1-2 m) stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued)

Cluster	Plot Mean	PCA Axis I	PCA Axis II	PCA Axis III
	Plot			
7	26	97.953	97.312	59.777
	29	100.000	100.000	31.956
	Mean	98.976	98.656	45.866
8	27	95.204	62.653	85.684
9	11	1.007	29.971	0.000
10	16	62.283	0.000	100.000
	18	62.294	2.251	69.373
	Mean	62.288	1.126	84.686

Appendix XV. Principal component (PCA) ordination species scores for shrub (1-2 m) stratum production plots in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	26.527	84.419	97.280
	Vaccinium stamineum	34.943	86.705	96.085
	Ulmus alata	31.327	71.914	77.069
	Vaccinium arboreum	37.519	77.994	85.933
	Pinus virginiana	11.540	83.690	89.896
	Lichen	9.586	82.177	88.572
	Juniperus virginiana	7.189	100.000	100.000
	Mean	22.660	83.843	90.691
2	*Cornus florida*	73.360	85.488	83.535
	Cercis canadensis	92.242	78.388	64.316
	Parthenocissus quinquefolia	93.413	77.827	68.577
	Lonicera japonica	100.00	71.739	58.826
	Viburnum pranifolium	94.713	66.016	73.247
	Diospyros virginiana	86.731	47.204	90.381
	Mean	90.076	71.110	73.147
3	*Platanus occidentalis*	45.301	67.924	55.795
	Carpinus caroliniana	48.495	58.321	57.600
	Quercus coccinea	45.348	47.805	54.923
	Robinia pseudacacia	74.657	68.519	46.693
	Quercus alba	58.333	61.825	36.457
	Mean	54.427	60.879	50.294
4	*Fraxinus pennsylvanica*	83.311	84.274	21.643
	Albizzia juliprissin	90.234	87.277	29.505
	Verbesina alternifolia	79.366	82.443	35.511
	Vitis sp.	94.434	89.678	40.535
	Mean	86.836	85.918	31.799
5	*Campsis radicans*	40.015	79.575	30.870
	Rhus radicans	67.164	93.177	20.416
	Mean	53.589	86.376	25.643
6	*Acer rubrum*	9.909	67.868	52.500
	Liquidambar styraciflua	0.000	69.502	65.303

Appendix XV. Principal component (PCA) ordination species scores for shrub (1-2 m) stratum production plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Species	I	II	III
6	*Quercus falcata*	6.149	45.186	37.678
	Mean	5.353	60.852	51.827
7	*Nyssa sylvatica*	13.873	53.353	0.000
	Fagus grandifolia	16.929	36.087	8.822
	Quercus velutina	12.700	38.785	9.069
	Mean	14.501	42.742	5.964
8	*Liriodendron tulipifera*	81.530	33.436	67.418
	Prunus serotina	65.004	19.061	64.344
	Mean	73.267	26.248	65.881
9	*Oxydendrum arboreum*	65.139	7.989	90.663
	Rhus copallinum	68.227	0.000	92.710
	Smilax glauca	60.137	17.035	95.052
	Mean	64.501	8.341	92.808
10	*Smilax rotundifolia*	45.056	9.313	39.544

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[a] $$\text{Species scores} = \frac{\text{Original PCA Score - Minimum Score}}{\text{(Maximum - Minimum)/100}}$$

Appendix XVI. Correlations of plot variables and plot scores for shrub (1-2 m) stratum production plots in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	0.65125**	0.20428	-0.24878	0.65813**	0.21182	-0.16946
BATOT	-0.28231	-0.00495	-0.31839+	-0.19655	-0.09754	-0.30443
BAMID	-0.23732	-0.00708	-0.06557	-0.30574	0.01256	-0.09929
TH	-0.55675**	-0.01144	0.03451	-0.50649**	0.13302	0.04674
TP	-0.47245**	-0.01106	-0.16498	-0.47336**	-0.17609	-0.27971
SI	-0.15098	0.08646	-0.38718*	-0.15421	0.05050	-0.53110**
COSAS	0.17063	0.16359	-0.36915*	0.16270	0.08160	-0.38136*
SLOPE	0.37828*	-0.18748	0.06158	0.36689+	-0.28190	0.06325
SRANK	-0.06936	0.28531	-0.28799	-0.20247	0.30956	0.28512
CANOV	-0.36160+	0.05262	-0.07701	-0.42424*	0.01404	-0.13944
PIEL	-0.06305	0.23815	0.22273	-0.04335	0.31133+	0.22808

\+ Significant, p < .10.

* Significant, p < .05.

** Significant, p < .01.

Appendix XVII. Principal component (PCA) ordination scores for overstory plots in loblolly pine plantations in the Virginia Piedmont.

	Cluster	Plot Mean	PCA Axis			Total Percent
			I	II	III	
Percent Eigenvalue			17.34	15.77	12.62	45.72
		Plot				
	1	1	12.893	57.193	74.021	
		29	12.893	57.193	74.021	
		23	15.462	64.535	72.996	
		6	12.712	53.354	66.394	
		7	15.818	49.965	72.178	
		28	20.446	49.432	77.094	
		4	33.635	49.604	74.143	
		17	25.149	55.205	76.669	
		26	25.340	55.836	60.903	
		27	27.187	57.779	68.139	
		Mean	20.153	55.010	71.656	
		Plot				
	2	2	5.603	56.782	49.849	
		10	8.190	39.130	65.396	
		Mean	6.896	47.956	57.623	
		Plot				
	3	9	15.790	18.737	53.605	
		16	0.000	24.910	51.519	
		Mean	7.895	21.823	52.562	
		Plot				
	4	18	19.226	83.211	17.656	
	5	24	14.830	47.268	0.000	
	6	3	26.882	84.706	82.384	
		25	32.124	73.612	77.449	
		20	39.645	83.147	61.035	
		19	42.607	100.000	84.259	
		Mean	35.315	85.366	76.282	
		Plot				
	7	21	31.925	72.189	93.506	
		22	36.884	62.532	95.804	
		Mean	34.405	67.360	94.655	

Appendix XVII. Principal component (PCA) ordination scores for overstory plots in loblolly pine plantations in the Virginia Piedmont. (continued).

Cluster	Plot Mean	PCA Axis I	II	III
8	8	38.151	24.480	60.117
	11	56.495	0.000	68.770
	Mean	47.323	12.240	64.444
	Plot			
9	12	37.542	42.230	90.365
	13	39.420	42.683	94.084
	14	54.371	39.200	98.084
	15	44.557	33.591	100.000
	Mean	43.973	39.426	95.633
	Plot			
10	5	100.000	60.007	6.467

Appendix XVIII. Principal component (PCA) ordination species scores for overstory plots in loblolly pine plantations in the Virginia Piedmont.[a]

		Species Scores		
		PCA Axis		
Cluster	Species	I	II	III
1	*Pinus taeda*	0.000	43.642	59.215
	Quercus coccinea	26.150	29.031	56.833
	Nyssa sylvatica	39.848	6.183	43.648
	Juniperus virginiana	44.482	0.000	35.901
	Mean	27.620	19.714	48.899
2	*Acer rubrum*	72.551	9.495	76.417
	Liquidambar styraciflua	74.342	10.255	100.000
	Cornus florida	73.418	52.508	90.744
	Robinia pseudoacacia	54.722	50.362	94.795
	Mean	68.758	30.655	90.489
3	*Pinus virginiana*	57.800	100.000	72.897
	Diospyros virginiana	52.986	99.184	77.239
	Mean	55.393	99.592	75.068
4	*Liriodendron tulipifera*	100.000	46.084	41.200
	Platanus occidentalis	91.216	56.077	27.244
	Mean	95.608	51.080	34.222
5	*Prunus serotina*	31.719	50.181	26.730
	Fraxinus pennsylvanica	36.671	74.339	43.398
	Carpinus caroliniana	60.184	72.027	0.000
	Mean	42.858	65.516	23.376

[a] $$\text{Species scores} = \frac{\text{Original PCA Score - Minimum Score}}{(\text{Maximum - Minimum})/100}$$

Appendix XIX. Correlations of plot scores and plot variables for overstory plots in loblolly pine plantations in the Virginia Piedmont.

	Pearson			Spearman		
	PCA Axis			PCA Axis		
	I	II	III	I	II	III
PRODUC	-0.20813	0.28736	-0.06585	-0.14977	0.25915	-0.11036
BATOT	0.58933**	-0.33980^{+}	-0.00462	0.45621*	-0.19707	0.13746
BAMID	0.28667	-0.38067*	0.32088^{+}	0.39522*	-0.46150*	0.10373
TH	0.33659^{+}	-0.51810**	0.03002	0.19148	-0.47397**	-0.02139
TP	0.40942*	0.11743	0.27323	0.47762**	0.03438	0.47811**
SI	0.38875*	-0.42763*	-0.19185	0.14326	-0.39382*	0.00801
COSAS	-0.19953	-0.12622	0.16083	-0.11921	-0.01171	-0.01861
SLOPE	-0.17423	0.45008*	-0.11944	-0.09637	0.53546**	-0.17445
SRANK	0.28048	-0.24785	0.07771	0.08669	-0.40097*	0.16234
CANOV	0.44802*	-0.27642	-0.12848	0.23408	-0.24467	0.04139
PIEL	-0.02331	0.21773	0.00904	0.08449	0.20815	0.00517

\+ Significant, $p < .10$

* Significant, $p < .05$

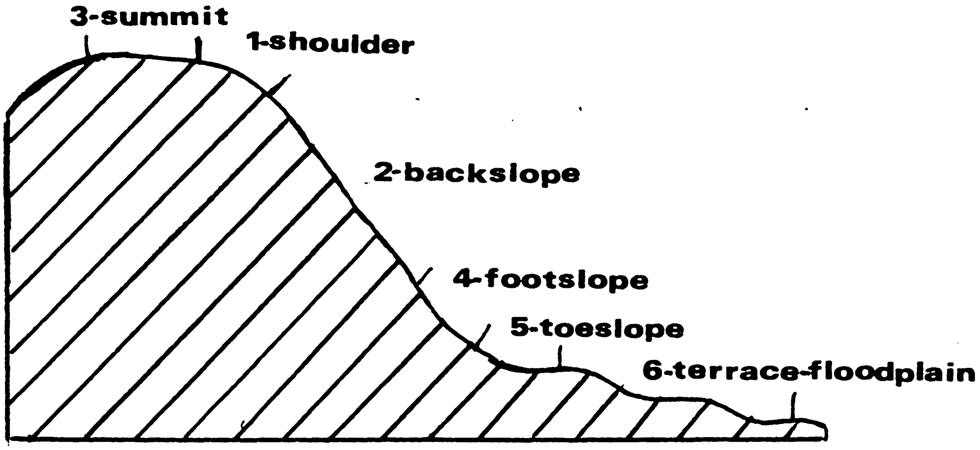
** Significant, $p < .01$

Appendix XX. Mean nutrient values of forage species for all areas in loblolly pine plantations in the Virginia Piedmont.

Species	Plant Part	Gross Energy (cal/g)			Dry Matter Digestibility (DDM) (percent)			Crude Protein (percent)		
		Mean	N	SD	Mean	N	SD	Mean	N	SD
Acer rubrum	Leaves	4906.87	2	91.36	39.31	3	0.90	11.45	3	0.31
	Twigs	4522.13	2	55.43	22.42	4	3.81	3.17	3	0.56
Nyssa sylvatica	Leaves	4317.38	2	80.24	40.80	3	6.37	11.27	3	0.56
	Twigs	4620.49	2	33.68	24.83	3	10.3	4.70	3	0.15
Cornus florida	Leaves	4388.31	2	276.79	37.18	1	--	9.13	3	0.75
	Twigs	4620.49	2	33.68	32.76	3	0.62	2.20	3	0.99
Juniperus virginiana	Leaves	5020.08	2	12.91	45.63	3	0.52	6.33	3	0.02
Quercus spp.	Leaves	4876.53	2	57.31	19.3	3	6.81	14.77	6	0.44
	Twigs	4800.89	2	391.10	16.62	3	2.47	4.25	6	0.42
Compositae	Leaves	4377.28	2	42.61	41.77	3	0.28	7.10	3	0.35
Chimophila spp.	Leaves	4955.37	2	81.59	47.91	3	5.27	11.63	3	0.66
	Twigs	4506.22	2	46.57	48.04	3	4.69	8.60	3	0.62
Fabaceae	Leaves	4825.85	2	115.62	--	-	--	23.22	3	0.14
	Twigs	4497.87	2	117.63	37.23	3	4.00	8.64	3	0.21
Fragaria spp.	Leaves	4572.87	2	43.04	35.13	6	2.85	11.14	3	0.28
Ilex spp.	Leaves	4990.65	2	79.86	38.35	-	--	6.76	3	0.63
	Twigs	4825.67	1	--	--	-	--	5.42	3	1.30
Lonicera japonica	Leaves	4502.25	32	635.42	50.64	35	5.06	9.60	15	3.05
	Twigs	4614.13	2	115.54	38.77	32	6.45	4.00	15	2.53
Pinus spp.	Leaves	4976.55	4	202.19	39.12	3	9.45	9.59	3	0.54
	Twigs	5094.87	2	44.66	36.43	3	5.21	4.57	6	1.32

Appendix XX. Mean nutrient values of forage species for all areas in loblolly pine plantations in the Virginia Piedmont (continued).

Species	Plant Part	Gross Energy (cal/g)			Dry Matter Digestibility (DDM) (percent)			Crude Protein (percent)		
		Mean	N	SD	Mean	N	SD	Mean	N	SD
Rhus radicans	Leaves	4577.00	2	297.84	34.62	3	8.49	14.65	3	0.73
	Twigs	3593.34	2	517.55	38.56	3	0.88	6.82	3	0.38
	Fruits	5979.58	2	45.66	58.14	3	9.73	7.73	3	0.23
Smilax spp.	Leaves	4810.09	2	27.26	51.39	3	11.82	13.83	3	1.63
	Twigs	4824.63	2	158.91	35.23	3	1.132	4.89	3	0.53
Vaccinum spp.	Leaves	5133.96	2	81.12	29.85	24	8.19	10.81	13	2.17
	Twigs	4997.28	2	60.16	32.55	17	7.10	4.70	13	0.56
	Fruits	5090.44	2	387.93	58.14	--	--	5.05	2	0.47
Vitis spp.	Leaves	4460.0	2	24.17	25.30	3	1.46	12.88	3	0.51
	Twigs	4630.9	2	15.90	26.83	2	14.93	4.34	3	1.95
Grass	Leaves	4330.73	6	296.8	47.97	12	9.36	7.56	5	0.56
Fungi	Leaves	4727.6	2	685.3	--	--	--	7.78	3	0.92
Rubus spp.	Leaves	4396.38	4	135.61	37.46	22	6.23	12.72	14	1.15
	Twigs	5158.17	2	452.20	38.63	9	4.48	5.83	3	0.59



Appendix XXI. Slope position ranking (SRANK), based on a hypothetical production gradient (Smith and Burkhart 1976) for understory vegetation in loblolly pine plantations in the Virginia Piedmont.

RELATIONSHIP OF UNDERSTORY DEVELOPMENT IN THINNED LOBLOLLY PINE PLANTATIONS TO OVERSTORY STRUCTURE AND SITE CHARACTERISTICS IN THE VIRGINIA PIEDMONT

by

Michael J. Conroy

(ABSTRACT)

Understory forage production, species composition, and nutrient concentrations were studied in relation to overstory structure and site characteristics in thinned loblolly pine *(Pinus taeda)* plantations in the Virginia Piedmont. Stands exhibited a wide range in overstory basal areas (18.8 to 43.5 m^2/ha) and site indices (14.2 to 23.8 m at base age 25 years). Understory forage production for the 0 to 2 m stratum averaged 610 kg/ha and ranged from 154 to 1690 kg/ha. Initially, differential models were used to develop prediction equations relating understory production to overstory characteristics, but an empirical prediction equation proved to be somewhat superior. Forage production was most predictable from total overstory basal area, canopy cover, and slope position. Understory species composition was analyzed with respect to overstory structural and site gradients, using vegetation ordination techniques. Species composition was less closely related to these gradients than was production; however, the greatest species diversity appeared to occur during the period following thinning but before crown closure, when successional and mid-tolerant species coexisted. Nutrient concentrations in forage material averaged 4643 cal/g for gross energy, 38.3 percent for *invitro* dry matter digestibility by white-tailed deer *(Odocoileus virginiana)* and 8.4 percent for crude protein. There were no apparent trends of these nutrient concentrations with respect to overstory structural or site characteristics. Forage based carrying capacities for white-tailed deer were computed using values from this study for production and nutrient concentrations, and values from the literature for deer forage preferences and nutrient requirements. Results indicated that the pine habitat could support 0.03 to 0.19 lactating does per ha during the summer season, and that energy and not protein is likely the limiting nutritive parameter. Suggestions are made for future research in pine overstory-understory and wildlife habitat relationships. These include the use of experimental overstory manipulation followed by periodic remeasurements to directly observe changes in understory production and species composition, intensive sampling to determine specific local wildlife forage preferences, and the quantification of wildlife movements and population dynamics.