MODELING WHITE-TAILED DEER HABITAT QUALITY AND VEGETATION RESPONSE TO SUCCESSION AND MANAGEMENT

by

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Thesis submitted to the faculty of
Virginia Tech University in partial
fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Wildlife Science

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April, 1994
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(ABSTRACT)

A habitat suitability index (HSI) model for white-tailed deer (Odocoileus virginianus) was tested to determine the relationship between habitat quality predicted by the model and habitat quality suggested by the condition of 1.5 year-old bucks on Quantico Marine Corps Base, Virginia. Additionally, new models were developed that predict the response of habitat variables important to a variety of species to succession and management.

Habitat quality predicted by the white-tailed deer HSI model for 11 different deer management units was not strongly correlated with body weight (Spearman's r = -0.40, P = 0.221, n = 11), beam diameter (r_s = 0.06, P = 0.851, n = 11), beam length (r_s = 0.37, P = 0.265, n = 11), and number of points (r_s = -0.24, P = 0.473, n = 11). The area within each management unit with HSI > 0.5 was weakly correlated (r_s = 0.48, P = 0.13) with beam diameter and beam length.

We attempted to model the response of vegetation to succession and management. The strength of the relationship between habitat changes and stand age (succession) varied depending on the variable and cover type being modeled. R^2_{adj} values were highest on average for habitat

parameters associated with overstory trees, including basal area, dbh, density, and height. R^2_{adj} values were low ($R^2_{adj} < 0.5$) and regressions nonsignificant ($\underline{P} > 0.10$) for models associated with shrubs and herbaceous vegetation. In general, the response of habitat parameters was most predictable in loblolly-shortleaf pine plantations that were hand planted and not subject to the same variation associated with naturally regenerated stands.

Acknowledgements

Many thanks go to Dean Stauffer, story teller extraordinaire, for giving me this opportunity and the freedom to make the most of it. As my advisor, Dean encouraged me to think and act independently and to laugh at my mistakes (I laughed a lot in the last 2 1/2 years). Luckily, Dean understood that hunting, fishing, and spending time at the gym were keys to success for some people, especially me.

I thank Dr. Roy Kirkpatrick for sharing his expertise and time. His willingness to listen and ability to put things in perspective helped me to keep my head on straight.

I greatly appreciated the valuable input provided by Dr. Rich Oderwald. He helped me to get back on track when I had lost my way and showed me how to look at things in ways I would not have otherwise.

Financial and logistical support for this project was provided by the U.S. Fish and Wildlife Service. I especially appreciate all of the assistance and advice provided by Brian Cade and Bart Prose of the National Ecology Research Center. Further financial support was provided by the U.S. Department of the Navy through the Natural Resources and Environmental Affairs Branch at Quantico Marine Corps Base. Special thanks to Tim Stamps, who was instrumental in obtaining funding and enthusiastically provided important logistical and moral support. Also Mary Geil, Ben Fulton, Tom Faleski, Mack Garner and Eueul Tritt, who did everything they could to make our work at Quantico successful and enjoyable.

I could not have completed this project without the help of my incredible crew of field technicians. Thanks to Joe Ferdinandsen, Carrie Stengle, Bonnie Brewer, Darl Fletcher, Mike Chamberlain, and Jim Bennet for braving the heat, ticks, bees and bombs. Thanks also to Jerry Hish, Martha Hawksworth and Joe Ferdinandsen for volunteer help in the lab.

Two super people, Judy Baker and Nancy Wade, shared their lab with me and taught me what was necessary to complete my analyses. Their humor and patience made an otherwise tedious task enjoyable. Thanks also to Dr. Scott Carr, Donnie Bell, Anne Robinson, Dave Hewitt, and Alice Chung-McCoubrey for sharing their lab expertise as well. I also appreciate the extra brain power provided by Dave Hewitt, Kurt Newman, Joe Lucas, Scott Staelgraeve, and especially Mike Tonkovich, who wouldn't let me be stupid. Thanks to Ed Mullins for preparing and repairing vehicles that we relied on so heavily.

It would be impossible for me to fully express my gratitude to Mike and Margaret Tonkovich. They made every aspect of my time in Blacksburg better. I cannot imagine what I would have done without them. I am very lucky to have them as friends.

Finally, and most importantly, I thank my biggest fans, my family. Their support and enthusiasm for what I was trying to accomplish was amazing. I could not have achieved anything without their love and encouragement.

The students, faculty, and staff in the Department of Fisheries and Wildlife Sciences are an amazing group of people. Their ability to work hard and play hard made it a great environment to work in. Thanks.

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CHAPTER I:

MODELING WINTER WHITE-TAILED DEER HABITAT QUALITY

INTRODUCTION

Habitat has been selected as the basis for modeling efforts to assist in planning studies. Habitat provides an integration of the concepts of population and carrying capacity. Additionally, habitat analysis can provide a consistent basis for baseline, impact assessment, mitigation, and monitoring studies (Schamberger and O'Neil 1986). The need to assess the impacts of increasing urban, industrial, and agricultural development on wildlife has resulted in the creation of wildlife habitat assessment approaches. Habitat suitability index (HSI) models have been developed and used in the context of determining habitat quality and predicting the impact of human disturbance on wildlife (Schamberger and O'Neil 1986). The U.S. Fish and Wildlife Service developed the Habitat Evaluation Procedures (HEP) that use HSI models to determine suitability of habitats, assess impacts of habitat modification, and provide guidelines for compensation and mitigation (Irwin and Cook 1985). These models have been criticized because some species may have inconspicuous, but important, requirements not reflected in the model. Additionally, many HSI models are based on literature review and expert opinion rather than intensive field studies. Thus, HSI models should be field tested to determine whether they incorporate appropriate habitat variables that are shown to influence populations and to determine correlation between model outputs and indices of population dynamics that reflect habitat conditions (Irwin and Cook 1985).

In 1987, the U.S. Fish and Wildlife Service recognized that HSI models were being developed at a greater rate than they were being tested. Consequently, field testing of models was made a higher priority while the development of new models was de-emphasized. Model testing, or validation, is the process of comparing predicted and observed test consequences (Romesburg 1981). Testing wildlife habitat models should be a requirement for their use in management (Hurley 1986, Chalk 1986, Bunnell 1989), but so far this has seldom been the case. Many wildlife HSI models represent hypotheses of animals' relations to habitat that have not been tested against empirical data (Chalk 1986). Complete testing of HSI models should occur in 2 steps (U.S. Fish and Wildlife Service 1987). The first stage is to evaluate the inputs and assumptions of the models; secondly, field testing of the model is carried out once the inputs and assumptions are deemed appropriate, or necessary changes or improvements have been made to the model.

I carried out a field test of the HSI model for white-tailed deer (Odocoileus virginianus) in the Gulf of Mexico and south Atlantic coastal plains (Short 1986). The inputs and assumptions of this model have been evaluated (Stauffer 1990), so this project represents the final phase of testing for this model, or a third iteration of model development.

Modeling white-tailed deer habitat represents a special problem because deer are flexible in their habitat requirements and have shown considerable ability to adapt, and even thrive, as their habitat is modified by human development. The white-tailed deer is by far the widest ranging species of deer in North America, occupying habitats ranging from sub-tropical to north-temperate areas (Baker 1984). The white-tailed deer's status as a habitat generalist makes it particularly difficult to isolate specific habitat requirements that may be used to assess the relative quality of habitat for deer.

The white-tailed deer HSI model developed by Short (1986) was intended for use in the Gulf of Mexico and south Atlantic coastal plain, including regions of Texas, Arkansas, Mississippi, Tennessee, Kentucky, Alabama, Florida, Georgia, South Carolina, North Carolina, Virginia and Maryland. The model uses quantity and quality of forages and available metabolizable energy in autumn-winter (15 November to 15 February) to predict habitat quality for deer. While many HSI models assess presence or absence of important foods (along with other variables) for a given species, direct measurement of available energy and forage quantity as indicators of habitat quality is a unique approach for HSI models. Forage quality and quantity also have been used to assess habitat for moose (Alces alces) (Allen et al. 1987), mule deer (Odocoileus hemionus) (Wallmo et al. 1977), and elk (Cervis elaphus) (Hobbs et al. 1982).

The objectives of this study were to:

1). Determine the degree of correspondence between the output of a modified white-tailed deer habitat suitability index model and observed deer condition.

2). Determine the change in available energy for deer in winter in response to succession.

Model Overview

The HSI model for white-tailed deer consists of 3 sub-models. Sub-model I estimates the carrying capacity of habitats during autumn-winter on the basis of the energy requirements for deer during these seasons. Sub-model I would be used when an explicit statement about the probable quality of a habitat for deer in autumn-winter is required. This energetics model requires intensive field sampling and provides a rationale for developing sub-models II and III and a way to assess how these models compare to sub-model I. An HSI for sub-model I is derived from the following equation:

$$\mathrm{HSI} = \frac{\sum_{i=1}^{n} (QF_i \times DF_i \times EV_i)}{100{,}000 \text{ kcal ME/ha}}$$

where $i=1,...n$ = The classes of suitable forages existing in measurable quantities on a hectare of habitat,

QF_i = Quantity of individual classes of suitable forages available within 1.5 m of the ground on each hectare of habitat to be evaluated,

DF_i = The apparent dry matter digestibility of each class of suitable forage. A digestibility of a forage for deer in autumn-winter < 41% is considered to be a digestibility of 0,

EV_i = The energy value of each forage class is equal to the apparent gross energy value of suitable forages times the constant 0.8, which converts digestible energy to metabolizable energy.

The denominator of the above equation, 100,000 kcal ME/ha, is the amount of metabolizable energy available to deer in a "standard" habitat. A standard hectare of habitat provides 45.5 kg of food that is 64% digestible and contains 4.3 kcal/g, or 100,000 kcal ME/ha. This standard unit of habitat could provide about 41-42 deer-days use for a deer unit (2 does, 1 buck), or support about 46 deer for a 90-day autumn-winter season per square kilometer of habitat (Short 1986).

Quantities of the 7 forage classes considered suitable for deer (at least 41% digestibility) were collected to provide the data necessary for applying the model.

1. Current year's twigs growth and needles from pines
2. Leaves of current year fallen from perennial woody species
3. Leafy browse composed of evergreen or tardily deciduous leaves *in situ* on perennial woody species
4. Mast from all vegetative layers including acorns, fleshy fruits, and seeds from many agricultural crops
5. Leguminous seeds
6. Cool season grasses and forbs (succulent) including growing herbaceous agricultural crops
7. Mushrooms

Ground pine (*Lycopodium clavatum*) and running cedar (*Lycopodium digitatum*), here collectively referred to as ground pine, was not included as a forage in the original deer model, but because it was so abundant, it was tentatively included in the sample. After fiber analyses, it was determined that ground pine qualified as a suitable forage (predicted DDM > 41%). In addition, browsing of ground pine was evident and biologists at Quantico reported finding ground pine in the mouths and stomachs of harvested deer, especially during poor mast years (T. Stamps, personal communication). Sub-model II is derived from sub-model I, but is of lower resolution. It also provides an explicit statement of habitat quality. Suitability indices (SI's) for the quantity (V1) (Fig. 1) and digestibility (V2) of forages (Fig. 2) are used in sub-model II to derive an HSI value. An HSI value for sub-model II is derived from combining SI's in the following equation:

$$HSI = \sum_{i=1}^{n} (SIV1_i \times SIV2_i)^{1/2}$$

where $i=1...n$ = The classes of suitable forages existing in measurable quantities on a ha of habitat,

$SIV1_i$ = The quantity (QF) of each type of suitable forage on each ha of habitat to be evaluated as represented by the appropriate SI value,

$SIV2_i$ = The apparent digestibility of each class of suitable forage as represented by the appropriate SI value.

Sub-model III is of lower resolution than II and III and provides a general statement about the probable value of habitat for deer. Model III uses the relative abundance of foods on a habitat block to derive an HSI value. It is used when only general information about forage abundance is available from a habitat block. Average dry matter yield of suitable forage per 1-m^2 plot (SIWF) (Fig 3) and number of stems/ha of species of woody shrubs and trees that provide mast to deer during autumn-winter (SIWM) (Fig. 4) are combined to generate an HSI in the

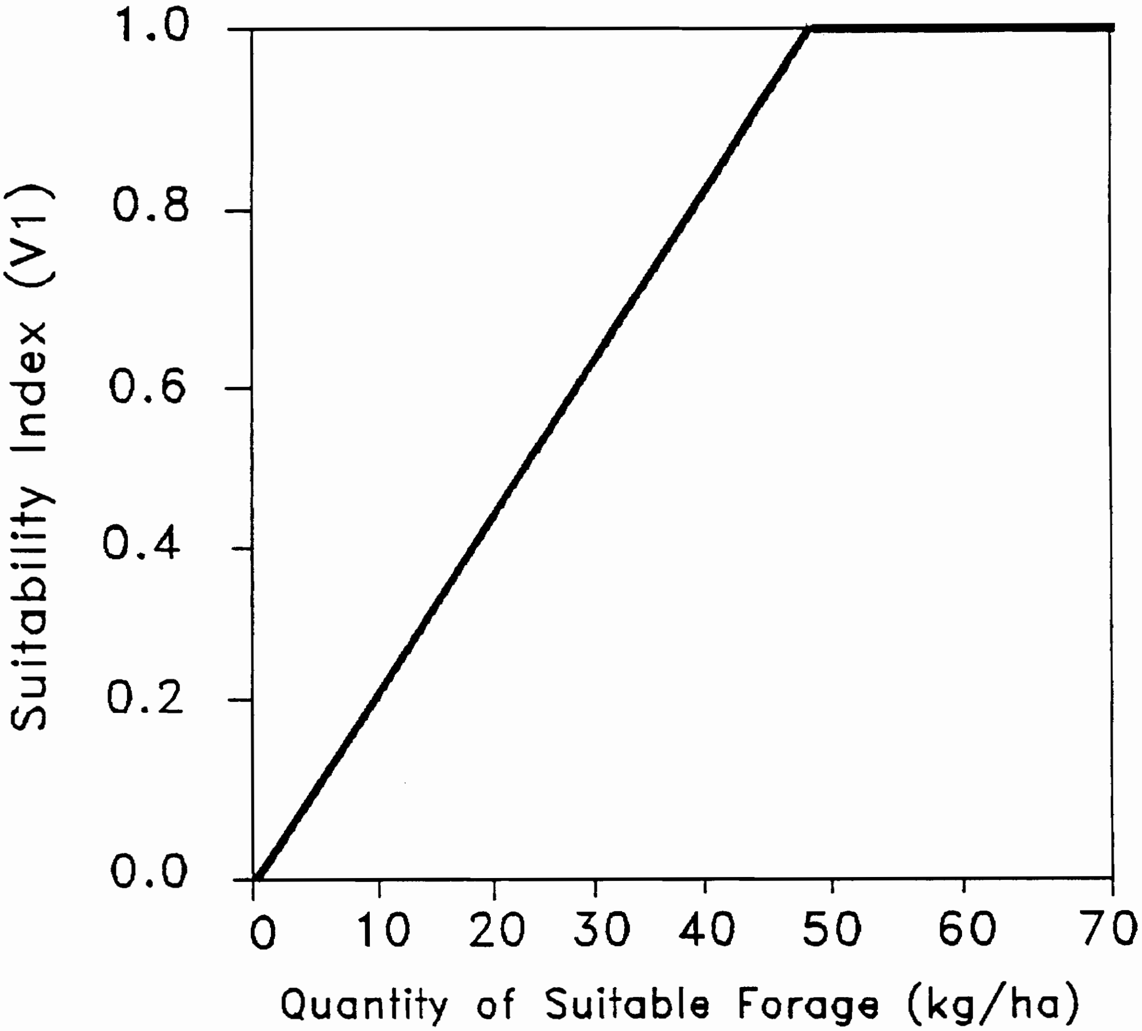

Figure 1 Suitability index determination for quantity of suitable forage (kg/ha) available to deer in autumn-winter for sub-model II of the white-tailed deer HSI model.

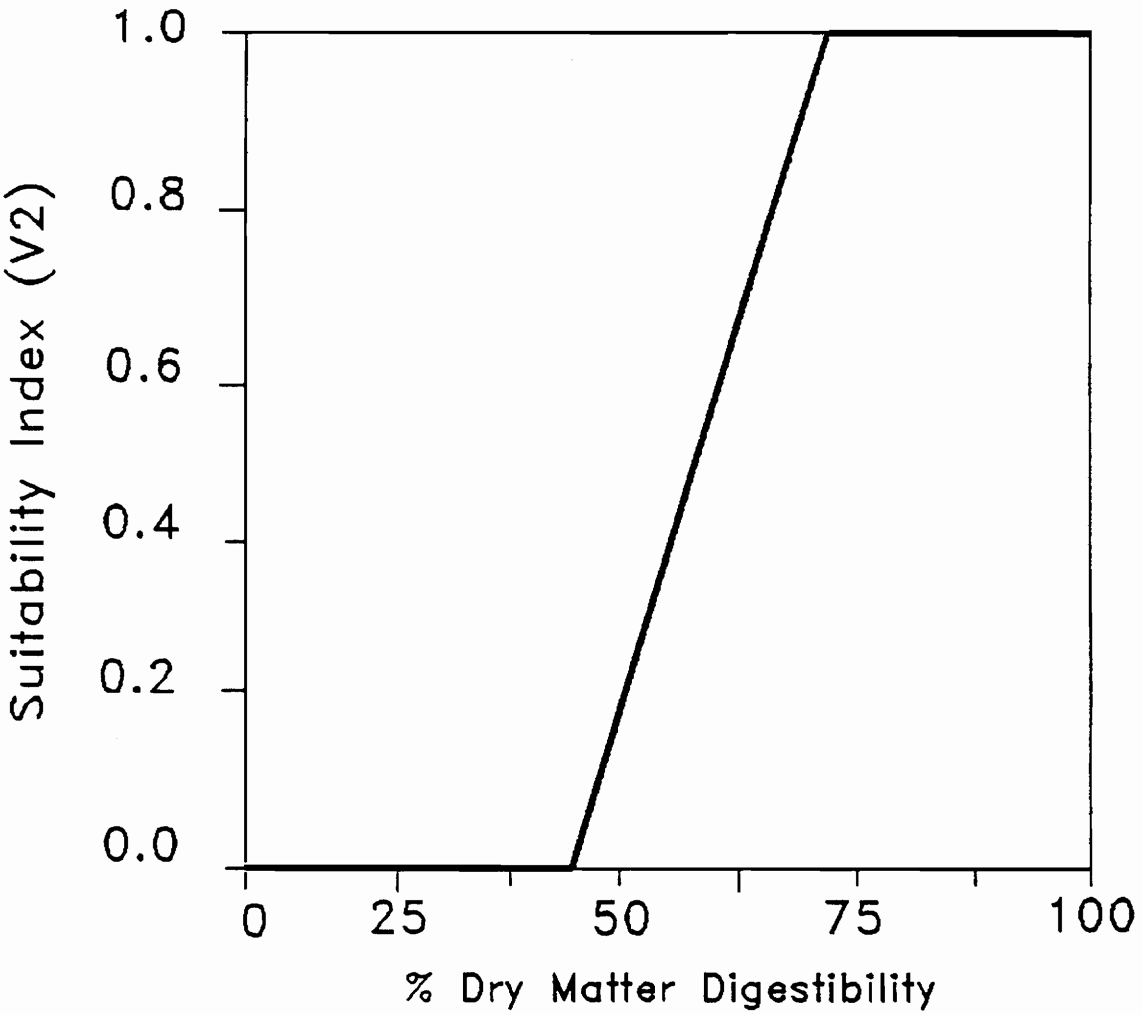

Figure 2. Suitability index determination for percent dry matter digestibility of forages available to deer in autumn-winter for submodel II of the white-tailed deer HSI model.

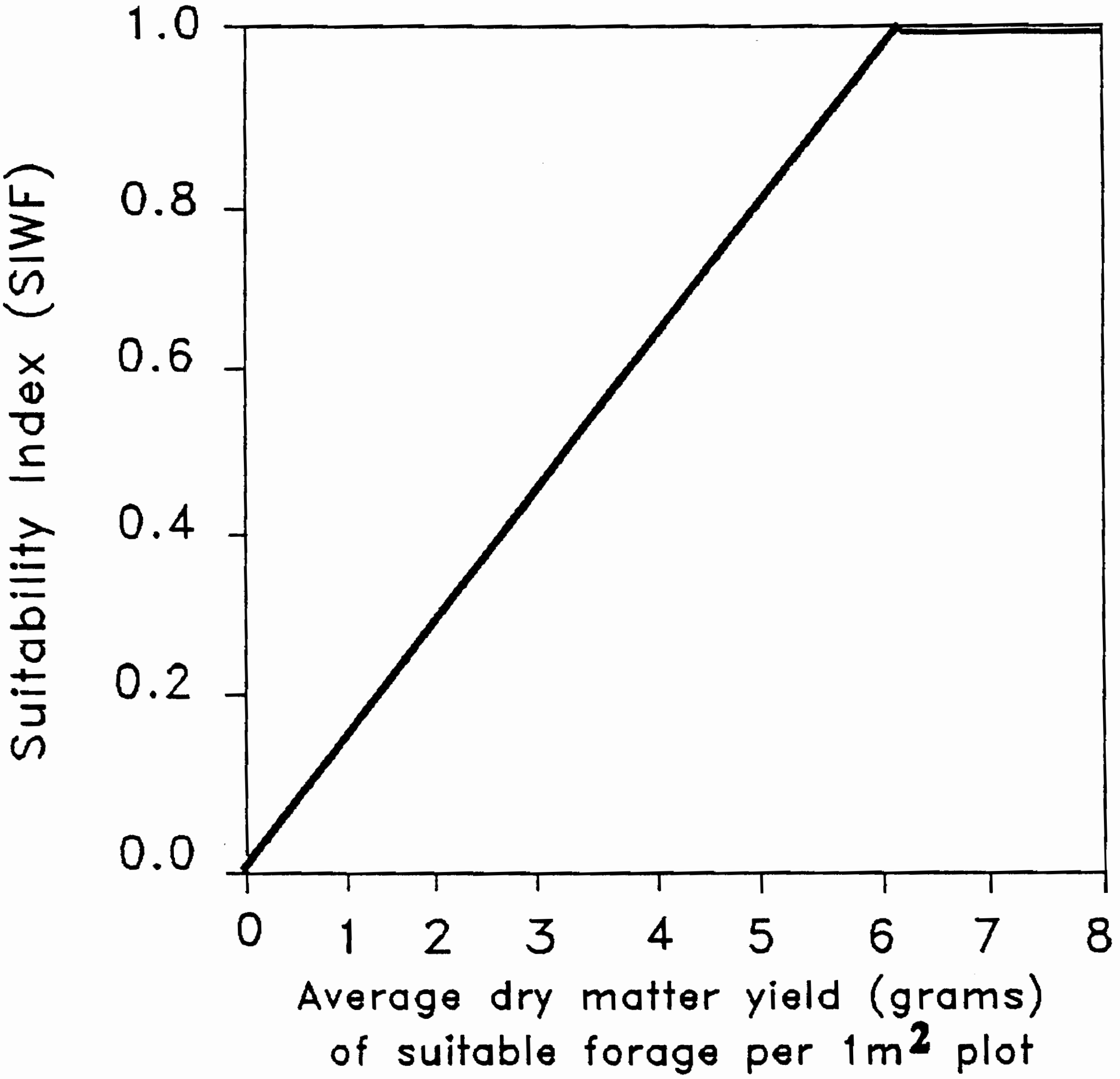

Figure 3. Suitability index determination for average dry matter yield of suitable forages (g/m^2 plot) available to deer in autumn-winter for sub-model III of the white-tailed deer HSI model.

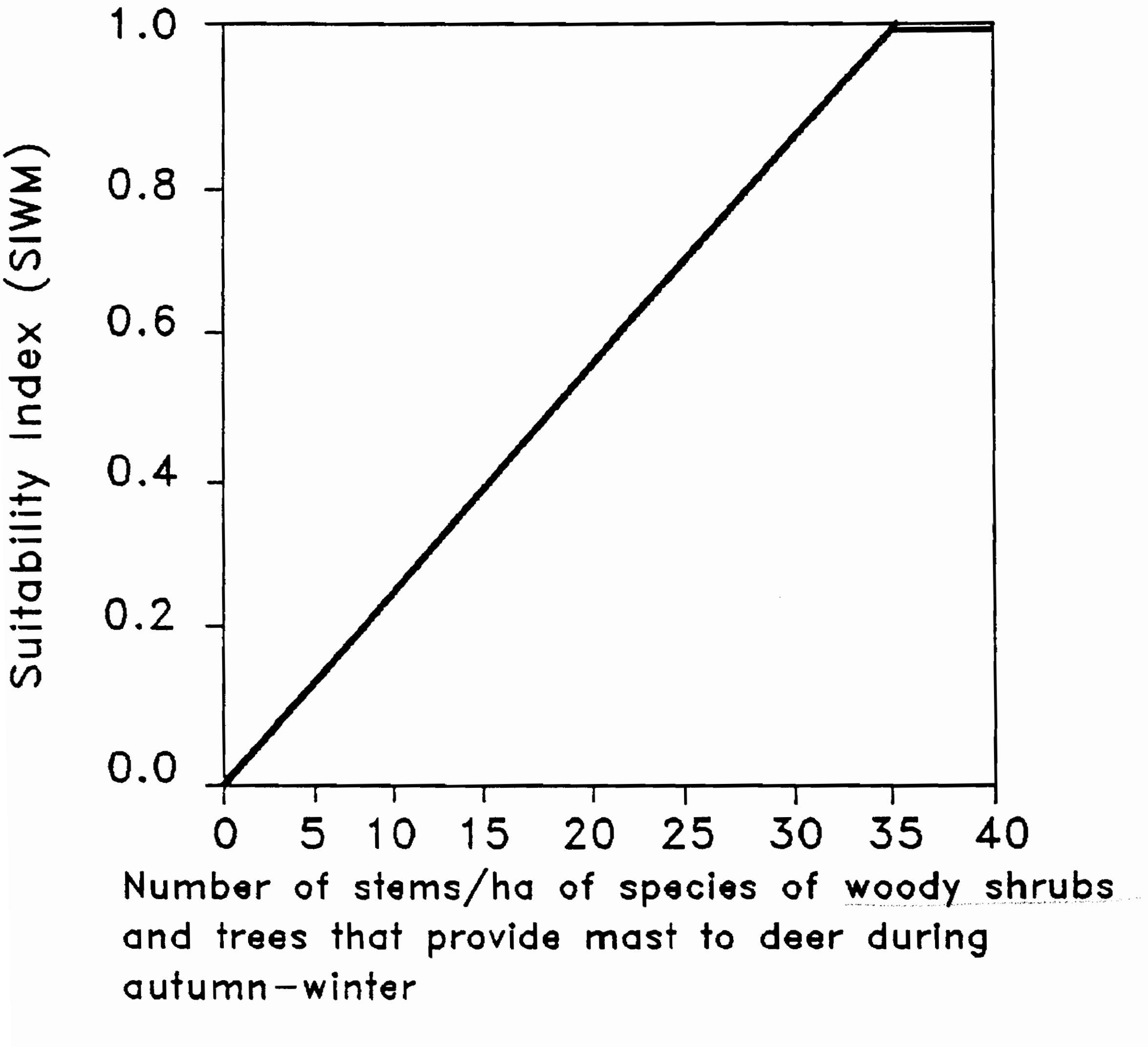

Figure 4. Suitability index determination for number of stems/ha of woody shrub and trees that provide mast to deer in autumn-winter for sub-model III of the white-tailed deer HSI model.

following equation:

HSI = SIWF (winter forage) + SIWM (winter mast).

Model Evaluation

This project represents the second phase of testing the original whitetail model. Stauffer (1990) used data from habitats in Louisiana, Mississippi, Alabama, South Carolina, North Carolina and Virginia to evaluate model inputs and assumptions. When evaluation of the model was completed, several modifications were suggested. New percent digestibility and energy values of forages were presented, but were not used in my analyses because digestibility and energy values were re-calculated with data from this study. The most important suggested modification of the original model was the assignment of utilization rates (percent of available forage expected to be consumed by deer) to each forage class. Utilization rates were necessary because an HSI of 1.0 was calculated for every transect sampled in his evaluation. Following the application of utilization rates, the model resulted in a range of HSI values across the sites sampled. Utilization rates suggested in the model evaluation and used in this study were current year twigs and needles, 5%; dried, fallen leaves, 0.5%; leafy browse, 20%; mast, 50%; cool season grasses and forbs, 20%; mushrooms, 50%.

STUDY AREA

This study was conducted on Quantico Marine Corps Base located in parts of Stafford, Prince William, and Fauquier counties, Virginia. Quantico is 21,538 ha in area, including approximately 16,194 ha of forested land, and is situated on the eastern edge of the Piedmont plateau physiographic region. Topography of the area is characterized by rolling hills and long, low ridges. Average elevation is about 120 meters. Soils are generally clay loams with varying amounts of sand and gravel and usually are acidic, low in organic matter and poor in natural fertility. Major impoundments include Lunga Reservoir, Breckenridge Reservoir, and Aquia Reservoir. Larger streams include Chopawamsic Creek, Cedar Run, Beaverdam Run, and Aquia Creek. Streams that empty into the Potomac River at the eastern edge of the base, especially Chopawamsic Creek, are tidally influenced for 2 km or more upstream.

Every forest stand on Quantico had been assigned a Society of American Foresters' cover type code. We assigned each stand to 1 of 4 general cover types: hardwood, open (stands < 5 years old, old fields and maintained openings), pine-hardwood, or pine. Oaks (Quercus spp.), hickories (Carya spp.), yellow poplar (Liriodendron tulipifera), sweetgum (Liquidambar styraciflua) and red maple (Acer rubrum) dominated the overstory of most hardwood stands sampled. Open habitats included any stand < 5 years of age (clear-cuts) and grassland-scrub/shrub habitats. Pine-hardwood stands consisted of mixed Virginia pine (P. virginianus) and oak. Pine habitats were either mixed loblolly (P. taeda) and shortleaf (Pinus echinata) pine or Virginia pine. The study area was divided into 17 management areas varying in size from 430 ha to 3300 ha, of which 11 were used for this study (Fig. 5). Each management area was divided into forest compartments composed of individual forest stands (Table 1). Agricultural activities, clear-cutting, and prescribed burning have resulted in diversity of habitat types and seral

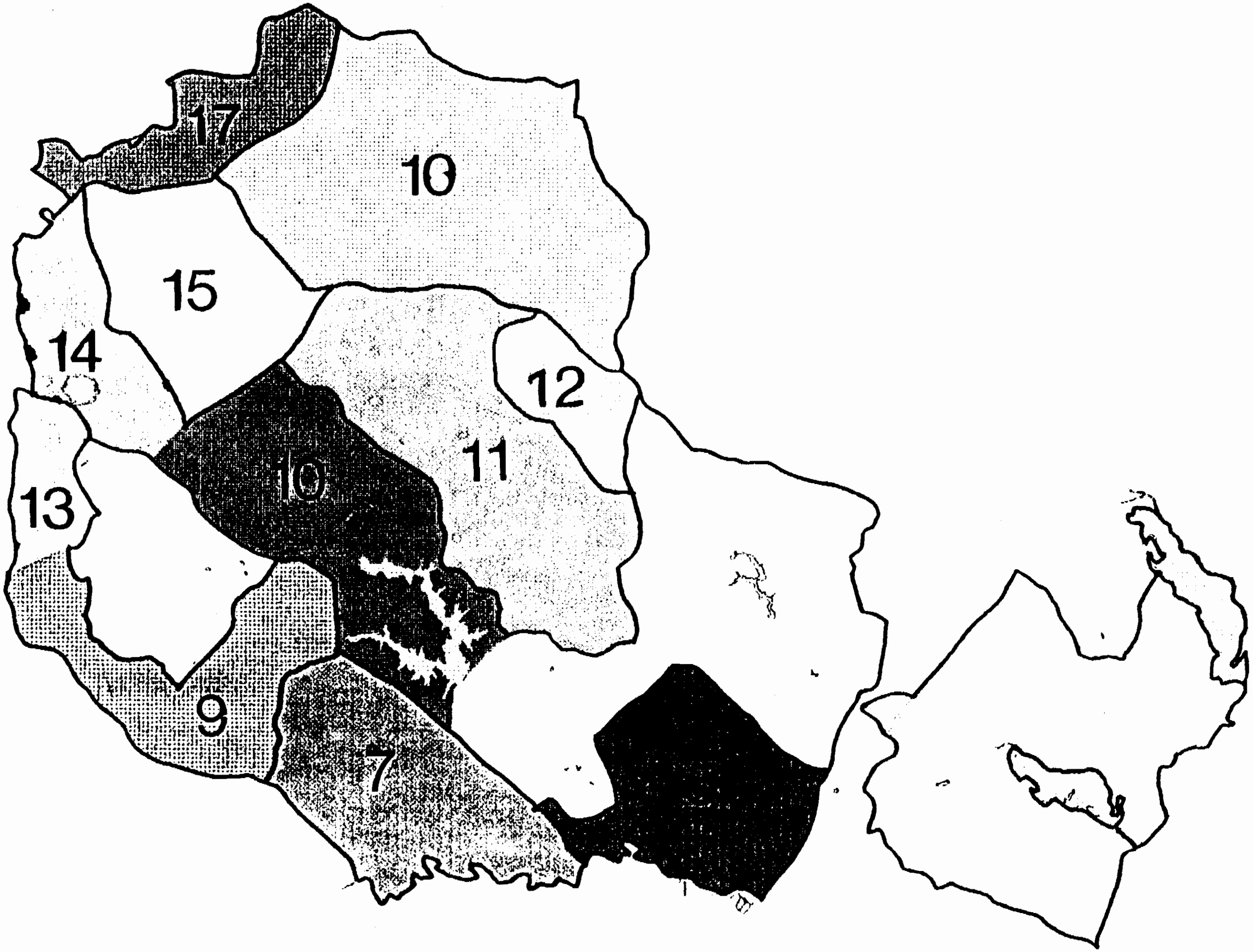

Figure 5. Map of Quantico Marine Corps Base showing relative sizes and positions of 11 deer management units used in this study.

Table 1. Number of stands, total area (hectares), and area of hardwood, open, pine and pine-hardwood habitat types for 11 deer management units on Quantico Marine Corps Base, Virginia, 1993.

		Area (ha)				
Management Unit	Number of stands	Total[a]	Hardwood	Open	Pine-hardwood	Pine
5	113	1482	836	124	155	340
7	120	1519	920	93	160	337
9	88	1022	572	84	139	223
10	169	2586	1145	100	433	356
11	213	2820	1573	55	378	535
12	37	432	243	26	52	110
13	38	436	201	4	78	150
14	82	921	328	79	201	272
15	165	1694	604	150	497	380
16	277	3267	1890	48	475	792
17	112	1139	449	118	190	257

[a] Sum of habitat areas will not equal total area of management unit due to developed areas and small agricultural plots not included in habitat types.

stages on Quantico. This diversity facilitates the intensive management of a variety of game and non-game wildlife, including white-tailed deer, wild turkeys (Maleagris gallopavo), northern bobwhite (Colinus virginianus), cottontail rabbits (Syvilagus floridanus), mourning doves (Zenaida macroura), Canada geese (Branta canadensis) and other waterfowl, songbirds, and birds of prey.

METHODS

Forage Sampling

Sampling for winter white-tailed deer forages was conducted from January 4 to March 10, 1993. Stratified random sampling was used to select a sample of stands from different ages of each cover type across the study area (Freese 1962). Stands were grouped by the following age classes: 1-4 years, 5-10 years, 11-20 years, 21-30 years, 31-40 years, 41-50 years, 51-60 years, 61-70 years, 71-80 years, 81-90 years, >91 years.

One 200m transect was randomly located in each stand with the constraint that all sampling points had to fall within a single cover type. Sampling points were located at 50m intervals along the transect. At each of the 5 sampling points, 3 1-m^2 plots were established. The first plot was located at a random azimuth 5m from the transect and the 2 subsequent plots were placed at 120° angles from the first.

Within each plot, we ocularly estimated wet weight for each of the 7 forage items to a height of 1.5m. We clipped and collected the vegetation for each of the forage items in every third plot to provide estimates of wet and dry weights. A rank-set sampling approach was used to decide which plots were clipped (Martin et al. 1990). With this procedure, the 3 plots at each sampling point were ranked in terms of total estimated biomass. At the first point, the plot with the highest estimated biomass was clipped and bagged and wet weights measured; biomass was only estimated for the other 2 plots. At the next point, the plot with the second highest estimated biomass was clipped, and at the third point the plot with the least amount of vegetation was clipped. Rank-set sampling has been shown to be more efficient than simple random sampling, allowing for fewer samples to be collected with an increase in precision. The rank-set sample also gives an unbiased estimate regardless of ranking errors (Martin et al. 1990, Dell and Clutter 1972). In order to avoid the effects of free water as much as possible, we avoided sampling on days when vegetation was saturated by rain or snow. All clipped samples were brought back to the lab at Virginia Tech and dried in a drying oven at 60°C for 48 hours, after which dry weights were measured. All samples then were ground in a Wiley mill to pass a 1mm screen in preparation for fiber analyses.

Fiber Analyses

Calculation of an HSI value under sub-models I and II required the estimation of percent digestible dry matter (DDM) for each forage category. The detergent system of separating fibrous feeds into cell contents and structural components was used for the analyses (Goering and Van Soest 1970). NDF, NDS, and lignin values were combined in the following equation (Mould and Robbins 1982) to obtain an estimate of percent DDM:

$$\% \text{ DDM} = (1.06 * \text{NDS} - 18.06) + \frac{(161.39 - 36.95 * \ln[\text{lignin}])}{100}$$

The first step for determining forage digestibility was to prepare neutral detergent fiber (NDF) from each sample after which percent neutral detergent solubles (NDS) could also be determined. NDF includes cell wall structural components, primarily lignin, cellulose, and hemicellulose. NDS includes cellular contents, primarily lipids, sugars, starch, and soluble proteins (Van Soest 1982). Two steps were required

Two steps were required to determine the lignin content of each sample. First, acid detergent fiber was prepared for each sample and dried in an oven for at least 4 hours. Treatment with acid detergent removes hemicellulose and any fiber bound proteins; cellulose and lignin are left as residues. Two procedures are commonly used for determining the lignin content of ADF: potassium-permanganate oxidation and 72% sulfuric acid (H_2SO_4) treatment. The permanganate method was chosen because it is relatively less hazardous to perform, requires less time, and apparently provides values that are closer to a true lignin figure (Van Soest 1982). The permanganate method was appropriate also because Mould and Robbins (1982) followed this method to determine the lignin component of the equation that we used. Procedures for determining permanganate lignin are described by Goering and Van Soest (1970).

Gross Energy

An estimate of gross energy was necessary for the calculation of metabolizable energy in the evaluation of the deer model. Forages were pelleted and a bomb calorimeter was used to determine the gross energy value for each forage class.

Analysis

Estimating Dry Weights

I considered transects to be the basic sampling unit; the stations and plots within each transect were treated as subsamples and were summarized to provide estimates for each transect. A total of 780 plots on 52 transects was sampled. Vegetation was clipped and weighed at 260 plots. This required that I estimate the dry weight of forages at the 520 plots for which we only estimated wet weight. I developed regressions, using data from clipped plots, that predicted the dry weight of each forage based upon estimates of wet weights. Because of potential variation among habitats, equations were developed for each forage category in each habitat type. Analysis of covariance (ANCOVA) was conducted (alpha = 0.05) to determine if slope and intercept of the regressions were different among habitats for each forage. For each forage, if the slope and intercept were not different, the data were combined across habitats to provide a predictive equation based upon a larger sample size (Table 2). Once the minimum necessary number of regression equations was determined, the dry weight of forages in the 520 unclipped plots was estimated.

Habitat Suitability Index values

Once the data necessary for calculating the suitability index (SI) values for sub-models I-III had been prepared, an HSI was calculated for each transect for each model. From these data I calculated an HSI value

Table 2. Slope and intercept for equations developed to convert estimates of wet weight (EWW) to dry weight (DW) for 7 forage categories in 4 different habitats.

Forage category	*n*	Intercept	*P*	Slope	*P*	R^2_{adj}
Current years growth						
Hardwood/Pine-hardwood[a]	129	0.76	0.269	0.35	0.001	0.94
Pine/Pine-hardwood[b]	128	0.56	0.395	0.35	0.001	0.94
Hardwood/Open[c]	119	2.25	0.024	0.38	0.001	0.92
Fallen leaves						
Pine/Pine-hardwood	129	8.15	0.118	0.60	0.001	0.69
Hardwood	69	80.79	0.001	0.25	0.001	0.33
Open	49	4.02	0.422	0.93	0.001	0.62
Leafy browse						
Hardwood/Pine-hardwood	129	0.28	0.280	0.40	0.001	0.75
Open	49	-0.29	0.780	0.89	0.001	0.86
Pine	69	-0.03	0.970	0.70	0.001	0.91
Mast[d]	249	0.003	0.510	1.04	0.001	0.99
Grasses and forbs[d]	249	-0.27	0.590	0.62	0.001	0.78
Mushrooms[d]	249	0.001	0.780	0.55	0.001	0.86
Ground pine[d]	249	1.00	0.168	0.39		0.78

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[a] Data pooled to predict forage dry weight for hardwood habitats

[b] Data pooled to predict forage dry weight for pine habitats

[c] Data pooled to predict forage dry weight for open habitats

[d] All habitats pooled (ANCOVAs not significant) for 11 age classes of

stands within the 4 habitat types for each model. A weighted HSI for each management unit was calculated by multiplying the area of each age and cover type combination within the management unit by the corresponding HSI value, summing these values, and dividing by the total area to get an HSI value weighted by the area of each cover type.

Deer Condition Indices

Age, sex, dressed carcass weight (kg), number of antler points, beam diameter (mm) and beam length (cm) were recorded from deer killed during the 1990-1992 hunting seasons on the Quantico Marine Corps Base. Age was determined using wear and replacement patterns of teeth from lower jaws. The management unit in which the deer was harvested also was recorded for each deer. I used dressed carcass weight, number of antler points, beam diameter and beam length of 1.5 year-old bucks as indices to deer condition for each management unit. Body weight and antler size are influenced by dietary energy intake, particularly in yearlings, and can be used as practical indices to deer condition (Rasmussen 1985, Severinghaus 1983, Ullrey 1982, Hesselton 1973). I assumed that deer condition improves as dietary energy intake increases. Dressed carcass weight and antler characteristics of 1.5 year-old bucks also are used by biologists at Quantico Marine Corps Base and the surrounding area to evaluate the physical condition of the deer herd (T. Stamps and R. Bush, Personal communication).

The final analysis was to compare model output (HSI's) with deer condition,thereby assessing the ability of the deer model to estimate the suitability of habitat for deer. Spearman's rank correlation was used to determine the degree of correspondence among deer condition indices and HSI values for each management unit. The same procedure was used to determine degree of correlation among HSI values generated by the 3 sub-models, and between condition indices.

RESULTS

Forage Quantity

A total of 13 models was developed for estimating dry weight of forages from ocular estimates of wet weight (Table 2). Two categories of forages, cool season grasses and forbs and ground pine, required only 1 regression each because there was no variation among habitat types (ANCOVA, $P > 0.05$). Data for mast and mushrooms were combined across habitat types because sample sizes were too small to develop equations when the data were divided among habitat types.

Of those forage categories where significant variation in regression coefficients did occur among habitat types, adjusted R^2 values of regressions for fallen leaves (R^2_{adj}=0.33, R^2_{adj}=0.62 and R^2_{adj}=0.69) were relatively low (Table 2). Adjusted R^2 values for all other models were > 0.75, suggesting that one can have reasonable confidence in the extrapolated values for dry weight based upon the predictive equations.

In all habitat types, current year fallen leaves constituted the greatest proportion of available dry matter, ranging from 258.9 kg/ha in open stands to 1446.6 kg/ha in hardwood stands (Table 3). Ground pine contributed the second highest values to available dry matter, ranging from 69.2 kg/ha in pine stands to 103.1 kg/ha in pine-hardwood stands.

Table 3. Estimated amount (kg/ha) of 7 classes of winter deer forages in 4 different habitat types on Quantico Marine Corps Base, VA, 1993.

	Habitat type							
	Hardwood (n=14)		Open (n=10)		Pine-hardwood (n=14)		Pine (n=15)	
Forage category	Weight (kg/ha)	SE	Weight (kg/ha)	SE	Weight (kg/ha)	SE	Weight (kg/ha)	SE
Twigs and needles	21.6	2.53	189.4	72.15	92.7	55.34	15.7	4.03
Dry leaves	1446.6	98.02	258.9	48.49	964.9	101.22	471.2	62.69
Leafy browse	16.6	5.79	90.6	47.99	26.3	7.86	40.1	14.59
Mast (Acorns)	2.5	2.49	0.0	_	0.3	0.14	0.05	0.04
Grasses and forbs	8.3	3.54	118.2	61.71	4.9	2.45	6.8	3.79
Mushrooms	0.05	0.05	1.1	0.76	0.0	-	0.2	0.26
Ground pine	71.8	0.01	0.0	-	103.1	0.01	69.2	0.01

An exception was open habitats, where current years growth of stems and needles contributed the second highest value to total dry matter, 189.4 kg/ha. Varying amounts of the other forages were collected from each habitat type. Mast and fungi occurred infrequently (3 samples each), and no leguminous seeds were collected (Table 3).

Hardwood habitats had the greatest amount of available dry matter (1567.5 kg/ha) due to the abundance of fallen leaves. Pine-hardwood, open and pine habitats averaged 1192.3 kg/ha, 658.2 kg/ha and 603.2 kg/ha of available dry matter, respectively (Table 3).

Neutral Detergent Fiber and Solubles

Neutral detergent fiber was highest for mast (76.0%), however, the sample size was very low (n=3). Mushrooms were second highest in NDF (70.5%). Current year growth was next highest in NDF (63.8%), followed by grasses and forbs (60.4%), fallen leaves (59.6%), ground pine (47.6%), and leafy browse (37.9%) (Table 4).

Leafy browse was highest in neutral detergent solubles (NDS) (62%), followed by ground pine (52%) and fallen leaves (40%). Mast was lowest in NDS (24%) (Table 5).

Acid Detergent Fiber

Acid detergent fiber was calculated as a preliminary step for determining percent lignin. ADF was highest for mast (61.5%), followed by fallen leaves (60.4%), current years growth of twigs and needles (48.5%), grasses and forbs (42.6%), ground pine (30.3%) and leafy browse (29.0%) (Table 6).

Table 4. Mean percent neutral detergent fiber (NDF) content (percent dry matter basis) for 7 classes of winter white-tailed deer forages in 4 habitat types at Quantico Marine Corps Base, Virginia, 1993.

	Habitat type														
	Hardwood			Open			Pine-hardwood			Pine			All habitats		
Forage category	n	%DM NDF	SE	n	%DM NDF	SE	n	%DM NDF	SE	n	%DM NDF	SE	n	%DM NDF	SE
Twigs and needles	22	65.7	0.63	32	60.9	0.52	22	62.9	0.64	21	65.5	0.64	97	63.4	0.90
Fallen leaves	34	59.6	0.43	30	54.5	0.50	32	62.7	0.40	40	61.6	0.36	136	59.8	0.57
Leafy browse	21	30.7	0.67	15	35.6	0.84	18	41.8	0.92	24	43.3	0.72	78	38.1	1.47
Mast (acorns)	1	76.0	-	0	-	-	2	76.0	1.19	0	-	-	3	76.0	1.15
Grasses/Forbs	10	61.1	0.95	16	64.3	0.87	3	51.3	1.39	7	64.9	1.49	36	62.4	1.97
Mushrooms	2	79.0	1.46	1	62.0	-	0	-	-	0	-	-	3	73.3	5.92
Ground pine	14	48.4	0.83	0	-	-	15	46.5	0.41	8	47.8	0.81	37	47.5	1.07

Table 5. Mean percent neutral detergent solubles (NDS) content (percent dry matter basis) for 7 classes of winter white-tailed deer forages in 4 habitat types at Quantico Marine Corps Base, Virginia, 1993.

	Habitat type														
	Hardwood			Open			Pine-hardwood			Pine			All habitats		
Forage category	n	%DM NDS	SE	n	%DM NDS	SE	n	%DM NDS	SE	n	%DM NDS	SE	n	%DM NDS	SE
Twigs and needles	22	34.3	1.87	32	29.1	1.53	22	37.1	1.93	21	34.5	1.87	97	36.6	0.90
Fallen leaves	34	40.4	1.09	30	45.5	1.39	32	37.3	0.89	40	38.4	0.81	136	40.2	0.57
Leafy browse	21	69.3	2.07	15	64.4	2.73	18	58.2	3.55	24	56.7	2.57	78	61.9	1.47
Mast	1	24.0	-	0	-	-	2	24.0	2.00	0	-	-	3	24.0	1.15
Grasses/Forbs	10	38.9	2.85	16	35.7	3.03	3	48.7	3.33	7	35.1	5.84	36	37.6	1.97
Mushrooms	2	21.0	3.00	1	38.0	-	0	-	-	0	-	-	3	26.7	5.92
Ground pine	14	51.6	2.59	0	-	-	15	53.5	0.66	8	52.3	1.87	37	52.5	1.07

Table 6. Mean percent acid detergent fiber (ADF) content (percent dry matter basis) for 7 classes of winter white-tailed deer forages in 4 habitat types at Quantico Marine Corps Base, Virginia, 1993.

	Habitat type														
	Hardwood			Open			Pine-hardwood			Pine			All habitats		
Forage category	n	%DM ADF	SE	n	%DM ADF	SE	n	%DM ADF	SE	n	%DM ADF	SE	N	%DM LIG	SE
Twigs and needles	12	51.1	0.73	22	43.2	0.59	15	46.4	0.75	11	53.1	0.77	60	47.5	1.06
Fallen leaves	32	60.6	0.50	26	56.8	0.63	23	62.9	0.49	37	61.1	0.48	118	60.4	0.78
Leafy browse	5	21.6	1.45	12	22.7	0.97	8	32.8	1.07	13	38.9	0.69	38	30.2	1.88
Mast	1	60.0	-	0	-	-	2	63.0	0.84	0	-	-	3	62.0	1.15
Grass/forbs	7	43.4	1.09	12	36.5	0.77	2	45.0	0.84	3	45.3	1.01	24	40.3	1.57
Mushrooms	1	34.0	2.99	0	-	-	0	-	-	0	-	-	1	34.0	-
Ground pine	12	30.5	1.48	0	-	-	13	30.0	0.64	8	30.3	1.22	33	30.2	0.64

Lignin

Percent lignin content of dry matter was highest for current year fallen leaves in all habitat types (23.7%). Mast had the second highest lignin content (15.3%), followed by current years growth of twigs and needles (12.1%), mushrooms (12.0%), grasses and forbs (11.3%), leafy browse (9.2%), and ground pine (8.5%) (Table 7).

Lignin content of forages (average of the 7 forage classes) collected from pine habitats (16.7%) was greater ($F = 2.63$, 3,378 df, $\underline{P} \leq 0.05$) than hardwood habitats (13.7%). Lignin content of forages was 15.8% and 14.9% for pine-hardwood and open habitats, respectively.

Digestible Dry Matter

Evergreen or tardily deciduous leafy browse was highest in digestible dry matter (77.5%). Ground pine was slightly less digestible than leafy browse (76.8%), followed by grasses and forbs (67.3%), current year's growth of twigs and needles (65.4%), mushrooms (60.3%), Mast (53.4%), and current years fallen leaves (52.1%) (Table 8).

DDM was significantly greater ($F = 4.79$, 3,378 df, $\underline{P} \leq 0.05$) in forages collected in hardwood habitats (68.1%) than in forages collected in pine or pine-hardwood habitats (62.8% and 61.5%, respectively).

Gross Energy

The model required that separate gross energy values be determined for non-mast forages (roughages) and mast. Since no mast samples were available for determining energy values, I used the energy value for mast (5.1 kcal/g) suggested in Stauffer's (1990) evaluation of model inputs. I determined an energy value of 4.35 Kcal/g ($n = 25$, SE =0.89)

Table 7. Mean lignin content (percent dry matter) for 7 classes of winter white-tailed deer forages in 4 habitat types at Quantico Marine Corps Base, Virginia, 1993.

	Habitat type														
	Hardwood[1]			Open			Pine-hardwood			Pine			All habitats		
Forage category	n	%DM LIG	SE	n	%DM LIG	SE	n	%DM LIG	SE	n	%DM LIG	SE	n	%DM LIG	SE
Twigs and needles*	22	9.3a	0.44	32	12.2a	0.52	22	12.9	0.60	21	14.9ab	0.97	97	12.3	3.64
Fallen leaves	32	24.4	1.17	30	24.3	1.06	32	24.9	0.77	40	22.4	1.12	134	23.9	6.14
Leafy browse*	21	7.5a	0.58	15	7.8a	1.09	18	8.3c	0.67	24	12.3abc	0.31	78	9.2	3.45
Mast	1	14.0	-	0	-	-	1	16.0	-	0	-	-	3	15.3	1.15
Grass/Forbs*	7	9.7a	1.77	16	9.42a	1.09	3	19.0ab	0.58	7	14.0	1.31	33	11.3	4.98
Mushrooms	1	12.0	-	0	-	-	0	-	-	0	-	-	1	12.0	-
Ground pine*	14	7.7a	0.36	0	-	-	15	9.1a	0.32	8	8.8	0.65	37	8.5	1.50

[1] forages in hard-mast hardwood habitats were significantly lower in lignin content than pine habitats (F = 2.63, 3,378 df, $P \leq 0.05$).

* Means with the same letter are significantly different ($P \leq 0.05$).

Table 8. Estimated mean percent digestible dry matter content for 7 classes of winter white-tailed deer forages collected from 4 habitat types at Quantico Marine Corps Base, Virginia, 1993.

	Habitat Type														
	Hardwood[1]			Open			Pine-Hardwood			Pine			All habitats		
Forage category	n	%DDM	SE	n	%DDM	SE	n	%DDM	SE	n	%DDM	SE	n	%DM	SE
Twigs and needles[*]	22	71.4abc	1.27	32	66.2ad	0.89	22	63.6b	1.43	21	60.0cd	1.62	97	65.4	7.27
Fallen leaves	32	51.9	1.77	30	54.4	1.34	32	48.7	1.18	40	53.2	1.74	134	52.1	9.24
Leafy browse[*]	21	81.6a	1.37	15	80.8b	2.58	18	77.5	2.10	24	71.8ab	1.13	78	77.5	8.47
Mast	1	55.9	-	0	-	-	2	52.1	0.94	0	-	-	3	53.4	2.36
Grasses	7	73.7	4.89	16	68.7	2.74	3	60.6	1.27	7	61.3	1.31	32	67.5	10.8
Mushrooms	1	60.3	-	0	-	-	0	-	-	0	-	-	1	60.3	-
Ground pine	14	78.1	1.32	0	-	-	15	75.9	0.63	8	76.2	1.65	37	76.8	4.06

[1] Forages in hard-mast hardwood stands were significantly more digestible than forages in pine-hardwood or pine habitats (F = 4.79, 3,378 $P \leq 0.05$).

[*] Means with the same letter are significantly different ($P \leq 0.05$).

for roughages. My energy value for roughages was comparable to the values of 4.3 kcal/g, 4.4 kcal/g and 4.5 kcal/ha suggested by Short (1986), Stauffer (1990), and Walmo et al. (1977), respectively.

Metabolizable energy

Determination of an HSI value for sub-model I required the estimation of the amount of metabolizable (ME) energy metabolically available to deer on the study area and a comparison of that estimate to the amount of ME available to deer on a standard unit of habitat (100,000 kcal/ha). Hardwood habitat types had the greatest amount of metabolizable energy (2,929,407 kcal/ha), followed by pine-hardwood (2,368,145 kcal/ha), open (1,436,256 kcal/ha) and pine (1,195,059 kcal/ha) habitats. No clear trend in amount of ME was apparent across seral stage and habitat type. However, there was a tendency for ME to be highest in the very early seral stages (1-10 years) when grasses, leafy browse, and twigs are very abundant, and in the late seral stages (70+ years), when there is a great abundance of fallen leaves from mature trees (Figure 6). When utilization rates were applied to each forage category, a clear trend in ME/hectare occurred. Amount of metabolizable energy tended to be greatest in stands 5 to 10 years of age, reach a minimum between 20 and 30 years, increase again until 50 to 70 years, and then decrease. This pattern was consistent across habitat types (Figure 7).

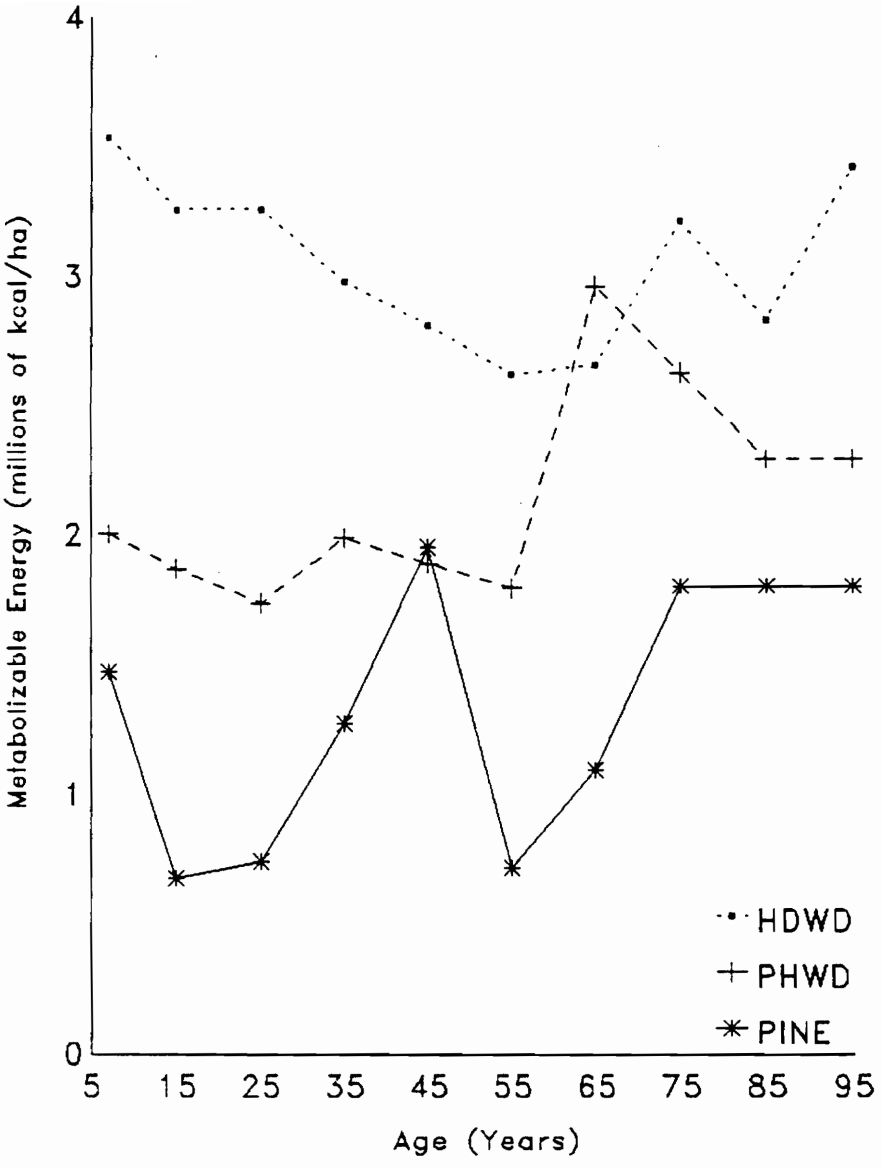

Figure 6. Relationship of available metabolizable energy in winter to stand age for 3 habitat types (hardwood=HDWD, pine-hardwood=PHWD) using the unmodified white-tailed deer HSI model at Quantico Marine Corps Base Virginia.

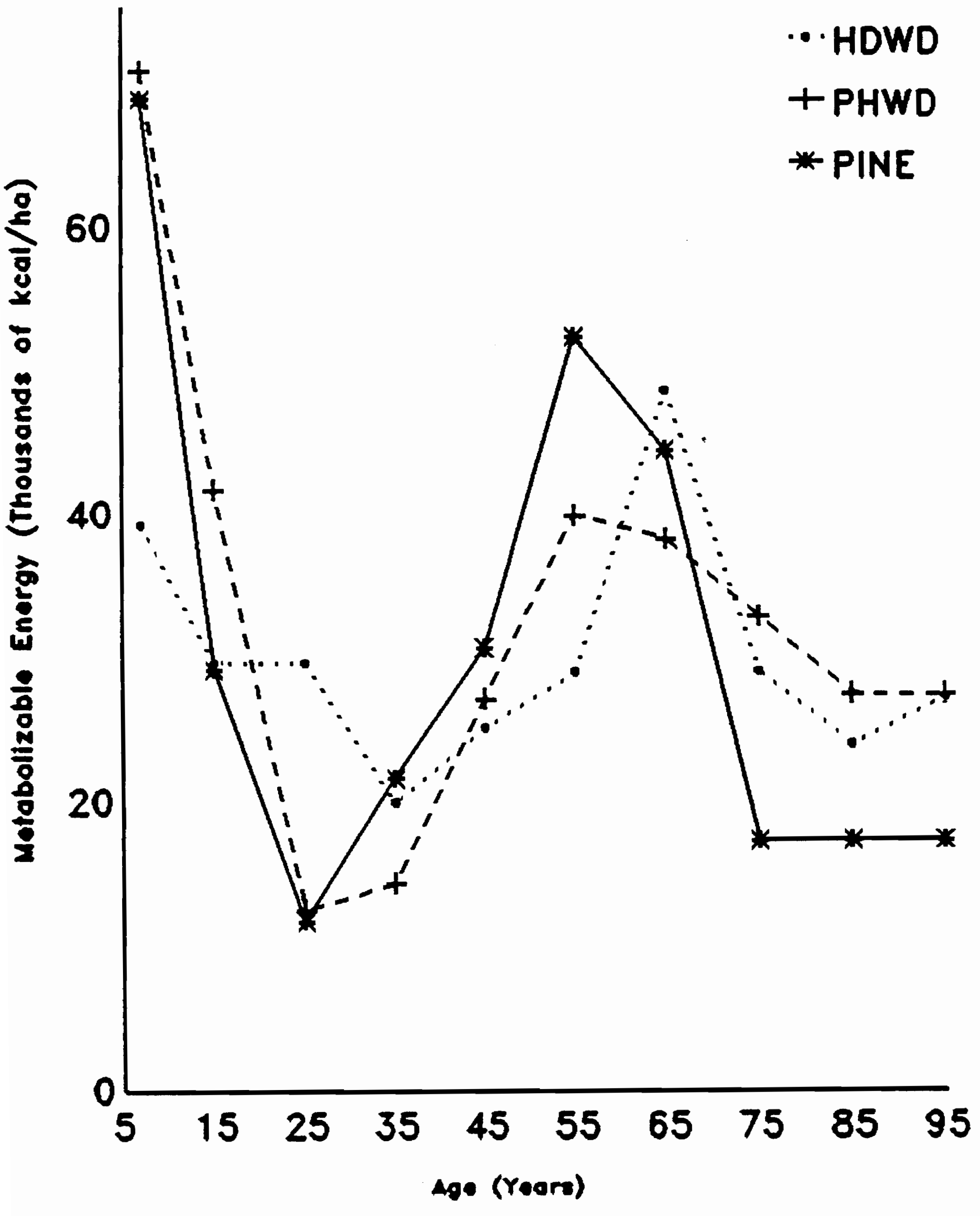

Figure 7. Relationship of metabolizable energy to stand age for 3 habitat types (hardwood=HDWD, pine-hardwood=PHWD) using the modified white-tailed deer HSI model at Quantico Marine Corps Base, Virginia.

HSI Values

Sub-model I

Data on forage quantity, percent digestible dry matter, and gross energy were combined in sub-model I to determine an HSI value for each management unit. Short's (1986) model yielded HSI's of 1.0 for every transect. Stauffer (1990) reported a similar result for his data. However, when estimated utilization rates (Stauffer 1990) for each forage were applied to my data, HSI values for transects ranged from 0.06 to 1.0.

There was little variation in HSI values between management units, however. HSI values ranged from 0.29 (Unit 15) to 0.34 (Unit 14), suggesting that poor quality habitat was more abundant than higher quality habitat and that the management units were homogeneous in terms of available metabolizable energy for deer (Table 9).

The model indicated that considerable variation in habitat suitability occurred within habitat types. HSI's for hardwood habitats ranged from 0.48 in 60-70 year-old stands to 0.20 in 30-40 year-old stands (Table 10). HSI's in pine-hardwood habitats ranged from 0.71 in 5-9 year-old stands to 0.13 in 20-30 year-old stands. In pine habitats, HSI's ranged from 0.58 in 5-9 year-old stands to 0.12 in 20-30 year old-stands. Open habitats, 1-4 years-old, had an HSI of 0.68.

Sub-model II

Sub-model II required that suitability indices (SI) be derived from quantity of forage (kg/ha) (V1) and apparent dry matter digestibility of

Table 9. White-tailed deer HSI values and deer condition measurements from deer harvested from 1990 to 1992 for 11 deer management units on Quantico Marine Corps Base, Virginia.

	HSI		Mean condition index								
Unit	Model I	Model II	n	Weight[1] (KG)	SE	Beam diameter (mm)	SE	Beam length (cm)	SE	Points	SE
5	0.33	0.48	38	35.4	0.93	23.7	1.03	11.5	0.92	3.3	0.24
7	0.32	0.48	64	36.4	0.71	21.3	0.84	11.2	0.77	3.0	0.19
9	0.33	0.48	45	35.2	0.87	22.3	1.14	11.4	0.95	3.2	0.26
10	0.33	0.48	51	35.9	0.94	23.4	1.19	13.1	1.02	3.5	0.26
11	0.34	0.49	36	33.7[ab]	0.88	23.7	1.12	13.1	0.83	3.3	0.23
12	0.31	0.46	12	34.8	1.89	20.6	3.00	10.1	1.72	2.8	0.30
13	0.30	0.46	17	37.5	1.49	22.7	1.69	12.2	1.63	3.5	0.50
14	0.34	0.48	22	37.7	1.11	23.6	1.68	12.8	1.27	3.3	0.30
15	0.29	0.42	41	39.1[a]	1.20	23.7	1.27	11.9	0.94	3.4	0.28
16	0.32	0.48	64	36.6	0.85	24.0	0.99	12.7	0.75	3.6	0.22
17	0.31	0.44	33	39.3[b]	0.85	24.0	0.98	12.1	0.63	3.6	0.25

[1] Means with the same letter are significantly different ($P \le 0.05$).

Table 10. HSI's (n) for combinations of habitat type and age classes sampled on Quantico Marine Corps Base, Virginia, 1993.

	Habitat type			
Age groups	Hardmast Hardwood	Pine-hardwood	Pine	Open
1-4	-	-	-	0.68
5-10	0.39 (1)	0.71 (2)	0.58 (2)	-
11-20	0.30 (1)	0.42 (1)	0.29 (2)	-
21-30	0.30 (1)	0.13 (2)	0.12 (3)	-
31-40	0.20 (4)	0.14 (1)	0.22 (3)	-
41-50	0.25 (1)	0.27 (1)	0.31 (2)	-
51-60	0.29 (1)	0.40 (2)	0.52 (1)	-
61-70	0.48 (4)	0.38 (6)	0.45 (1)	-
71-80	0.29 (1)	0.33 (1)	0.17 (1)	-
81-90	0.24 (1)	0.28 (1)	0.17 (1)	-
91+	0.27 (1)	0.28 (1)	0.17 (1)	-

forages (V2) to arrive at a final HSI. As with sub-model I, the unaltered Short (1986) model yielded HSI's of 1.0 for every transect, so utilization rates were applied to available dry matter as in sub-model I. Values for V1 and V2 ranged from 0.0 kg/ha to 118.0 kg/ha and 52.1% DDM to 77.5% DDM, respectively. HSI's for each management unit using sub-model II were slightly higher on average than sub-model I (Table 9), but again there was little variation among management units. HSI's ranged from 0.42 (Unit 15) to 0.49 (Unit 11). HSI values for management units from sub-models I and II were highly correlated (Spearman's r = 0.92, $\underline{n}$ = 11, $\underline{P}$ = 0.0001).

Sub-model III

Sub-model III required that SI's be derived from the amount of dry matter per 1-m plot (SIWF) and from the number of stems/ha of mast producing trees and shrubs (SIWM) to arrive at a final HSI. Average dry matter yield of suitable forages/m^2 plot ranged from 13.0 g/m^2 to 221.8 g/m^2; therefore, SIWF was 1.0 for every transect. Likewise, SIWM was never < 1.0, even when size restrictions were placed on mast producing trees (only trees > 20cm DBH were considered to be of mast producing size). My data supports the conclusion by Stauffer (1990) that these surrogate measures as presented in the model are not appropriate for predicting habitat suitability for deer.

Deer Condition

Dressed body weight, beam diameter, beam length, and number of points for 1.5 year-old bucks harvested during Quantico's 1990-1992 deer seasons were used as indices to deer condition in each management unit

(Table 9). Mean body weights ranged from 32.7 kg in unit 8 to 39.3 kg in unit 17. Mean body weight in unit 11 (33.6 kg) was significantly (F = 2.65, 12,460 df, $\underline{P} \leq 0.05$) lower than in units 15 (39.1 kg) and 17. There were no other statistical differences in body weight between units.

There were no statistical differences in beam diameter (F = 0.77, 12,460 df, $\underline{P} = 0.68$) beam length (F = 0.63, 12,460 df, $\underline{P} = 0.82$) or number of points (F = 0.79, 12,460 df, $\underline{P} = 0.67$) between units. Average measurements ranged from 20.6 mm to 24.1 mm for beam diameter, 10.1 cm to 13.4 cm for beam length, and 2.8 to 3.5 for number of points (Table 9).

HSI-Condition comparisons

HSI values generated by sub-model I for each management unit were poorly correlated with body weight ($r = -0.40$, $\underline{P} = 0.221$), beam diameter ($r = 0.06$, $P = 0.851$), beam length ($r = 0.36$, $\underline{P} = 0.265$), and number of points ($r = -0.24$, $\underline{P} = 0.472$) for 1.5 year-old bucks in each management unit (Table 11).

HSI values generated with model II were also poorly correlated with mean body weight ($r = -0.49$, $\underline{P} = 0.122$), beam diameter ($r = -0.02$, $\underline{P} = 0.96$), beam length ($r = 0.40$, $\underline{P} = 0.226$), and number of points ($r = -0.260$, $\underline{P} = 0.440$) for each unit (Table 11).

DISCUSSION

Forage Quantity

Current year fallen leaves contributed the most to forage quantity (dry weight) in all habitat types, but is probably the least used by

Table 11. Spearman's rank correlation coefficients and significance from comparison of habitat suitability indices from sub-models I and II (modified with utilization rates) with deer condition indices for 11 management units.

	Habitat suitability index			
	Sub-model I		Sub-model II	
Condition index	r_s	$\underline{P}$	r_s	$\underline{P}$
Body weight	-0.40	0.221	-0.50	0.122
Beam diameter	0.06	0.851	-0.02	0.957
Beam length	0.37	0.265	0.40	0.226
Number of points	-0.24	0.473	-0.26	0.440

deer of the 7 forage classes collected. Wet weight of current year fallen leaves was the most difficult to ocularly estimate in the field. Variation in species of leaves, depth of the leaf litter, and the moisture content of leaves contributed to inconsistencies in estimating wet weight of leaves. As a result, R^2_{adj} values were relatively low when dry weight of leaves was regressed on estimated wet weight. Wet weight estimates were much more consistent for the other forages that occurred in smaller quantities and were less affected by moisture. Consequently, R^2_{adj} values for dry weight regressed with estimated wet weights were > 0.75 for the other forages (Table 2). Current year's growth of twigs and needles contributed nearly 30% of the total biomass in open habitat types compared to 1-8% in the other 3 habitat types. Dense saplings and young pines made twig tips and needles, which were heavily browsed (personal observation), particularly accessible to deer in young, open stands.

Ground pine contributed as much as 103 kg/ha in pine-hardwood stands. No ground pine was found in open habitats, as it is generally associated with moist, shaded areas. In most years, ground pine probably constitutes a small percent of a deer's diet and need not be included in sampling. Total forage quantity ranged from 603 kg/ha in pine habitats to 1567 kg/ha in hardwood stands. Low leaf litter, dense canopy cover, and burning probably account for the relatively low forage availability in pine stands. Heavy leaf litter contributed most of the biomass in hardwood stands (Table 3).

Estimates of forage quantity from this study are likely to be conservative. Mast was scarce in the fall of 1992, and what did occur was probably consumed before sampling took place (Goodrum et al. 1971). In a good year, mast would probably contribute much more to quantities of available forage. Honeysuckle, another important and preferred forage (Crawford and Marchinton 1989, Cushwa et al. 1970), did occur regularly in our sample, but in small quantities. Dense thickets of honeysuckle browsed out of reach of deer were common. Honeysuckle and other forages may have been utilized more (and earlier) than usual because of the mast scarcity, thereby not contributing as much to the overall biomass as might normally be the case. Also, the timing of our sampling (beginning early January to avoid the hunting season) was such that the most preferred forages probably had been eaten.

Neutral Detergent Fiber

NDF was calculated as the first step in determining percent digestibility of forages; thus, NDF values have a direct bearing on the estimation of DDM. As expected, NDF varied with forage type (Table 4). More succulent forages such as evergreen, leafy browse and ground pine tended to be relatively low in NDF. With the exception of mast, NDF for all forages were comparable to other reported NDF values. NDF for current year growth of twigs and needles of 63.8% was similar to the value of 62.5% reported by Stauffer (1990) and 57.8% reported by Blair et al. (1977). NDF for current year fallen leaves was 59.6% compared to 63.3% reported by Stauffer (1990). NDF for leafy browse was 37.9%, similar to the values of 39.0% reported by Blair et al. (1977), but was somewhat lower than the value of 50.8% reported by Stauffer (1990).

Stauffer (1990) and Short and Epps (1976) reported NDF values of 61.0% and 47.0% for mast, respectively, suggesting that my value of 76.0% for mast NDF was too high. A small sample size (n=3) and difficulty with fine grinding of small samples probably contributed to the elevated NDF for acorns. NDF was 60.4% for grasses and forbs compared to 62.3% and 74.8% (forbs) to 84.6% (grasses) reported by Stauffer (1990) and Blair et al. (1977), respectively. A certain amount of variation is inherent in estimating NDF. Variation in NDF values is likely to be influenced by such factors as the extent to which the sample is ground, the species of vegetation being analyzed, phenological stage, plant part, the apparatus being used, and the expertise of the person conducting the analyses.

Lignin

Percent lignin varied between forage categories, with twigs and dead leaves being higher in lignin than more succulent leafy browse, grasses and forbs, and ground pine (Table 7). Lignin content was 12.3% percent for current year's growth of twigs and needles, the same value reported by Blair et al. (1977). Lignin content for mast was 15.3%, somewhat higher than, but comparable to, the value of 11.7% reported by Short and Epps (1976). Lignin was 11.3% for forbs and grasses. Blair et al. (1977) reported comparable lignin values of 10.3% and 14.6% for grasses and forbs, respectively.

Digestible Dry Matter

DDM of forages is an important component of the deer model, but could not be estimated directly. The calculation of percent DDM was dependent on estimates of NDF, NDS, and lignin combined in an equation by Mould and Robbins (1982). Percent DDM varied considerably between forage categories (Table 8). Leafy browse, forbs and grasses, and ground pine, succulent forages low in fiber and lignin, were the most digestible. My values for percent DDM were generally not comparable to the values suggested by Short (1986) in the deer model, but were similar to values reported from other sources. Stauffer (1990) reported DDM for current annual growth as 57.6% and Blair et al. (1977) from 55.6% to 67.2%, compared to 65.4% from this study. Stauffer (1990) reported DDM of current year fallen leaves as 59.8% compared to 52.1% for this study. The DDM value of 77.5% for leafy browse from this study was much higher than the value of 54.9% reported by Stauffer (1990). However, Short (1975) reported a DDM value of 74.0% for honeysuckle collected in November. Much of the leafy browse collected in this study was honeysuckle and other small, relatively succulent, evergreen species, as opposed to dried leaves that were included as leafy browse if they had not fallen yet. Only 3 samples (all acorns) were used to determine a DDM value of 53.4% for mast. Pekins and Mautz (1988) reported a similar DDM for acorns, 53.1%. However, Stauffer (1990) reported DDM for mast as 62.1%. Short and Epps (1976) reported values ranging from 59.8% to 68.5% depending on the species of acorn. These data indicate that my value is probably a little low, but not unreasonable. A DDM of 67.5% for forbs and grasses was similar to the value of 63.6% reported by Stauffer (1990) and 68.2% reported by Blair et al. (1977). No data were available for the comparison of DDM values for ground pine (76.8%).

Metabolizable Energy

Amount of metabolizable energy varied between habitats. Without assuming utilization rates < 100%, hardwood and pine hardwood had the greatest amount of forage and yielded the most ME, mainly because of heavy leaf litter. Although pine habitats produced more potential forage (by weight), open habitats yielded more ME, indicating the presence of higher quality (more digestible) forages.

When estimated utilization rates were factored in, the contribution of leaves was minimized and open habitats consistently yielded the most ME ($\bar{x}$ = 67,700 kcal/ha). This result makes sense given relatively high quality and highly utilized browse, including leafy browse (especially honeysuckle), and grasses and forbs that were found in open habitats. Because of the large amount of leaves in all but the earliest seral stages, the effects of succession on metabolizable energy provided by the other forages in the understory were masked (Fig. 6). However, when utilization rates were applied and the contribution of dried, fallen leaves minimized, logical changes in ME with increasing stand age occurred in all 3 forest habitats that did not occur without estimated utilization rates (Fig. 7). ME was highest in the earlier seral stages (1-15 years) probably for the same reason as for open habitats. Stands 5-10 years-old provided the most ME for all forest habitats. ME was lowest from 15 to 30 years for all habitats. At this stage, canopy cover approaches 100%, little browse is produced in the understory and most twigs and needles are out of reach. ME increased again after 40 years as the canopy presumably began to open up again and continued to increase up to age 70 when it leveled off or decreased slightly. The model, with utilization rates applied, seems to have the ability to detect changes in habitat quality based on ME.

As was the case in estimating forage quantity, ME estimates are probably conservative. Mast, honeysuckle and perhaps some other preferred forages may not have contributed as much to estimation of ME at the time of this study as might realistically be the case in years of good mast crops. Little honeysuckle was available, possibly due to heavier than usual browsing on honeysuckle because of the scarcity of mast. Harlow (1984) showed that ME available to South Carolina deer on a daily basis was 36% less in years of mast failure as compared to good mast years. ME in hardwood and pine-hardwood stands is probably affected the most when mast is scarce.

HSI values and deer condition

Correlations between the weighted HSI and deer condition for each management unit were low and not statistically significant (Table 11). One reason for lack of correlation between predicted and observed conditions may be that available metabolizable energy is not a reliable predictor of habitat quality for deer. Available energy may not be the limiting factor nutritionally for deer. If deer densities are maintained at a level below carrying capacity, then available energy alone may not adequately represent habitat quality for deer in autumn-winter. Mautz (1978) points out that, while winter food is often considered to be the limiting link for big game species, white-tailed deer have a number of mechanisms, such as lowered metabolic rate, highly insulative coats and changes in behavior, that tend to reduce the importance of winter food as the sole factor influencing winter condition of deer. Thill et al. (1990) concluded that deer in the southeast can maintain a reasonably uniform nutritional plane throughout the year through selective foraging. Additionally, Stauffer (1990) suggested that the winter period may not be the most limiting period in terms of nutrition for deer in the coastal plain. Late summer and early autumn may be nutritionally the most limiting period for does going into estrus. If does enter into estrus on a low nutritional plain, it is likely that reproductive output would be lowered (Stauffer 1990). Finally, deer have been shown to travel long distances on a daily basis to find preferred foods (Marchinton and Hirth 1984). The condition of a deer taken from any particular area may be a function of energy consumed outside of the evaluation area. Crawford and Marchinton (1989) suggest basal area of oak, number of oak species, site index, percentage of agricultural lands and distance from agricultural land to forest of shrub cover as important habitat variables for deer on the Piedmont of Virginia.

There was little variation in the HSI values generated by sub-models I and II for each management unit (Table 9). HSI values ranged from 0.29 to 0.34 and 0.42 to 0.49 for sub-models I and II, respectively. This low variation in HSI values indicates that the units of interest were fairly homogeneous in terms of available energy and mix of habitats. It obviously would have been advantageous if the 11 units being compared had been extremely heterogeneous and a wider range of HSI values had been calculated.

When calculating HSI values for each unit, I incorporated as much of the available habitat into the weighted mean as possible. There is an underlying assumption that all habitat is used equally and contributes to the HSI value and deer condition in proportion to its area. However, deer probably do not use all habitats in proportion to abundance. It is likely that deer use the areas that provide the greatest quantity and quality of forages (i.e. higher quality habitats) more than other areas. It also seems likely that, although overall habitat suitability for a given area may be low, deer condition might be related to the relative area of high quality habitat. Based on these ideas, I used sub-model I to calculate the area of habitat with HSI > 0.50 for each unit and looked at the correlations with deer conditions. For every condition index, correlations improved over the original HSI comparisons and beam diameter approached significance ($r = 0.49$, $\underline{n} = 11$, $\underline{P} = 0.129$) (Table 12), suggesting that the abundance of high quality habitat on an area rather than the overall habitat quality may be a better indicator of the suitability of a given area.

Unit 17 had a relatively large area in habitat types that we did not sample and that occurred only in small patches in the other units. Alfalfa and other high quality deer foods had also been planted in unit 17 and were unaccounted for in the determination of ME. Unit 17 had the lowest deer HSI value and the best deer condition according to all 4 indices, and was an obvious outlier. When unit 17 was removed form analyses, correlations improved further and beam diameter was

Table 12. Spearman's rank correlation coefficients and significance for comparison of area with HSI > 0.5 (based on sub-model I) with deer condition indices from 11 management unit.

	Habitat suitability index	
Condition index	r_s	*P*
Body weight	-0.05	0.873
Beam diameter	0.49	0.129
Beam length	0.48	0.136
Number of points	0.20	0.550

significantly correlated ($r = 0.68$, $\underline{n} = 11$, $\underline{P} = 0.030$) to area of habitat with HSI > 0.50. Final criteria when comparing 2 areas with this model or this energetics-based approached might be "percentage of area with suitability > 0.5 " (or some higher value), assuming that the area can be classified into habitat types as was done here.

CONCLUSIONS

The original white-tailed deer HSI model is not useful for predicting habitat quality for deer in autumn-winter. The data showed that there was far more available energy for deer from winter forages than was hypothesized to occur in a standard or optimum habitat in the original model. Consequently, the original model assigned each habitat a HSI of 1.0. By adjusting each forage category by the percentage of the available forage that is likely to be consumed by deer, it was possible to predict a range of habitat quality. The model also was able to predict trends in metabolizable energy with increasing stand age. Utilization rates should be used with caution since the percentages were based only on sparse data and expert opinion.

Even though the data suggested that habitat quality predicted by the model did not reflect actual conditions, low variation in HSI values and deer condition made it difficult to draw concrete conclusions concerning the usefulness of the model from correlation analyses. In addition, alternative methods of evaluating the data and removal of outliers as described above showed much stronger relationships between model output and deer condition.

The evaluation and field testing of the white-tailed deer HSI model for the south Atlantic coastal plain clearly showed it to be unreliable. In addition, sampling of forages for calculating model variables is relatively tedious and time consuming, another major shortcoming of this model if it is to be applied quickly.

Model Restructuring

Data from this study have suggested that habitat quality predicted by the modified white-tailed deer HSI model do not agree well with observed conditions, but the evidence does not support rejection of the energetics approach as a method of predicting deer habitat suitability in winter. The model may be more useful if some modifications are made.

Data from this study and from Stauffer (1990) suggest that the original HSI model presented by Short (1986) is of little value because no HSI values < 1.0 could be predicted. Our data indicated that the utilization rates suggested by Stauffer (1990) provide a logical range of HSI values and might reasonably be incorporated into the model.

Another logical improvement to the model might be to remove current year's fallen leaves from the list of forages and not include ground pine as we did. The abundance of leaves was what drove the original model to predict HSI = 1.0 , although leaves are the least important forage nutritionally of those included in the model. When leaves and ground pine were excluded from the analysis, the model predicted HSI's for each transect ranging from 0.13 to 1.0 without the use of utilization rates. HSI's for management units ranged from 0.73 to 0.87, but there was no improvement in correlations with deer condition indices (Table 13).

Table 13. Spearman's rank correlation coefficients and significance for comparison of habitat suitability indices from sub-models I with deer condition indices for 11 management units. Leaves and twigs have been excluded from the model and utilization rates were not used.

	Habitat suitability index			
	No leaves		No leaves or twigs	
Condition index	r_s	*P*	r_s	*P*
Body weight	-0.84	0.001	-0.35	0.298
Beam diameter	-0.09	0.788	0.07	0.830
Beam length	0.16	0.639	0.62	0.043
Number of points	-0.26	0.435	0.15	0.655

Woody twig ends are commonly accepted as important forages for deer in winter, but data from Cushwa et al. (1970) suggest that utilization of twig ends in winter may be nearly zero based on analysis of 489 deer rumina collected from deer killed throughout the Southeast. Therefore, it also may be reasonable to exclude woody twigs along with leaves. When the data were analyzed with twig ends and leaves excluded, HSI's for management units ranged from 0.52 to 0.61 and correlations with deer condition indices improved (Table 13), with beam length being significantly correlated with HSI ($r = 0.62$, $\underline{P} = 0.043$).

Forage digestibility data from this study and from Stauffer (1990) varied considerably from the values suggested in the original model. Variation in percent dry matter digestibility between studies may occur for several reasons. First, plant species differences may be an important source of variation in digestibility. Percent digestibility was determined for classes of forages, not for individual species. Therefore, the forage species that fall into each may be very different between study areas. Different species are likely to differ in digestibility (Short et al. 1972, Cook 1972, Klein 1970), therefore, substantially different digestibility values for the same forage class are possible.

Site condition and environment also may affect digestibility, even within the same species of plants (Klein 1970). Conditions such as shading, water and mineral availability in soil, topography, climate and frequency of burning change nutrient composition of the soil and cell wall structure, thereby altering the digestibility of plant tissue

(Short et al. 1972). While range of applicability of the white-tailed deer model is limited to a single physiographic region, significant differences in species composition, site condition and nutritional quality of forages for deer are likely to occur across this region. Therefore, no particular estimate of digestibility will be perfectly appropriate over the suggested range of applicability for this model. A range of digestibilities to cover several different "sub-regions" of the coastal plain may improve the accuracy of the model.

At the present time, I can only suggest digestibility values based on available data. New values for %DDM suggested in the model evaluation phase of testing the deer model were based upon empirical data from sites across the entire coastal plain region and extensive literature review. Because those values for %DDM were based upon a much larger and representative sample than in this study and because they did not differ radically from my %DDM values, I recommend incorporating into the model those values suggested by Stauffer (1990). These values are: Current annual growth - 55%, Current year leaves - 60%, Leafy browse - 55%, Mast - 68%, cool season herbs - 63%, and fungi - 95%. No data were available for leguminous seeds, but digestibility for this forage class is likely to be relatively high.

In summary, I believe that this HSI model can be useful for assessing autumn-winter white-tailed deer habitat quality in the south Atlantic coastal plain if the modifications suggested above are adopted by the user. The model is not likely to be useful if forage utilization by deer is ignored as in the original model. Forage digestibilities suggested above may be generally applicable anywhere in the coastal plain, but plant digestibilities corresponding specifically to the region of use, if available, would likely produce the most reliable model output.

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CHAPTER II:

MODELING VEGETATION RESPONSE TO SUCCESSION AND MANAGEMENT

INTRODUCTION

Pressures on natural resources due to human population expansion into rural areas and increased economic exploitation have created some serious challenges for today's wildlife managers. Predictive tools that can provide a realistic view of habitat conditions through time and space and the associated effects on wildlife are potential keys to successful resource management planning in the future (Mayer 1986). By combining wildlife and vegetation models, it is possible to predict the impacts of habitat manipulation and succession on many species of wildlife at the same time. The Habitat Management Evaluation Method (HMEM) is a system that links wildlife and vegetation models to simulate the effects of management and to identify which actions result in the greatest habitat gain at the least cost (Stauffer et al. 1991). One of the drawbacks of the system is that many of the predictions made by HMEM concerning changes in habitat are based upon inference rather than empirical data (Stauffer 1990). The purpose of this study was to collect data and develop models that reflect the response of habitat variables important to wildlife to succession and management, thereby providing some of the data necessary to make HMEM a truly useful system. The objectives of the study were to

1). Develop models that predict the response of habitat variables important to wildlife to succession and management, 2). Determine if changes in non-tree habitat variables, such as shrub and herbaceous cover and snags, can be predicted over time.

Changes in composition and appearance of vegetation with time during succession are caused by differences in growth and survival rates, competitive ability and longevity (Miles 1979). Modelers have used vegetation models such as TWIGS (Brand et al. 1986), DYNAST (Benson and Laudenslayer, Jr. 1986, Kirkman et al. 1986), FORHAB (Smith 1986), and HABSIM (Raedeke and Lehmkuhl 1986) to predict changes in habitat variables over time. These models have been developed for forestry applications and are not designed to predict changes in non-tree habitat parameters such as snags, herbaceous cover, shrub cover and density, and dead wood (Brand et al. 1986, Sweeney 1986, Stauffer 1990), which may be important habitat components for a wide variety of wildlife species. Further, timber models typically are developed for single tree species (Belcher et al. 1982) with data from intensively managed stands where understories may be burned or cut and overstories are thinned to enhance timber yield. I developed models that predict habitat measurements based on stand age and, in some instances, other habitat parameters that are related to the variable being estimated. These models are designed for predicting changes in wildlife habitat conditions over time when little information on stand dynamics is known and when effort cannot be spent measuring the variables directly.

STUDY AREA

This study was conducted on Quantico Marine Corps Base located in parts of Stafford, Prince William, and Fauquier counties, Virginia. Quantico is 21,538 ha in area, including approximately 16,194 ha of forested land, and is situated on the eastern edge of the Piedmont plateau physiographic region. Topography of the area is characterized by rolling hills and long, low ridges. Average elevation is approximately 400 feet. Soils are generally clay loams with varying amounts of sand and gravel and are usually acidic, low in organic matter and poor in natural fertility. Major impoundments include Lunga reservoir, Breckenridge reservoir, and Aquia reservoir. Larger streams include Chopawamsic creek, Cedar run, Beaverdam run, and Aquia creek. Streams that empty into the Potomac river at the eastern edge of the base, especially Chopawamsic creek, are tidally influenced for a distance of about 2 kilometers upstream.

The study area is divided into approximately 50 forest compartments (Fig. 8) that are composed of individual forest stands varying in age and cover type. Agricultural activities, clear-cutting, and prescribed burning have resulted in diversity of habitat types and seral stages on Quantico. This diversity facilitates the intensive management of a variety of game and non-game wildlife, including white-tailed deer, wild turkeys (Maleagris gallopavo), bobwhite quail (Colinus virginianus), cottontail rabbits (Syvilagus floridanus), mourning doves (Zenaida macroura), Canada geese (Branta canadensis) and other waterfowl, songbirds and birds of prey.

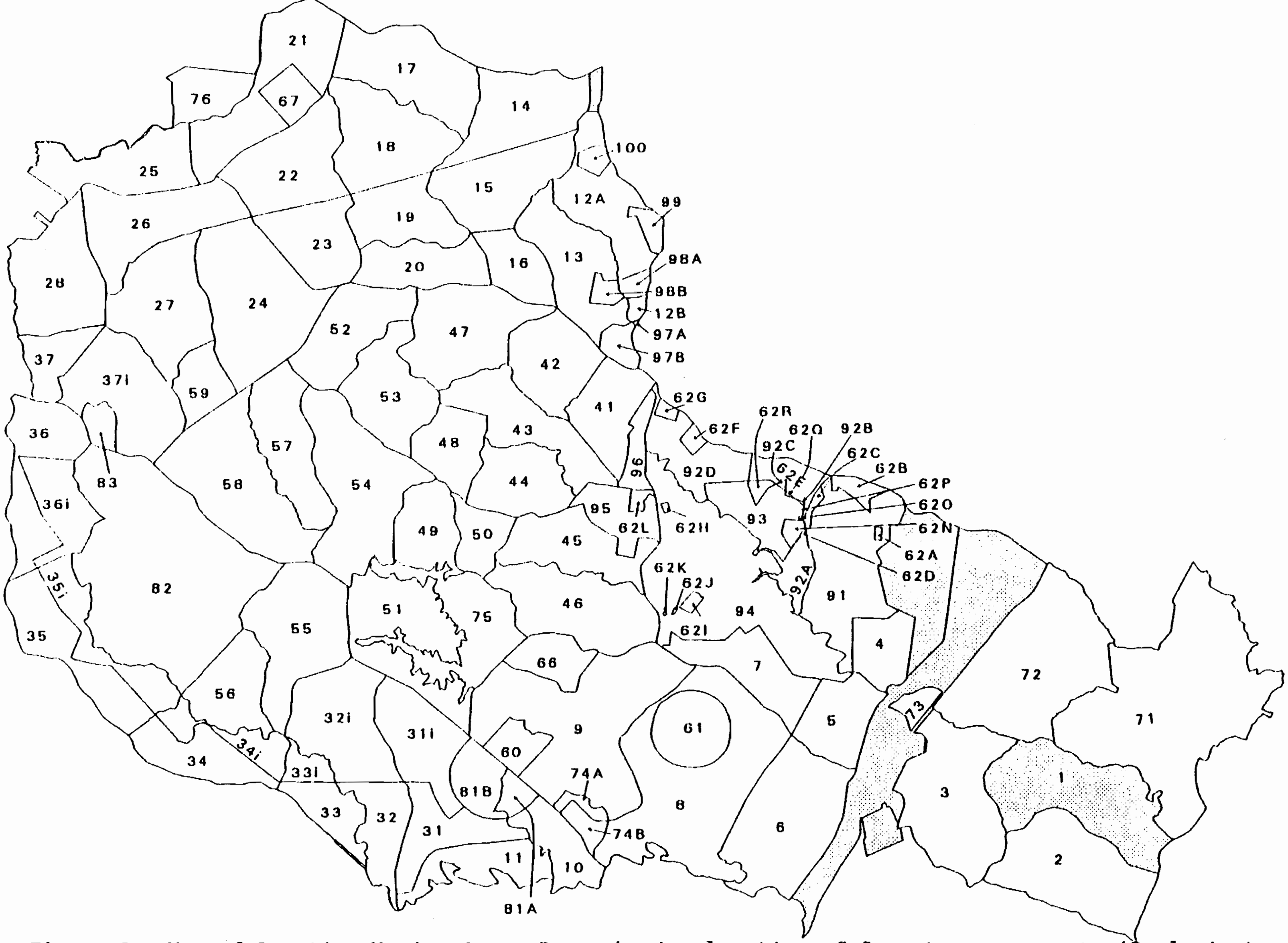

Figure 8. Map of Quantico Marine Corps Base showing location of forest compartments (Scale is too small to show individual forest stands).

METHODS

To determine the habitat variables that we would measure, I reviewed 52 HSI models for terrestrial species and tallied the number of times a given variable occurred in a model. Of 164 variables recorded, the 15 (Table 14) that were important for the greatest number of species were measured in this study. The other variables found in the models but not measured in this study for 1 or a combination of the following reasons: the variable was important to a single species or to species not found on or near the study area, such as for moose (Alces alces) or the cactus wren (Campylorhynchus brunneicapillus); the habitat parameter did not occur at all on the study area, such as percent sandy shoreline; the habitat variable could not realistically be modeled, such as successional stage or size of habitat block.

Habitat sampling at Quantico was conducted from May 15 to August 15, 1992 and 1993. Every forest stand on Quantico had been assigned a Society of American Foresters' cover type code. We assigned each stand to 1 of 5 general cover types: hard-mast hardwood (SAF type numbers 52, 59, 44, or 65) non-mast hardwood (SAF type numbers 25,57,61,87,94, or 108) pine-hardwood (SAF type number 78), loblolly-shortleaf pine (SAF type number 81), or virginia pine (SAF type number 79).

Hard-mast stands were composed mainly of oaks (Quercus spp.), hickories (Carya spp.), and beech (Fagus grandifolia). Yellow poplar (Liriodendron tulipifera), sweetgum (Liquidambar styraciflua), red maple (Acer rubrum), and sycamore (Platanus occidentalis) dominated the overstory of non-mast hardwood stands. Pine-hardwood stands consisted

Table 14. Habitat variables used in modeling vegetation response to succession and management on Quantico Marine Corps Base, Virginia. Variables were chosen according to their frequency of occurrence in habitat suitability index (HSI) models and in habitat studies in the literature.

Variable	Number of HSI models[a] including variable	Measurement technique
Trees > 5cm diameter		
Basal area	2	
Density	1	Plot count
Mean diameter	7	Biltmore stick
Overstory		
Canopy closure	17	Densiometer
Height, dominant trees	2	Clinometer
Shrubs < 1.5m tall		
% crown cover	14	Line intercept
Density	1	Plot count
Mean height	6	Graduated rod
Herbaceous vegetation		
% ground cover	5	Daubenmire plot
% bare or light litter	3	Daubenmire plot
% grass cover	2	Daubenmire plot
Height	6	Graduated rod
Snags		
Density	4	Plot count
Mean diameter	1	Biltmore stick
Density of woody stems < 5cm diameter	2	Plot count

[a] Based on review of 52 terrestrial HSI models

of mixed Virginia pine (Pinus virginianus) and oak. Pine habitats were dominated by mixed loblolly (Pinus taeda) and shortleaf (Pinus echinata) pine or Virginia pine. Blackgum (Nyssa sylvatica), flowering dogwood (Cornus florida), and American hornbeam (Carpinus caroliniana) were common understory tree species. Commonly occurring woody shrubs and vines included mapleleaf viburnum (Viburnum acerifolium), greenbriar (Smilax spp.), American hazlenut (Corylus americanus), hercules club (Aralia spinosa), poison ivy (Rhus radicans), and sumac (Rhus spp.). Stratified random sampling was used (Freese 1962) to select a sample of stands from different ages of each cover type (Table 15) across the base. Stands were grouped by the following age classes: 1-4 years, 5-10 years, 11-20 years, 21-30 years, 31-40 years, 41-50 years, 51-60 years, 61-70 years, 71-80 years, 81-90 years, 91 years or more. Stands in each age class within a habitat type were put in random order using the statistical analysis system (SAS) and a random sorter. Stands then were chosen for sampling in order of occurrence.

Two-hundred meter transects served as the sampling framework within each stand. Normally, 2 transects were established unless the stand was < 10 ha and it was determined that the stand could be adequately sampled using just 1 transect. Transects were randomly located with the constraint that all sampling points occurred entirely within one habitat type. We attempted to avoid edges, abrupt changes in habitat type within the stand, and disturbances caused by troop activity by referring to aerial photographs.

Five sampling points were established along each transect at 50

Table 15. Number of stands sampled by habitat type and age class for modeling vegetation response to succession and management on Quantico Marine Corps Base, Virginia.

	Habitat type					
Age class	Hard-mast hardwood	Loblolly-shortleaf pine	Non-mast hardwood	Pine-hardwood	Virginia pine	Total
1-10	7	19	-	7	-	33
11-20	7	3	-	2	1	13
21-30	3	5	1	7	8	24
31-40	8	-	1	3	2	15
41-50	3	-	4	3	4	14
51-60	2	-	4	2	4	12
61-70	2	-	4	4	4	14
71-80	2	-	1	1	3	7
81-90	6	-	2	2	1	11
91+	5	-	-	-	-	5
Total	45	27	17	31	27	148

meter intervals. Diameter at breast height (DBH) of every tree > 5 cm in diameter within a 0.04ha plot was measured with a biltmore stick to the nearest centimeter at each sampling point. In young stands (< 20 years-old) where trees were very dense, a 0.01 hectare plot was used to speed up the tree measuring process. Height of the dominant tree closest to the plot center was measured (meters) using a clinometer. Percent canopy cover of the overstory was measured at 25m intervals with a spherical densiometer. Woody stems < 5cm dbh were counted in 2 x 11.3m plots at 90° intervals about the plot center. Herbaceous vegetation characteristics were measured using a Daubenmire plot placed at 90° intervals 5 meters from the plot center.

A 50 meter tape was laid out between sampling points. Shrub cover (shrubs were defined as any woody vegetation between 0.2 and 1.5 meters tall) was measured using the line intercept method (Hays et al 1981). All shrubs were counted within 1 meter on either side of the tape (0.01 ha plot) to get an estimate of shrub density and the DBH and condition of any snags within 10 meters on either side (0.1 ha plot) were recorded. From these data, all habitat variables of interest could be calculated.

Analysis

Linear and non-linear least squares regression were used to model the response of each habitat variable to increasing stand age (succession). Plots of the raw data (habitat variable vs. age) were used to obtain a rough estimate of the shape of the curve that represented the relationship of the habitat variable to stand age. The curves then were compared to commonly used vegetation models (Avery and Burkhart 1983) to determine the most appropriate model. When > 1 model may have been appropriate, both models were fitted. The final model was the model giving the best fit (based on adjusted R^2). Where possible, other variables were added to the models if they improved prediction. R^2_{adj} and significance levels were used to determine how well each model fit the data. The shape of the curve generated by the final model also was used as an indication of the appropriateness of the model and to determine if the model was biologically realistic. Curves representing changes in variables for stand ages from 3 to 120 years were generated only for those models that were significant ($\underline{P} \leq 0.10$). For loblolly-shortleaf pine, for which the oldest stand sampled was 28 years, I extrapolated to 100 years only if the relationship appeared realistic. If the relationship between variable and stand age broke down, I extrapolated only to 30 years.

RESULTS

Basal Area

Basal area (BA) of trees (m^2/ha) increased rapidly in the early stages of forest growth, slowing in the later seral stages (Fig. 9). The following model was used to fit the data:

$$\ln BA = b_o + b_1 * \ln AGE$$

The relationship between basal area and stand age was relatively good for hard-mast hardwoods ($R^2_{adj} = 0.60$, 1,40 df, $\underline{P} = 0.0001$), loblolly-shortleaf pine ($R^2_{adj} = 0.78$, 1,22 df, $\underline{P} = 0.0001$), and pine-hardwood ($R^2_{adj} = 0.53$, 1,28 df, $\underline{P} = 0.0001$) habitats. The relationship between

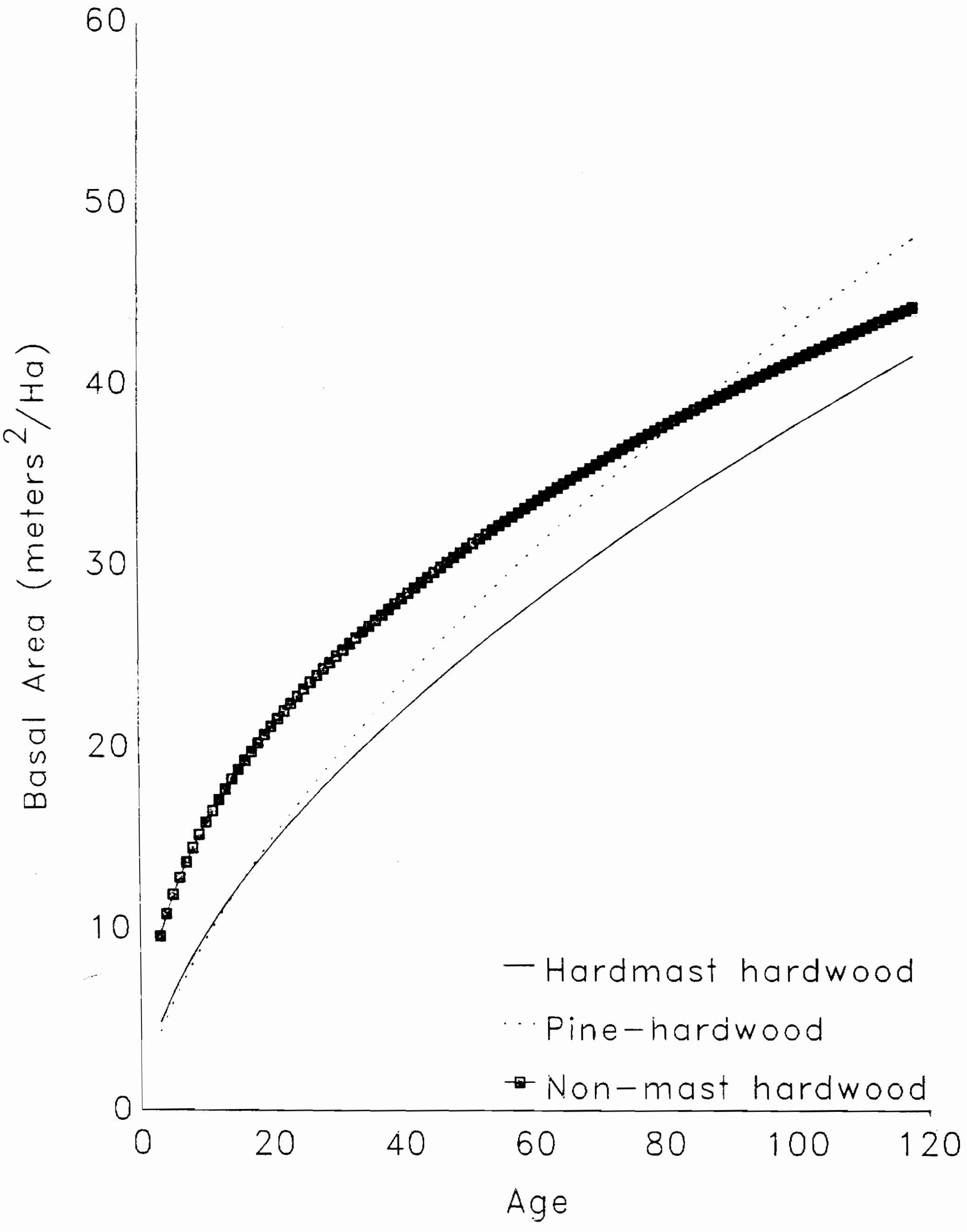

Figure 9. Predicted relationship of basal area to stand age in 4 habitat types at Quantico Marine Corps Base, Virginia.

basal area and stand age was poor for non-mast hardwood (R^2_{adj} = 0.13, 1,15 df, $\underline{P}$ = 0.0884) and Virginia pine (R^2_{adj} = -0.0419, 1,23 df, $\underline{P}$ = 0.8520) habitats (Table 16).

Density of trees

Density of trees (trees/ha) generally decreased with increasing stand age. An exception was loblolly-shortleaf pine, where tree density increased at a decreasing rate through 30 years (Fig. 10). The following model was fit to the tree density data:

$$\text{Tree density} = b_o + b_1/\text{AGE}$$

R^2_{adj} was highest for loblolly-shortleaf pine (R^2_{adj} = 0.52, 1,22 df, $\underline{P}$ = 0.0001). The relationship between tree density and stand age was relatively poor for hard-mast hardwood (R^2_{adj} = 0.05, 1,40 df, $\underline{P}$ = 0.0673), pine-hardwood (R^2_{adj} = 0.14, 1,28 df, $\underline{P}$ = 0.023), non-mast hardwood (R^2_{adj} = 0.03, 1,15 df, $\underline{P}$ = 0.4883), and Virginia pine (R^2_{adj} = 0.25, 1,23 df, $\underline{P}$ = 0.0059) habitats (Table 16).

Table 16. Linear regression models for predicting basal area (BA, meters^2/ha), trees/ha (TD), and tree diameter (cm) at breast height (DBH) from age of stand for 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	R^2_{adj}	P
Hard-mast hardwood (n=41)			
Basal area	lnBA = 0.92 + 0.59 lnAge	0.60	0.0001
Tree density	TD = 804.15 + 3919.08/Age	0.05	0.0673
Diameter	lnDBH = 1.12 + 0.45 lnAge	0.82	0.0001
Loblolly-shortleaf pine (n=23)			
Basal area	lnBA = -3.38 + 2.30 lnAge	0.78	0.0001
Tree density	TD = 2378.65 - 8333.76/Age	0.52	0.0001
Diameter	lnDBH = 1.28 + 0.42 lnAge	0.41	0.0004
Pine-hardwood (n=29)			
Basal area	lnBA = 0.73 + 0.66 lnAge	0.52	0.0001
Tree density	TD = 1016.94 + 7300.38/age	0.14	0.0253
Diameter	lnDBH = 1.17 + 0.41 lnAge	0.82	0.0001
Non-mast hardwood (n=16)			
Basal area	lnBA = 1.80 + 0.42 lnAge	0.13	0.0884
Tree density	TD = 890.50 - 7696.01/Age	0.03	0.4883
Diameter	lnDBH = 3.09 - 0.009 lnAge	0.00	0.9543
Virginia Pine (n=24)			
Basal area	lnBA = 3.06 + 0.07 lnAge	0.00	0.8520
Tree density	TD = 530.23 + 24873.0/Age	0.25	0.0059
Diameter	lnDBH = 2.08 + 0.20 lnAge	0.31	0.0040

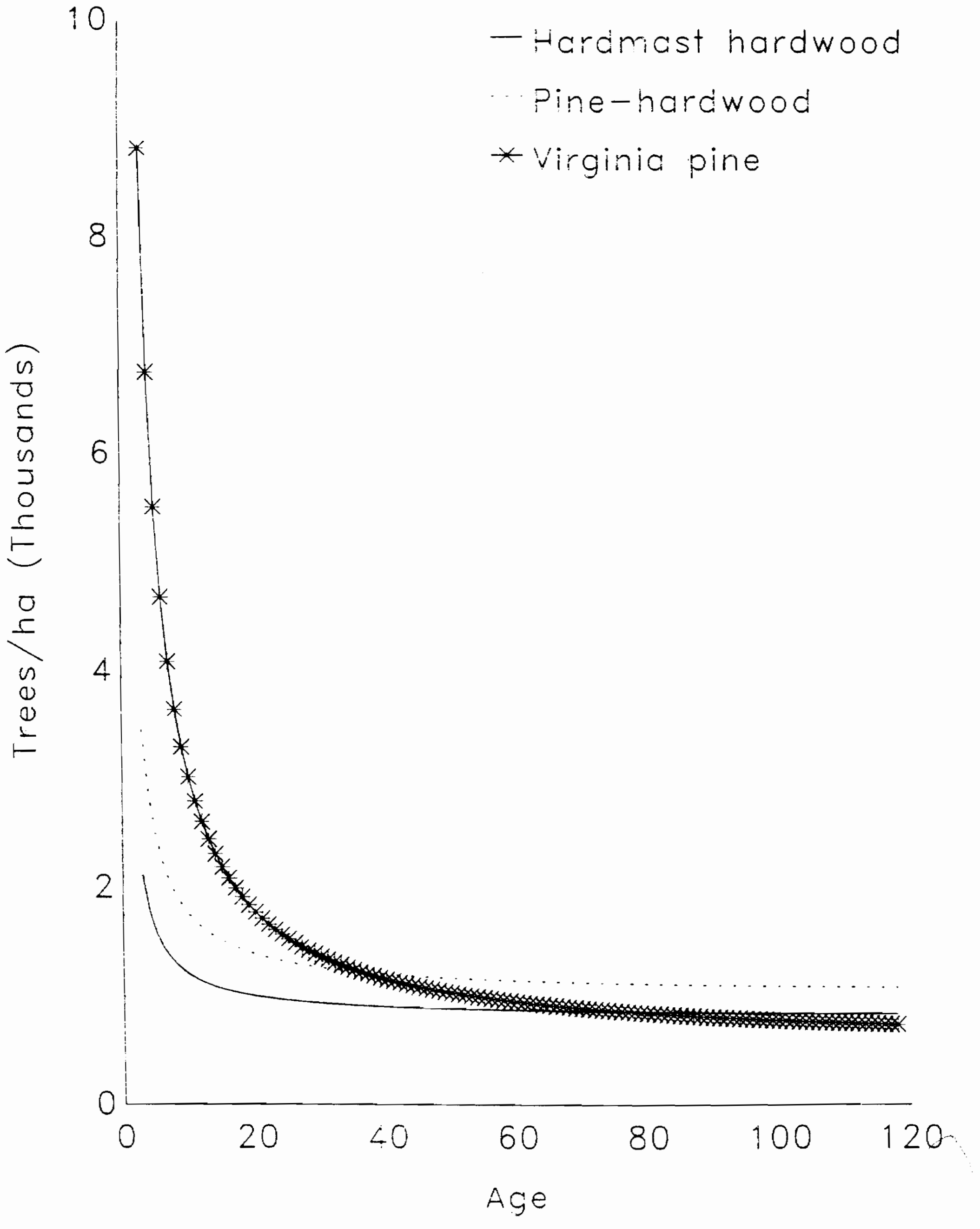

Figure 10. Predicted relationship of tree density to stand age in 4 habitat types at Quantico Marine Corps Base, Virginia.

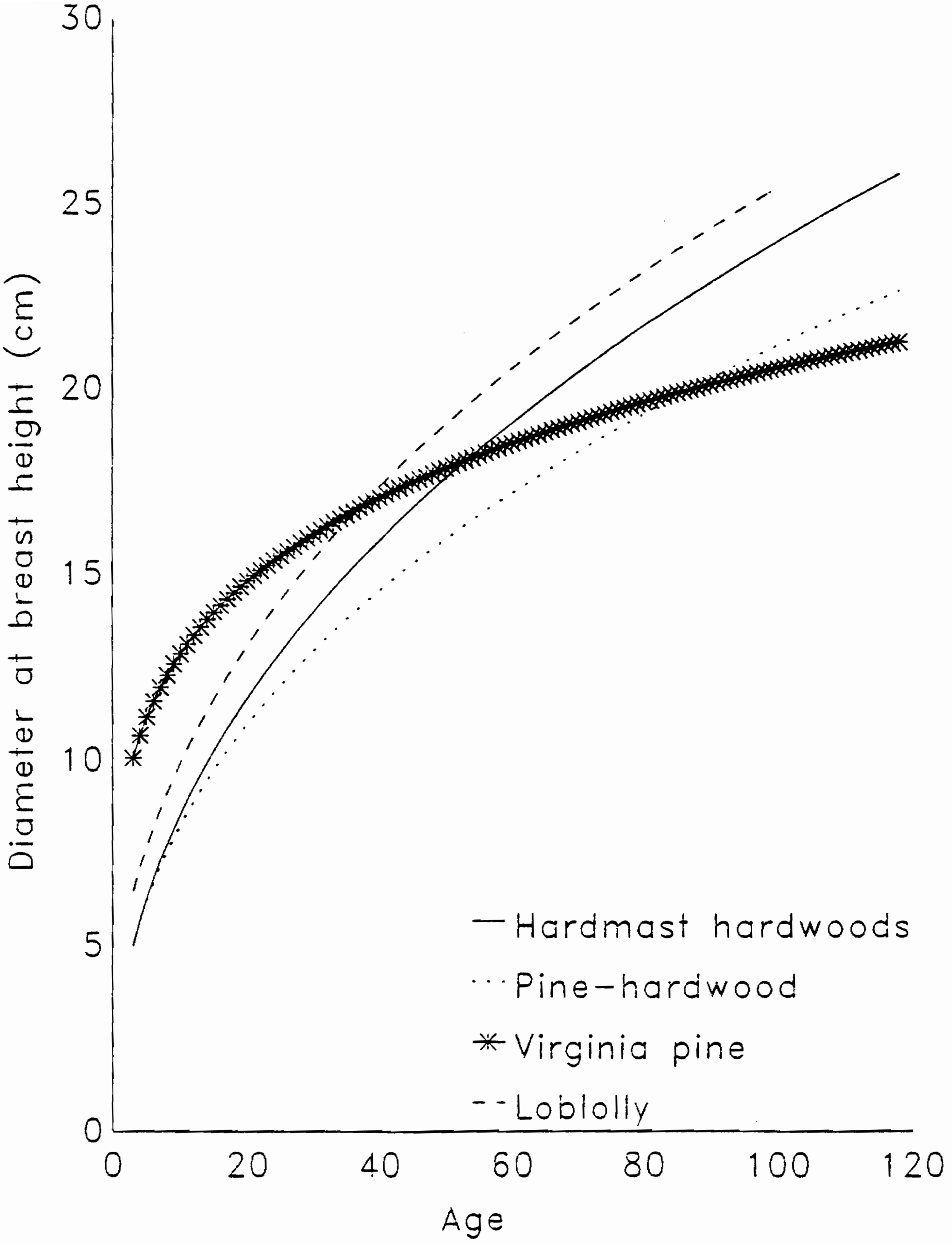

Figure 11. Predicted relationship of dbh to stand age in 4 habitat types at Quantico Marine Corps Base, Virginia.

DBH

Average DBH of trees increased with stand age, rapidly at first and slowing as the stands matured (Fig 11). The following model was used to fit the diameter data:

$$\ln DBH = b_o + b_1 * \ln AGE$$

R^2_{adj} was highest for hard-mast hardwood ($R^2_{adj} = 0.82$, 1,40 df, $\underline{P} = 0.0001$) and pine-hardwood habitats ($R^2_{adj} = 0.82$, 1,28 df, $\underline{P} = 0.0001$). The relationship between DBH and stand age was not as strong for loblolly-shortleaf pine ($R^2_{adj} = 0.41$, 1,22 df, $\underline{P} = 0.0004$) and Virginia pine ($R^2_{adj} = 0.31$, 1,23 df, $\underline{P} = 0.004$) habitats. There was no relationship between DBH and stand age ($R^2_{adj} = -0.07$, 1,15 df, $\underline{P} = 0.9545$) (Table 16).

Height of overstory trees

Height of dominant trees (H) increased rapidly in the early stages of stand growth, then leveled off and increased at a much slower rate as the stands matured (Fig. 12). The following model was used to fit the data:

$$\ln H = b_o + b_1/AGE$$

There was a strong relationship between stand age and tree height for hard-mast hardwoods ($R^2_{adj} = 0.79$, 1,37 df, $\underline{P} = 0.0001$), loblolly-shortleaf pine ($R^2_{adj} = 0.78$, 1,22 df, $\underline{P} = 0.0001$), and pine-hardwood ($R^2_{adj} = 0.87$, 1,26 df, $\underline{P} = 0.0001$) habitats. The relationship was not as strong for Virginia pine ($R^2_{adj} = 0.51$, 1,20 df, $\underline{P} = 0.0001$) and there was no relationship between tree height and stand age for non-mast hardwoods ($R^2_{adj} = 0.00$, 1,15 df, $\underline{P} = 0.3312$) (Table 17).

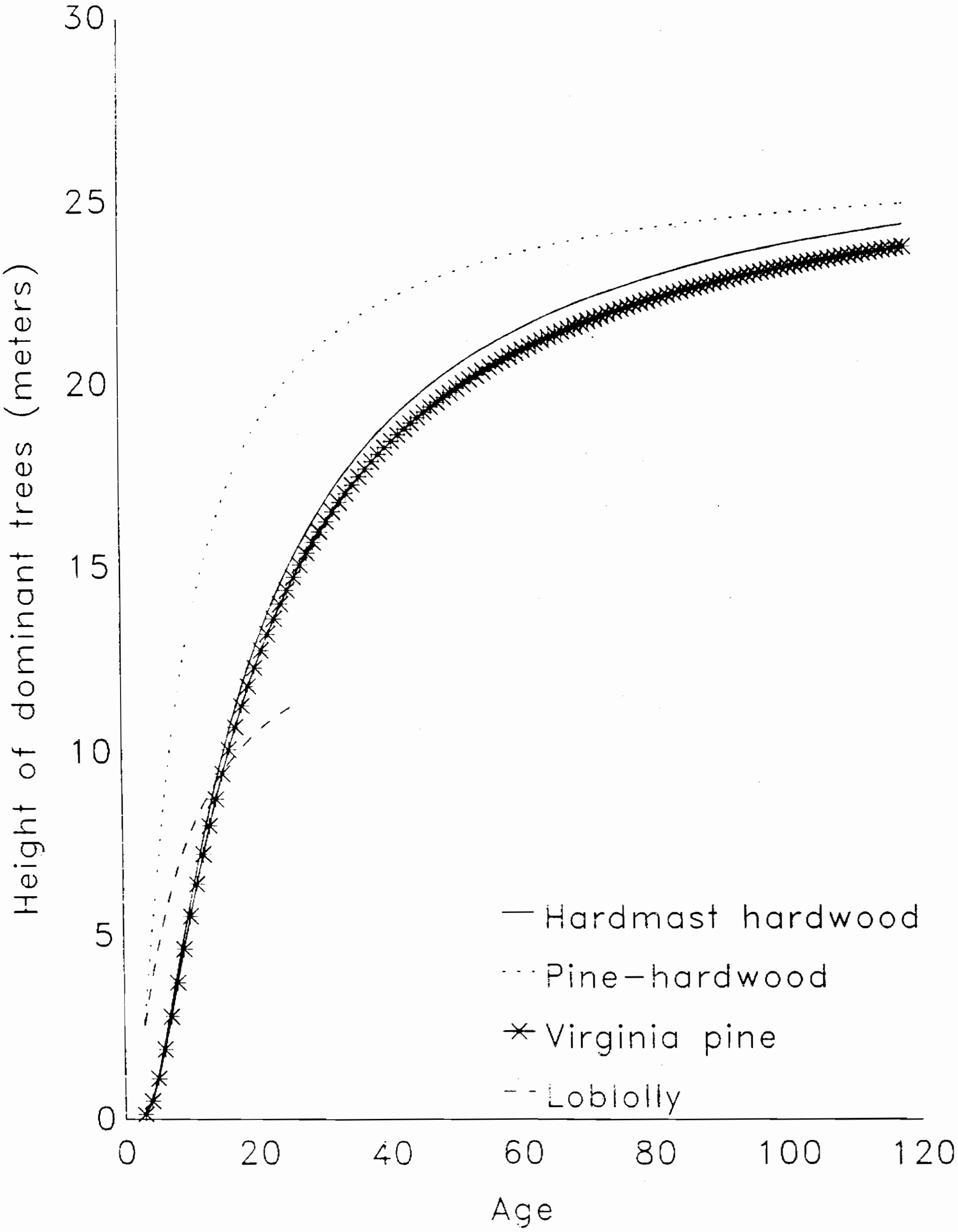

Figure 12. Predicted relationship of dominant tree height to stand age in 4 habitat types at Quantico Marine Corps Base, Virginia.

Table 17. Linear regression models for predicting height (meters) of overstory trees (H) from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	$\ln H = 3.33 - 15.50/Age$	38	0.79	0.0001
Loblolly-shortleaf pine	$\ln H = 2.68 - 6.96/Age$	23	0.78	0.0001
Pine-hardwood	$\ln H = 3.28 - 14.94/Age$	27	0.87	0.0001
Non-mast hardwood	$\ln H = 3.27 - 6.88/Age$	16	0.00	0.3312
Virginia pine	$\ln H = 3.30 - 15.92/Age$	21	0.51	0.0001

When DBH was added to the model as a predictor of tree height, R^2_{adj} improved slightly for hard-mast hardwood (R^2_{adj} = 0.83, 1,37 df, $\underline{P}$ = (0.0001), loblolly-shortleaf pine (R^2_{adj} = 0.87, 1,22 df, $\underline{P}$ = 0.0001), pine-hardwood (R^2_{adj} = 0.90, 1,26 df, $\underline{P}$ = 0.0001), and non-mast hardwood (R^2_{adj} = 0.20, 1,15 df, $\underline{P}$ = 0.0822) habitats (Table 18).

Density of woody stems < 5cm DBH

Woody stems < 5cm in diameter were generally very dense in the early seral stages, becoming progressively less dense at a decreasing rate with age (Fig. 13). The following model was used to fit the data:

$$\text{Stem density} = b_o + b_1/\text{AGE}$$

The relationship between stand age and stem density was relatively good for hard-mast hardwood (R^2_{adj} = 0.76, 1,40 df, $\underline{P}$ = 0.0001) and pine-hardwood (R^2_{adj} = 0.76, 1,29 df, $\underline{P}$ = 0.0001) habitats. The relationship was poorer, though still significant, for loblolly-shortleaf pine (R^2_{adj} = 0.08, 1,26 df, $\underline{P}$ = 0.0809) and Virginia pine (R^2_{adj} = 0.17, 1,24 df, $\underline{P}$ = 0.0194) habitats. There was no relationship between stem density and stand age for non-mast hardwood stands (R^2_{adj} = 0.00, 1,14 df, $\underline{P}$ = 0.9352) (Table 19).

Percent canopy cover

In general, canopy cover (CC) was low in the very early seral stages (1-10 years-old), then increased rapidly before leveling out sharply between 80% and 100% (Fig. 14). I used the following model to fit the data:

$$CC = b_o + b_1/\text{AGE} + b_2{*}\text{AGE}$$

Table 18. Linear regression models for predicting height (meters) of overstory trees (H) from stand age and mean diameter of trees in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	*n*	R^2_{adj}	*P*
Hard-mast hardwood	$\ln H = 2.69 - 11.64/\text{Age} + 0.03\ \text{DBH}$	38	0.83	0.0001
Loblolly-shortleaf pine	$\ln H = 1.41 - 3.32/\text{Age} + 0.08\ \text{DBH}$	22	0.87	0.0001
Pine-hardwood	$\ln H = 2.08 - 8.25/\text{Age} + 0.07\ \text{DBH}$	23	0.90	0.0001
Non-mast hardwood	$\ln H = 2.78 - 6.87/\text{Age} + 0.02\ \text{DBH}$	16	0.20	0.0822
Virginia pine	$\ln H = 3.44 - 16.77/\text{Age} - 0.01\ \text{DBH}$	19	0.47	0.0018

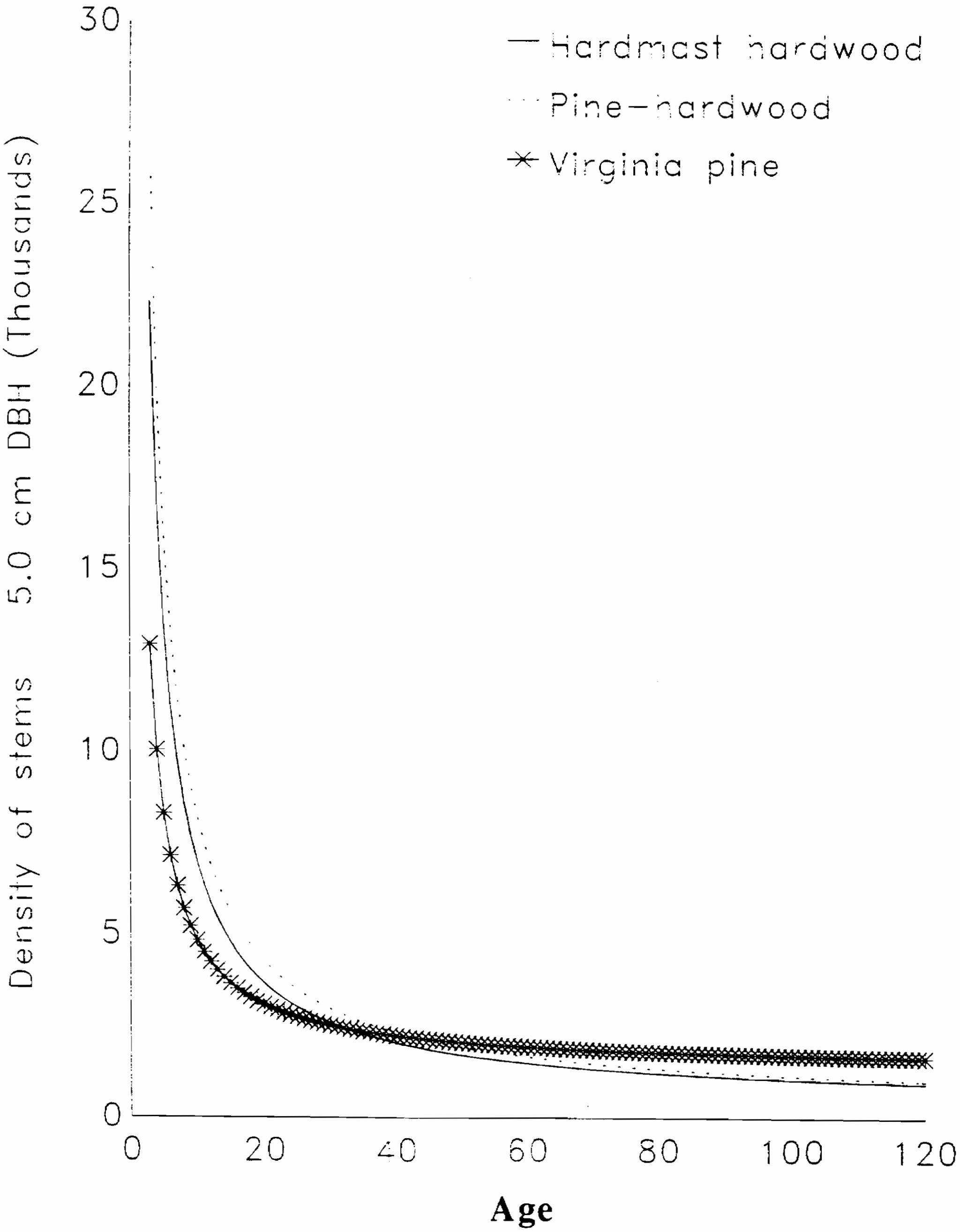

Figure 13. Predicted relationship of density of woody stems < 5cm dbh to stand age in 4 habitat types at Quantico Marine Corps Base, Virginia.

Table 19. Linear regression models for predicting density of stems < 5cm DBH/ha from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	Stems = 408.69 + 65739.00/Age	41	0.76	0.001
Loblolly-shortleaf pine	Stems = 5726.01 - 8881.98/Age	27	0.08	0.080
Pine-hardwood	Stems = 375.76 + 78441.00/Age	30	0.76	0.001
Non-mast hardwood	Stems = 2179.81 - 2815.66/Age	15	0.00	0.935
Virginia pine	Stems = 1376.43 + 34676.0/Age	25	0.17	0.019

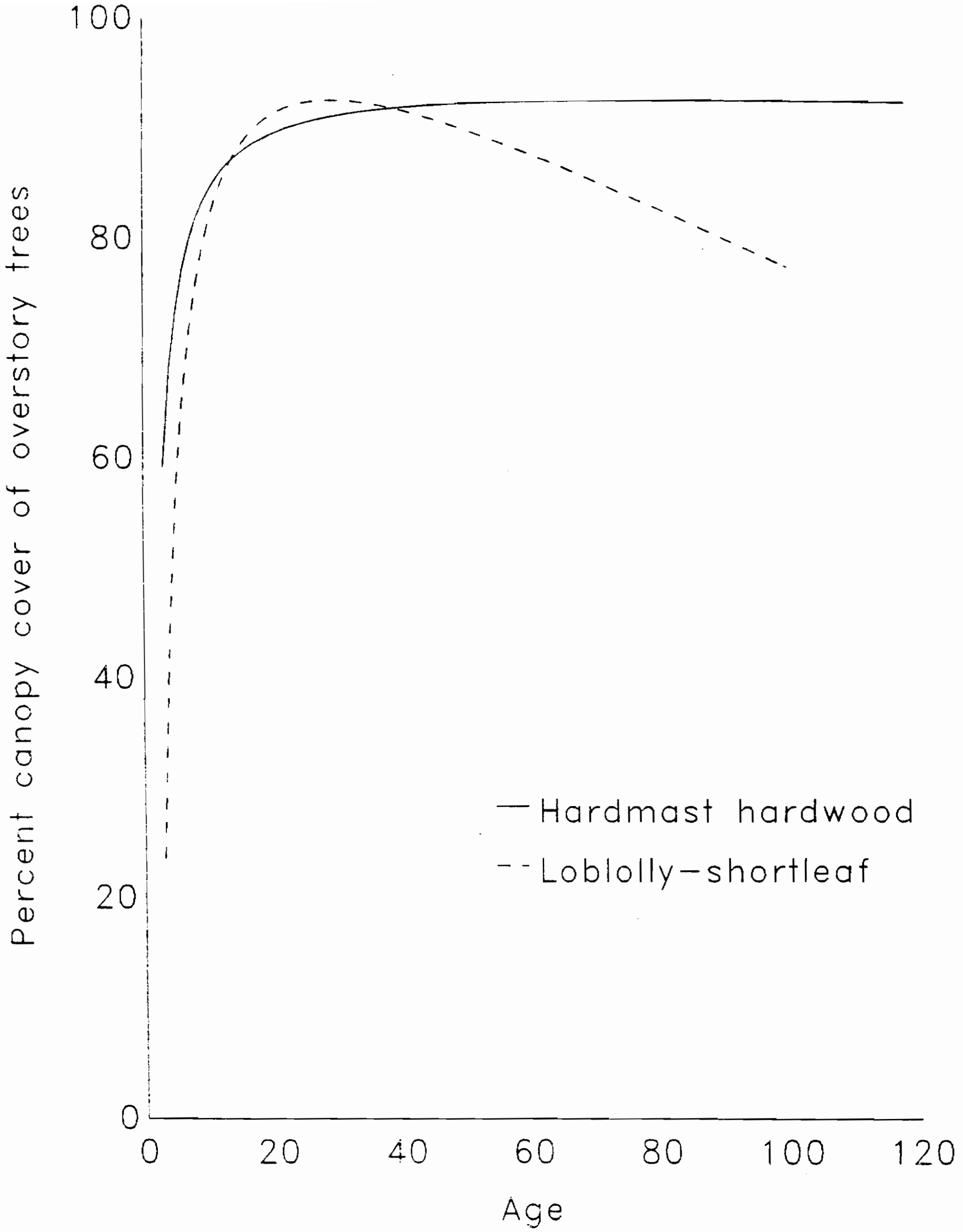

Figure 14. Predicted relationship of percent canopy cover of overstory trees to stand age in 2 habitat types at Quantico Marine Corps Base, Virginia.

The relationship between stand age and canopy cover was strongest for loblolly-shortleaf pine (R^2_{adj} = 0.85, 1,22 df, $\underline{P}$ = 0.0001) habitats. The relationship was poor but significant for pine-hardwood (R^2_{adj} = 0.26, 1,28, $\underline{P}$ = 0.0069) and Virginia pine (R^2_{adj} = 0.15, 1,26 df, $\underline{P}$ = 0.0497) habitats. There was no relationship between canopy cover and stand age for hard-mast hardwoods (R^2_{adj} = 0.08, 1,41 df, $\underline{P}$ = 0.0648) and non-mast hardwood (R^2_{adj} = 0.05, 1,14 df, $\underline{P}$ = 0.2791) habitats (Table 20).

Percent canopy cover of shrubs ≤ 1.5m tall

The relationship between percent shrub cover and stand age was not evident from plots of the data. I expected a tendency for shrub canopy cover (SCC) to be high at the early seral stages (1-10 years-old), decrease to a low between 10 and 30 years, and then increase again at the later seral stages (Fig. 15). Thus, I chose the following model to fit the expected relationship:

$$SCC = b_o + b_1\ AGE + B_2\ AGE^2$$

There was very little discernable relationship between shrub cover and stand age based on plots of the raw data. When the model was fitted, there was a weak relationship between shrub cover and stand age in loblolly-shortleaf pine stands (R^2_{adj} = 0.24, 1,29 df, $\underline{P}$ = 0.0076). There was no relationship between shrub cover and stand age (R^2_{adj} = 0.00, $\underline{P}$ > 0.25) in any of the other habitats (Table 21).

When shrub height was added to the model as a predictor of shrub density, more of the variation was accounted for in hard-mast hardwoods (R^2_{adj} = 0.13, 3,42 df, $\underline{P}$ = 0.029), loblolly-shortleaf pine (R^2_{adj} = 0.59,

Table 20. Linear regression models for predicting percent canopy cover of overstory trees (CC) from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	CC = 96.68 - 86.89/Age - 0.04 Age	42	0.07	0.064
Loblolly-shortleaf pine	CC = 110.22 - 257.48/Age - 0.30 Age	23	0.86	0.001
Pine-hardwood	CC = 95.34 - 108.37/Age - 0.02 Age	29	0.25	0.007
Non-mast hardwood	CC = 140.36 - 16.75/Age + 0.34 Age	15	0.05	0.279
Virginia pine	CC = 63.92 + 7.92/Age - 0.07 Age	27	0.15	0.050

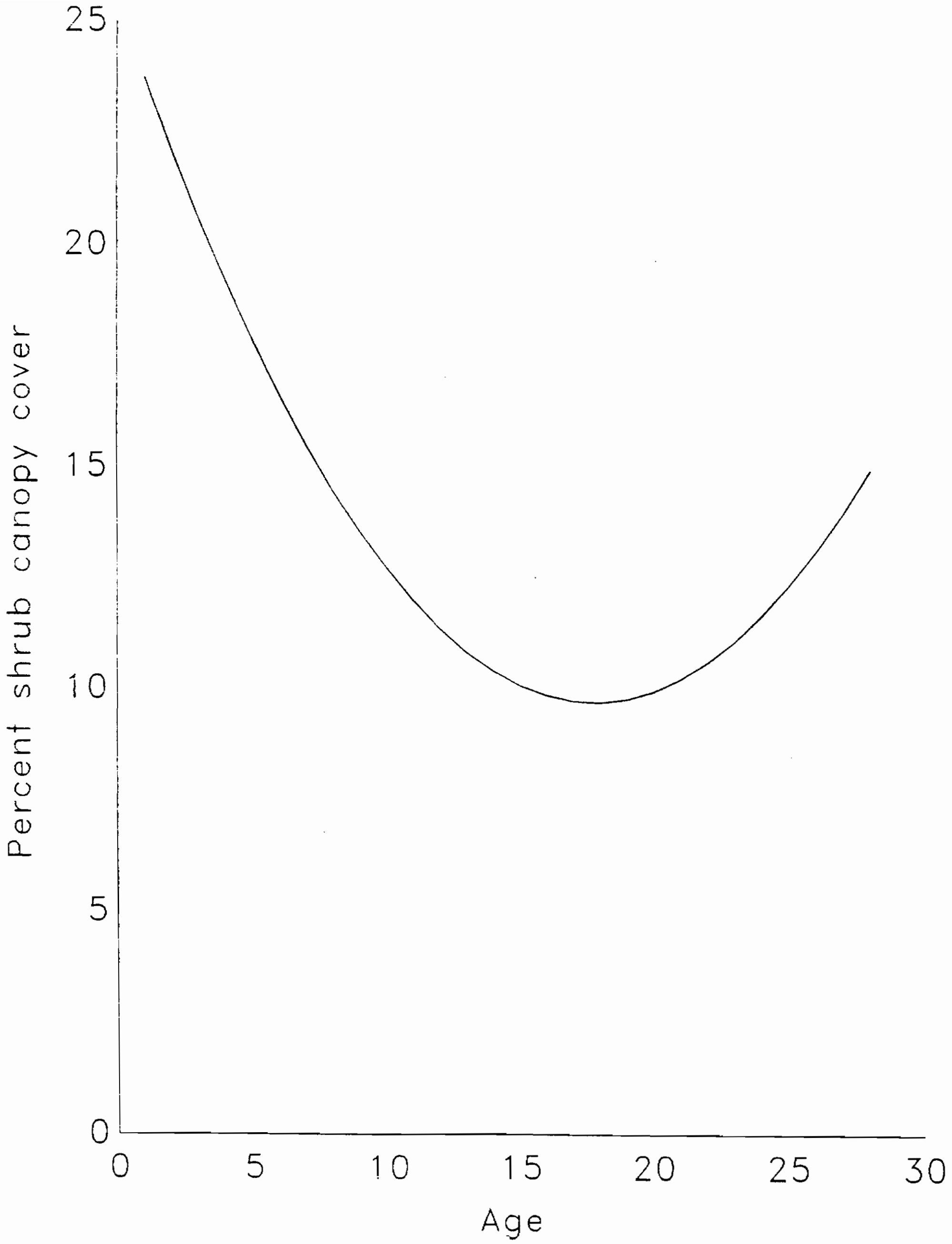

Figure 15. Predicted relationship of percent canopy cover of shrubs to stand age in loblolly-shortleaf pine stands at Quantico Marine Corps Base, Virginia.

Table 21. Linear regression models for predicting percent canopy cover of shrubs (SCC) $\leq$ 1.5m tall from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	*n*	R^2_{adj}	*P*
Hard-mast hardwood	SCC = 17.65 - 0.21 Age + 0.002$(Age)^2$	45	0.02	0.249
Loblolly-shortleaf pine	SCC = 29.24 - 1.98 Age + 0.05$(Age)^2$	30	0.24	0.007
Pine-hardwood	SCC = 16.13 - 18 Age + 0.002$(Age)^2$	28	0.00	0.438
Non-mast hardwood	SCC = 1.79 + 0.35 Age - 0.003$(Age)^2$	16	0.00	0.847
Virginia pine	SCC = -0.08 + 0.70 Age - 0.007$(Age)^2$	24	0.00	0.399

Table 22. Linear regression models for predicting percent canopy cover of shrubs (SCC) $\leq$ 1.5 tall from stand age and shrub height (SH) in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	SCC = 4.31 - 0.07 Age + 0.001(Age)^2 + 20.03 SH	45	0.13	0.029
Loblolly-shortleaf pine	SCC = -7.56 - 1.27 Age + 0.05(Age)^2 + 49.08 SH	30	0.59	0.001
Pine-hardwood	SCC = -5.36 + 0.08 Age - 0.0002(Age)^2 + 31.12 SH	28	0.11	0.116
Non-mast hardwood	SCC = -0.64 + 0.31 Age - 0.002(Age)^2 + 5.00 SH	16	0.00	0.929
Virginia pine	SCC = 2.68 + 0.86 Age - 0.009(Age)^2 - 11.71 SH	24	0.00	0.545

3,27 df, $\underline{P} = 0.0001$), and pine-hardwood ($R^2_{adj} = 0.11$, 3,25 df, $\underline{P} = 0.1155$) habitats, but the relationships were relatively poor (Table 22). Adding canopy cover of trees as a predictor of percent shrub cover had approximately the same effect as adding shrub height in hard-mast hardwood ($R^2_{adj} = 0.16$, 3,42 df, $\underline{P} = 0.020$) and loblolly-shortleaf pine ($R^2_{adj} = 0.33$, 3,27 df, $\underline{P} = 0.005$) habitats (Table 23). However, when tree canopy cover and shrub height were both added as predictors of shrub cover, R^2_{adj} values improved to 0.22, 0.62, and 0.33 ($\underline{P} < 0.008$) for hard-mast hardwood, loblolly-shortleaf pine and pine-hardwood habitats, respectively (Table 24).

Shrub height

Shrub height (SH) was expected to decline in general with stand age. While data plots showed this to be true for the early stages of stand growth (Fig. 16), the relationship fell apart at the older age classes. I used the following model to fit the data:

$$SH = b_o + b_1/AGE$$

R^2_{adj} was low but regressions were significant for loblolly-shortleaf ($R^2_{adj} = 0.09$, 1,29 df, $\underline{P} = 0.0515$), pine-hardwood ($R^2_{adj} = 0.12$, 1,27 df, $\underline{P} = 0.0345$) and Virginia pine ($R^2_{adj} = 0.14$, 1,23 df, $\underline{P} = 0.0345$) habitats (Table 25). There was no relationship between shrub height and stand age in hard-mast hardwood ($R^2_{adj} = 0.01$, 1,44 df, $\underline{P} = 0.2069$) and non-mast hardwood ($R^2_{adj} = 0.00$, 1,15 df, $\underline{P} = 0.7499$) habitats.

Shrub canopy cover accounted for more variation in shrub height when added as a predictor of shrub height in hard-mast hardwoods ($R^2_{adj} = 0.21$, 2,43 df, $\underline{P} = 0.004$) (Table 26).

Table 23. Linear regression models for predicting percent canopy cover of shrubs (SCC) $\leq$ 1.5 tall from stand age and canopy cover of overstory trees (CC) in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	$SCC = -9.43 - 0.39\ Age + 0.003(Age)^2 + 0.35\ CC$	45	0.16	0.020
Loblolly-shortleaf pine	$SCC = 25.21 - 4.07\ Age + 0.89(Age)^2 + 0.34\ CC$	30	0.33	0.005
Pine-hardwood	$SCC = -2.51 + 0.06\ Age - 0.0007(Age)^2 + 0.17\ CC$	28	0.00	0.756
Non-mast hardwood	$SCC = -20.93 + 0.35\ Age - 0.002(Age)^2 + 0.22\ CC$	16	0.00	0.830
Virginia pine	$SCC = 83.86 - 0.76\ Age - 0.008(Age)^2 - 0.58\ CC$	24	0.03	0.282

Table 24. Linear regression models for predicting percent canopy cover of shrubs (SCC) $\leq$ 1.5 tall from stand age, canopy cover of overstory trees (CC), and shrub height (SH) in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	$SCC = -13.48 - 0.26\ Age + 0.002(Age)^2 + 0.26\ CC + 16.42\ SH$	45	0.22	0.009
Loblolly-shortleaf pine	$SCC = -2.70 - 2.89\ AGE + 0.07(Age)^2 + 0.15\ CC + 46.33\ SH$	30	0.62	0.001
Pine-hardwood	$SCC = -25.53 + 0.23\ Age - 0.002(Age)^2 + 0.13\ CC + 35.40\ SH$	28	0.33	0.006
Non-mast hardwood	$SCC = -22.42 + 0.33\ Age - 0.002(Age)^2 + 0.26\ CC - 4.53\ SH$	16	0.00	0.923
Virginia pine	$SCC = 96.26 - 0.80\ Age - 0.009(Age)^2 - 0.57\ CC - 22.84\ SH$	24	0.06	0.245

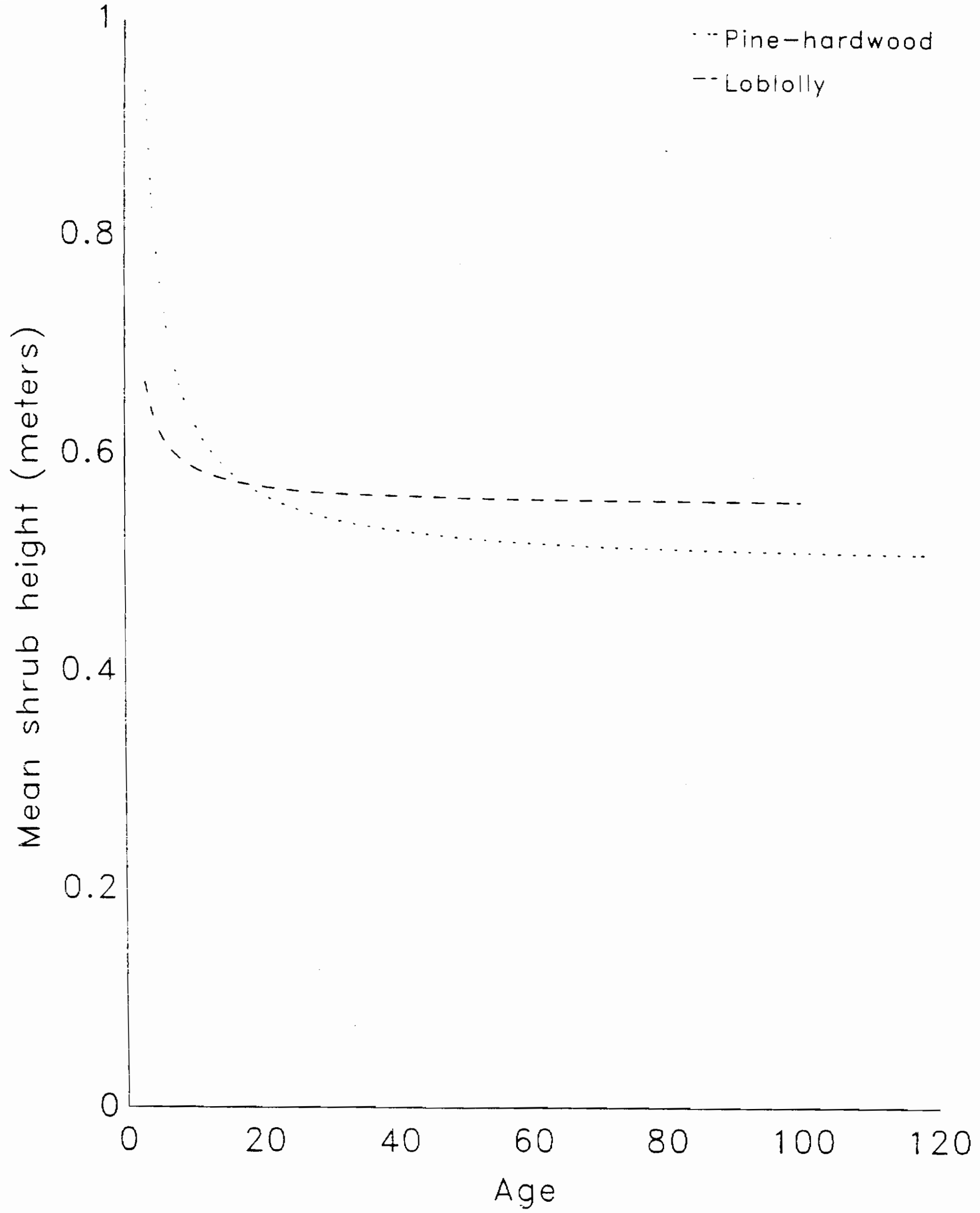

Figure 16. Predicted relationship of shrub height to stand age in 2 habitats at Quantico Marine Corps Base, Virginia.

Table 25. Linear regression models for predicting mean height of shrubs (SH) from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	SH = 0.50 + 0.31/Age	45	0.01	0.207
Loblolly-shortleaf pine	SH = 0.55 - 0.34/Age	30	0.09	0.052
Pine-hardwood	SH = 0.50 + 1.31/Age	28	0.12	0.035
Non-mast hardwood	SH = 0.60 - 1.53/Age	16	0.00	0.750
Virginia pine	SH = 0.67 - 3.88/Age	24	0.14	0.035

Table 26. Linear regression models for predicting mean height of shrubs (SH) from stand age and percent tree canopy cover (CC) in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	SH = -0.21 + 1.96/Age + 0.01 CC	45	0.21	0.004
Loblolly-shortleaf pine	SH = 0.39 + 0.40/Age + 0.003 CC	30	0.10	0.101
Pine-hardwood	SH = 0.34 + 1.62/Age + 0.002 CC	28	0.12	0.070
Non-mast hardwood	SH = -0.84 - 5.56/Age + 0.02 CC	16	0.06	0.259
Virginia pine	SH = 0.61 - 3.03/Age + 0.0004 CC	24	0.04	0.241

When tree canopy cover and shrub cover were added as predictors of shrub height, considerably more of the variation was accounted for in hard-mast hardwood (R^2_{adj} = 0.26, 3,42 df, $\underline{P}$ = 0.002), loblolly-shortleaf pine (R^2_{adj} = 0.62, 3,27 df, $\underline{P}$ = 0.0001) and pine-hardwood (R^2_{adj} = 0.49, 3,25 df, $\underline{P}$ = 0.0001) habitats (Table 27).

Shrub density

Plots of mean shrub density versus stand age in each habitat revealed no discernable patterns. Several models were fitted to the data, but none was significant and R^2_{adj} was nearly zero. Therefore, it was concluded that shrub density could not be predicted with any degree of certainty from these data. An example of the result of trying to model shrub density is provided in table 28.

When canopy cover was added as a predictor of shrub density, some variation was accounted for in loblolly-shortleaf pine (R^2_{adj} = 0.22, 3,24 df, $\underline{P}$ = 0.03). There was no improvement in the models for the other habitats.

Density of snags > 5cm DBH

Density of snags appeared to increase linearly with age based on data plots. The model that best fit the data was a simple linear function (Table 29, Fig. 17). The strongest relationship occurred in hard-mast hardwood (R^2_{adj} = 0.48, 1,19 df, $\underline{P}$ = 0.0003) and Virginia pine (R^2_{adj} = 0.19, 1,11 df, $\underline{P}$ = 0.08) habitats. R^2_{adj} was 0.22 for loblolly-shortleaf pine stands, but the regression was not significant ($\underline{P}$ = 0.16). R^2_{adj} was 0.00 ($\underline{P}$ > 0.34) for pine-hardwood and non-mast hardwood stands (Table 29).

Table 27. Linear regression models for predicting mean height of shrubs (SH) from stand age, percent tree canopy cover (CC), and percent canopy cover of shrubs (SCC) in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	P
Hard-mast hardwood	SH = -0.03 + 1.46/Age + 0.01 CC + 0.01 SCC	45	0.26	0.004
Loblolly-shortleaf pine	SH = 0.35 - 0.06/Age + 0.001 CC + 0.01 SCC	30	0.62	0.001
Pine-hardwood	SH = 0.29 + 1.92/Age + 0.001 CC + 0.01 SCC	28	0.49	0.001
Non-mast hardwood	SH = -0.84 - 5.91/Age + 0.02 CC - 0.001 SCC	16	0.00	0.448
Virginia pine	SH = 0.73 - 3.05/Age + 0.0006 CC - 0.002 SCC	24	0.03	0.309

Table 28. Linear regression models for predicting mean density of shrubs (SD) < 1.5m tall from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	n	R^2_{adj}	*P*
Hard-mast hardwood	$SD = 16319.0 - 66.89\ AGE + 0.53\ AGE^2$	44	0.00	0.844
Loblolly-shortleaf pine	$SD = 15697.0 - 295.09\ AGE + 14.6\ AGE^2$	31	0.00	0.544
Pine-hardwood	$SD = 19346.0 - 112.96\ AGE + 1.25\ AGE^2$	29	0.00	0.886
Non-mast hardwood	$SD = 7648.0 + 217.50\ AGE - 1.96\ AGE^2$	17	0.00	0.912
Virginia pine	$SD = 17405.0 - 10.49\ AGE - 0.54\ AGE^2$	24	0.00	0.640

Table 29. Linear regression models for predicting mean density (SDEN) and dbh (SDBH) of snags from stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	R^2_{adj}	*P*
Hard-mast hardwood (*n*=20)			
Snag density	SDEN = 8.94 + 0.18 AGE	0.48	0.0003
Snag diameter	lnSDBH = 0.77 + 0.72 lnAGE	0.34	0.0034
Loblolly-shortleaf pine (*n*=6)			
Snag density	SDEN = 4.07 + 0.36 AGE	0.22	0.1611
Snag diameter	lnSDBH = -0.64 + 1.28 lnAGE	0.50	0.0500
Pine-hardwood (*n*=10)			
Snag density	SDEN = 11.41 + 0.073936 AGE	0.00	0.0349
Snag diameter	lnSDBH = 1.09 + 0.80 lnAGE	0.34	0.0358
Non-mast hardwood (*n*=6)			
Snag density	SDEN = 33.34 - 0.17 AGE	0.00	0.3974
Snag diameter	lnSDBH = 2.85 + 0.19 lnAGE	0.00	0.5711
Virginia pine (*n*=12)			
Snag density	SDEN = 11.60 + 0.07 AGE	0.19	0.0752
Snag diameter	lnSDBH = -0.67 + 1.22 lnAGE	0.37	0.0169

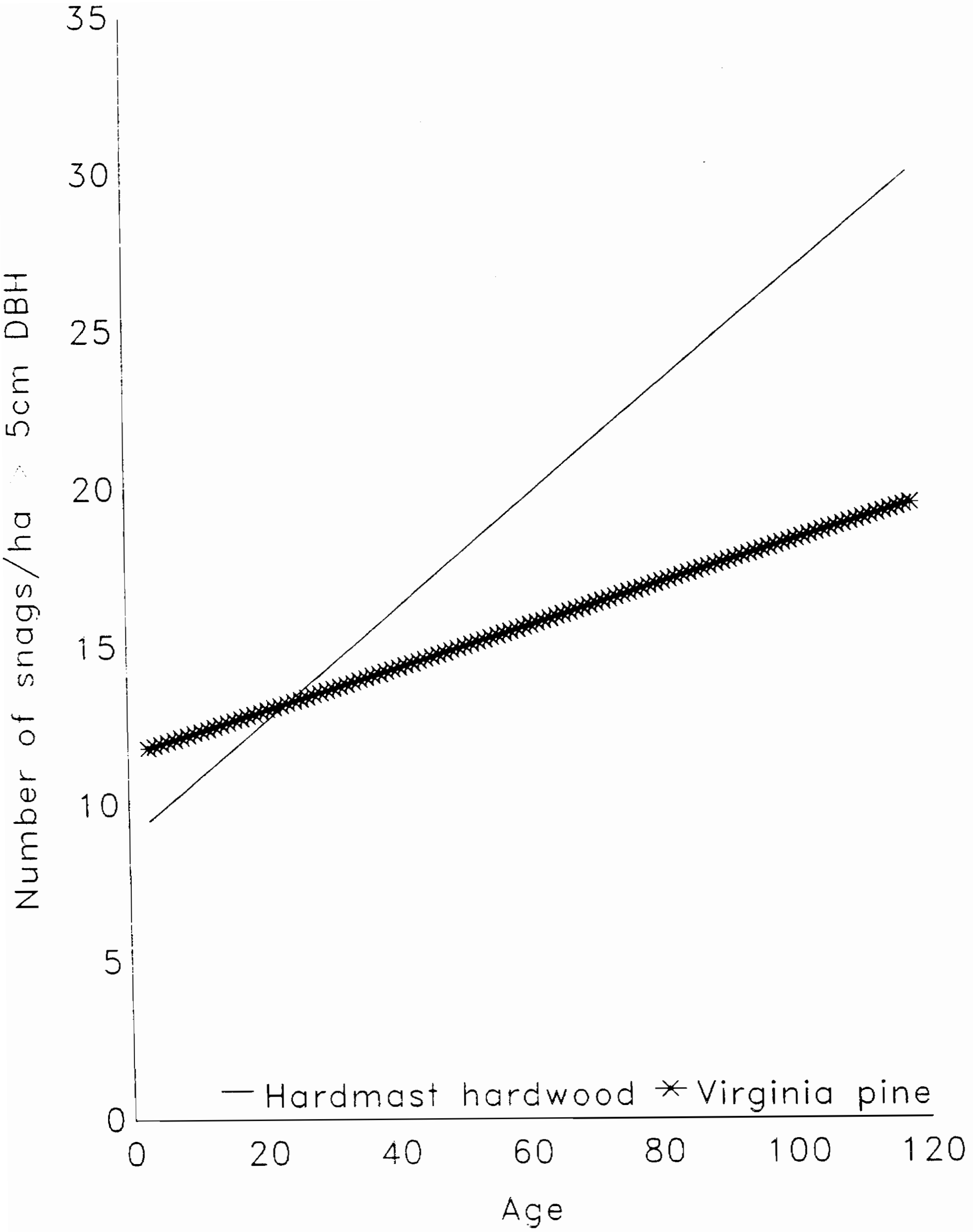

Figure 17. Predicted relationship of snag density to stand age in 2 habitats at Quantico Marine Corps Base, Virginia.

Snag diameter

Mean snag diameter (SDBH) increased with increasing stand age, with greater variation as the stand matured (Fig. 18). The following function was used to fit the data:

$$\ln SDBH = b_o + b_1 * \ln AGE$$

The relationships were poor but regressions were significant for hard-mast hardwood ($R^2_{adj} = 0.34$, 1,19 df, $\underline{P} = 0.0034$), loblolly-shortleaf pine ($R^2_{adj} = 0.50$, 1,5 df, $\underline{P} = 0.05$), pine-hardwood ($R^2_{adj} = 0.34$, 1,9 df, $\underline{P} = 0.0358$), and Virginia pine ($R^2_{adj} = 0.36$, 1,11 df, $\underline{P} = 0.0169$) habitats. There was no relationship between snag diameter and stand age in non-mast hardwood stands ($R^2_{adj} = 0.00$, 1,5 df, $\underline{P} = 0.5711$) (Table 29).

Percent herbaceous ground cover

Percent of ground covered by herbaceous vegetation (PGC) was high in the early seral stages (1-10 years-old), but declined rapidly as stand overstories became dense (Fig. 19). The following model was used to fit the data for percent ground cover:

$$PGC = b_o + b_1/AGE$$

There was a significant relationship between stand age and herbaceous cover in loblolly-pine habitats ($R^2_{adj} = 0.67$, 1,23 df, $\underline{P} = 0.0001$). R^2_{adj} was < 0.05 for all other habitats ($\underline{P} > 0.192$) (Table 30).

Percent bare ground or light litter

Because percentage of bare ground (BGLL) is inversely related to percent ground cover, the percentage of bare ground initially increases

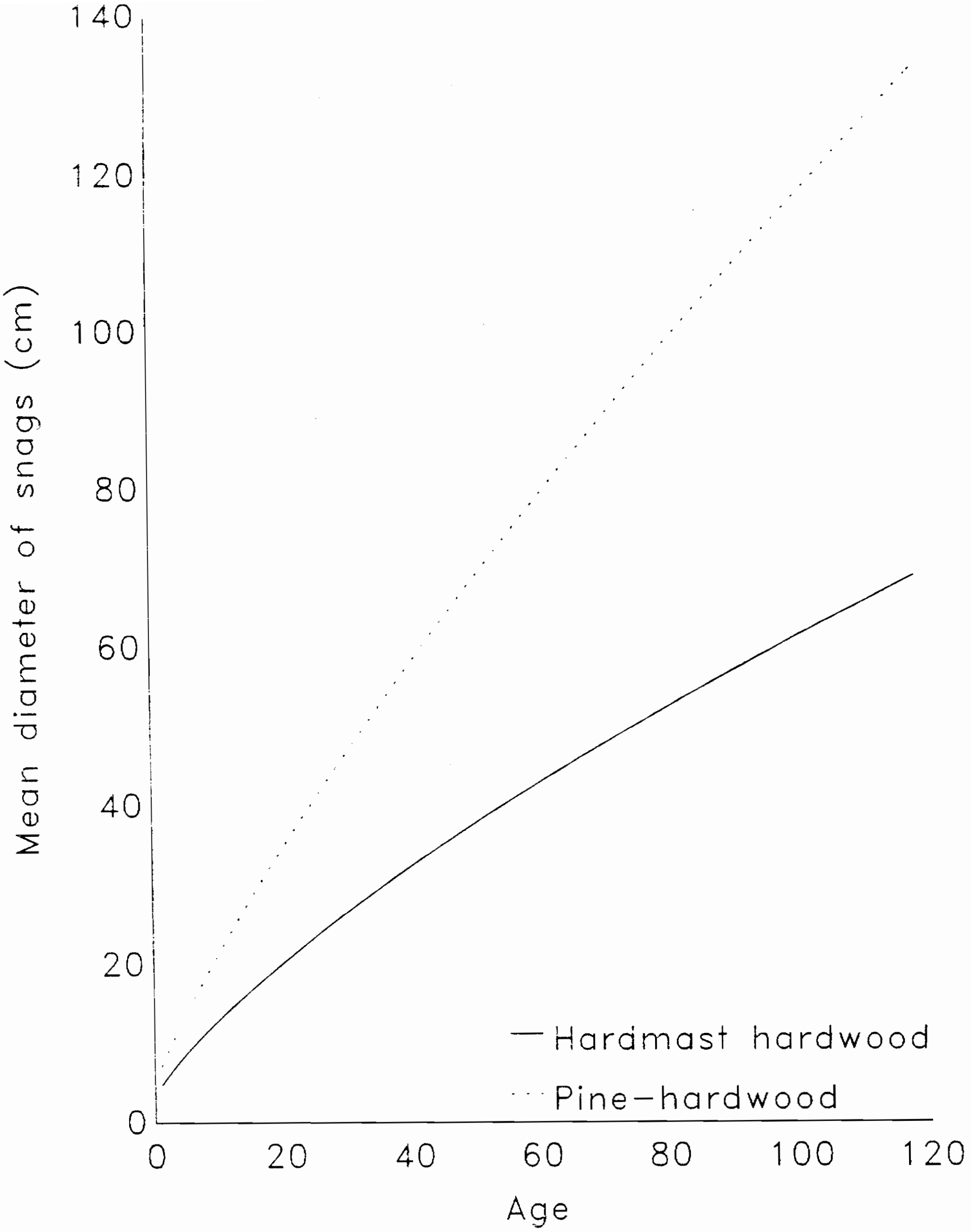

Figure 18. Predicted relationship of snag diameter to stand age in 2 habitats at Quantico Marine Corps Base, Virginia.

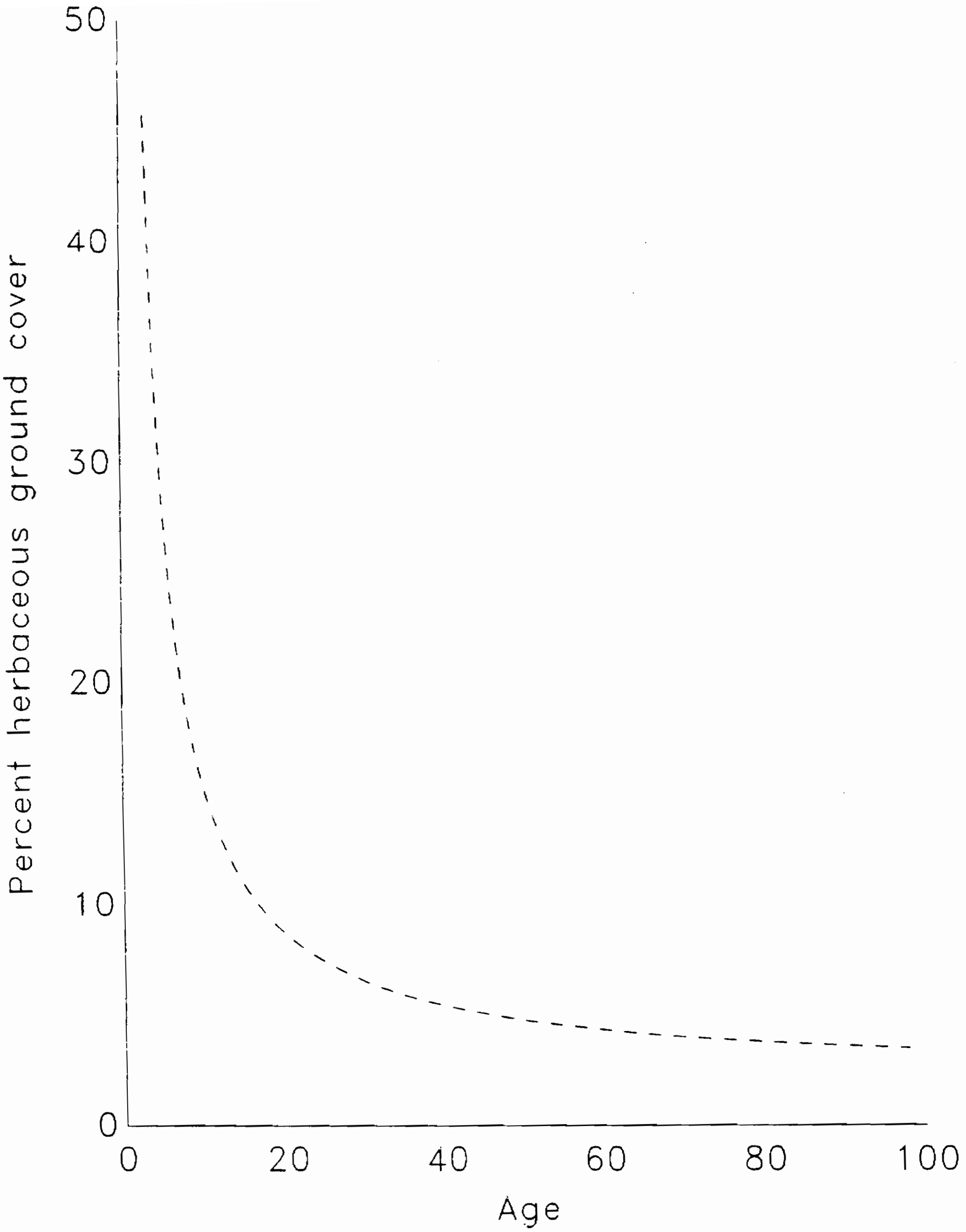

Figure 19. Predicted relationship of percent herbaceous ground cover to stand age in loblolly-shortleaf pine habitats at Quantico Marine Corps Base, Virginia.

Table 30. Linear regression models for predicting percent herbaceous ground cover (HC), bare ground (BGLL), grass cover (GC), and height of herbaceous cover (HH) stand age in 5 habitat types on Quantico Marine Corps Base, Virginia.

Habitat type	Model	R^2_{adj}	P
Hard-mast hardwood (n=27)			
%Herbaceous Cover	HC = 6.45 + 0.06/Age	0.00	0.348
%Bare ground or light litter	BGLL = 91.89 - 0.26 lnAGE	0.00	0.919
%Grass cover	GC = 1.81 + 10.90/Age	0.02	0.206
Height herb cover	HH = 0.07 + 0.42/Age	0.00	0.378
Loblolly-shortleaf pine (n=24)			
%Herbaceous cover	HC = 2.18 + 130.59/Age	0.67	0.001
%Bare ground or light litter	BGLL = 25.72 + 23.64 lnAge	0.67	0.001
%Grass cover	GC = 4.86 + 66.47/Age	0.34	0.001
Height herb cover	HH = 0.08 + 0.33/Age	0.13	0.044
Pine-hardwood (n=17)			
%Herbaceous cover	HC = 5.62 + 67.94/Age	0.05	0.192
%Bare ground or light litter	BGLL = 78.85 + 3.70 lnAge	0.04	0.203
%Grass cover	GC = 2.41 + 42.59/Age	0.01	0.306
Height herb cover	HH = 0.02 + 1.72/Age	0.02	0.264
Non-mast hardwood (n=14)			
%Herbaceous cover	HC = 25.75 + 254.43/Age	0.00	0.602
%Bare ground or light litter	BGLL = 33.96 + 8.79 lnAge	0.00	0.397
%Grass cover	GC = 0.53 + 549.11/Age	0.10	0.127
Height herb cover	HH = 0.07 + 6.63/Age	0.11	0.123

Table 30. (Cont.)

Habitat type	Model	R^2_{adj}	*P*
Virginia Pine (*n*=17)			
%Herbaceous cover	HC = 11.90 + 39.18/Age	0.00	0.912
%Bare ground or light litter	BGLL = 71.49 + 3.86 lnAge	0.00	0.695
%Grass cover	GC = -1.35 + 137.99/Age	0.29	0.013
Height herb cover	HH = 0.05 + 0.32/Age	0.00	0.708

with stand age. I used the following model to fit the data:

$$BGLL = b_o + b_1 * \ln AGE$$

The strength of the relationship was high for loblolly-shortleaf pine habitats ($R^2_{adj} = 0.67$, 1,23 df, $\underline{P} = 0.0001$). There was essentially no relationship between bare ground and stand age in the other habitats (Table 30).

Percent grass cover

Percent grass cover (GC) was closely related to overall herbaceous ground cover and followed the same general pattern with relation to stand age (Fig. 20). I used the following model to fit the data:

$$GC = b_o + b_1/AGE$$

The relationship between percent grass and stand age was best in loblolly-pine stands ($R^2_{adj} = 0.34$, 1,23 df, $\underline{P} = 0.0001$) and Virginia pine ($R^2_{adj} = 0.29$, 1,16 df, $\underline{P} = 0.0130$). R^2_{adj} was < 0.10 for the other habitats and regressions were not significant ($\underline{P} > 0.13$) (Table 30).

Height of herbaceous cover

Height of herbaceous vegetation (HH) also was closely related to percent ground cover and tended to decrease initially with stand growth (Fig. 21). I used the following model to fit the data:

$$HH = bo + bl/AGE$$

The relationship between stand age and height was weak but significant in loblolly-shortleaf pine habitats ($R^2_{adj} = 0.13$, 1,23 df, $\underline{P} = 0.044$). R^2_{adj} was < 0.11 in all other habitats ($\underline{P} > 0.123$) (Table 30).

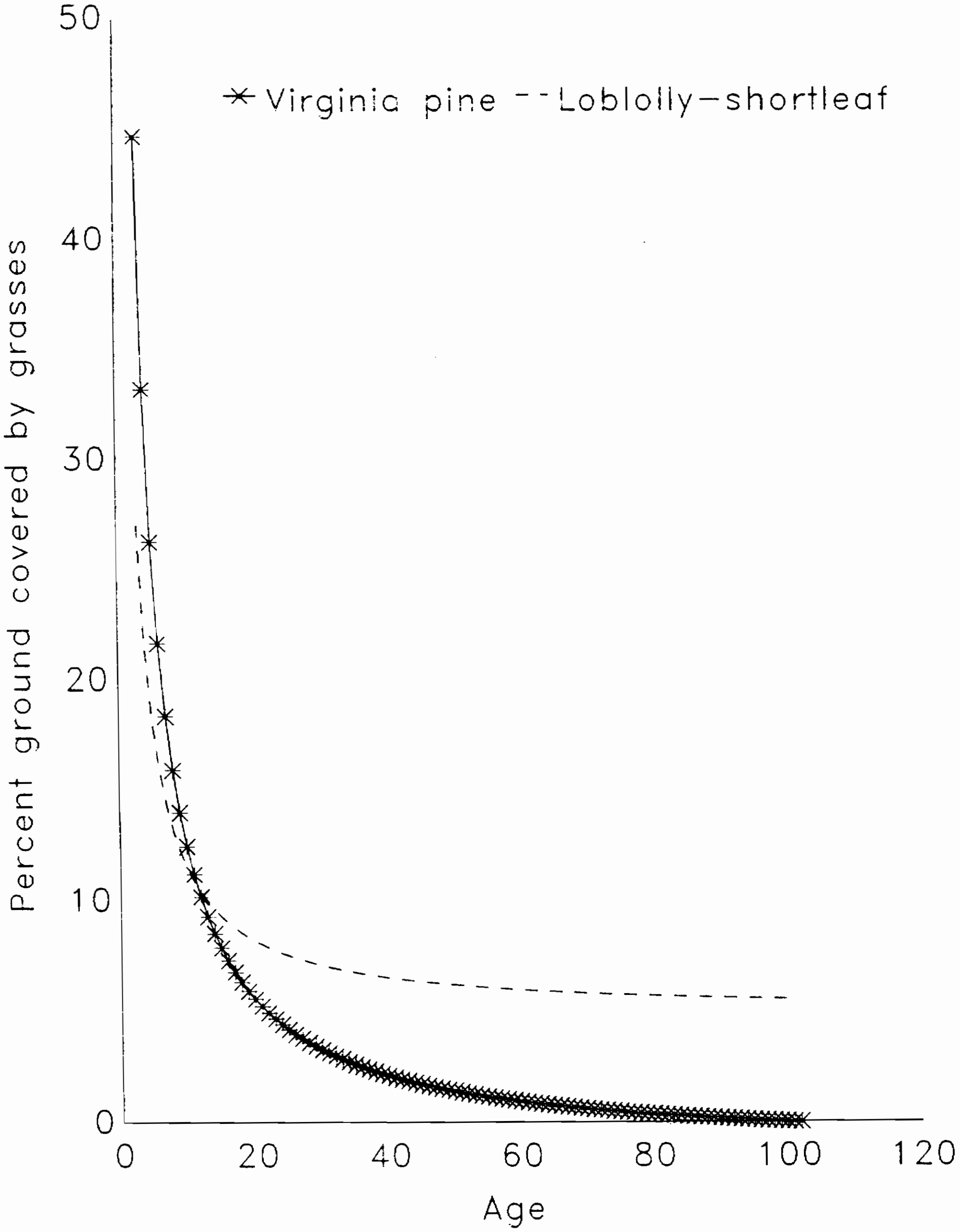

Figure 20. Predicted relationship of percent herbaceous ground cover composed of grass to stand age in loblolly-shortleaf pine and Virginia pine habitats at Quantico Marine Corps Base, Virginia.

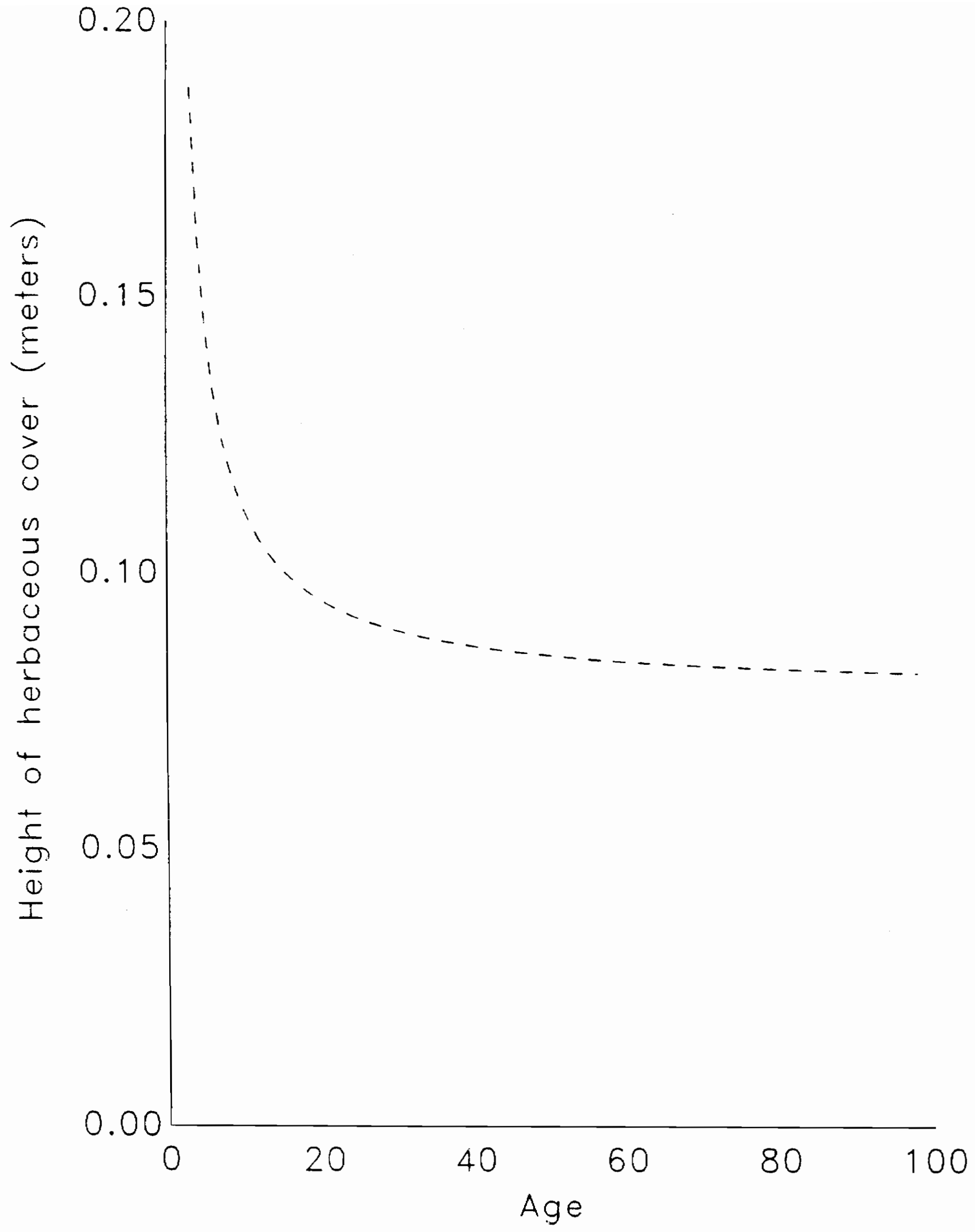

Figure 21. Predicted relationship of height of herbaceous ground cover to stand age in loblolly-shortleaf pine habitats at Quantico Marine Corps Base, Virginia.

DISCUSSION

Basal area

Habitat parameters associated with tree growth and spacing, such as basal area, density and dbh, were relatively predictable based on stand age. R^2_{adj} was > 0.50 for basal area in all but non-mast hardwood and Virginia pine habitats (Table 16). Based on my data and personal observation, diameter and spacing of trees (the main determinants of basal area/ha) in Virginia pine stands tended to vary more among stands of similar age than in other types. This variation also probably contributed to difficulty with predicting tree density and mean dbh. Nonetheless, curves produced by the final models, with the exception of loblolly-shortleaf pine habitats, were very similar and biologically reasonable, showing that basal area increases at a decreasing rate as the stand matures for hard-mast hardwood, pine-hardwood, and non-mast hardwood habitats (Fig. 9)

Tree density

Stand age was not a good indicator of tree density. R^2_{adj} was relatively low on average for density of trees, particularly in hard-mast and non-mast hardwood stands (Table 16). Plots of tree density versus stand age suggest that considerable variation in tree density occurred at the early seral stages (1-20 years). This may have been due initially to site conditions. Stand initiation may be influenced by variation in site conditions, available species, and type of initial disturbance (Oliver and Larson 1990). Therefore, number of saplings exceeding the > 5cm dbh size restriction may vary among stands of the same age (most notably between 6 and 10 years) depending on the conditions, thereby affecting greatly the calculated density of "trees" in young stands. Tree density curves generated by the final models (Fig. 10) suggest a logical relationship between tree density and stand age out to 120 years.

The relationship between stand age and tree density was strongest for loblolly-shortleaf pine habitats ($R^2_{adj} = 0.52$). However, because of apparent differences in stocking densities or planting failures in loblolly-shortleaf pine stands, the relationship between stand age and tree density was the opposite of the relationship in the other habitats, an unrealistic occurrance (R. Oderwald - Personal communication). Therefore, this model was considered to be useless.

DBH

There was a poor relationship between stand age and dbh within pine habitats compared to hardwood or pine-hardwood habitats (Table 16). Plots of the data revealed several outliers in the early seral stage loblolly-shortleaf pine habitats creating the appearance of a poor model fit when the relationship was probably much tighter. The outliers were all unusually high estimates and they may have been caused by unusually good site conditions (Oliver and Larson 1990). Mean diameter clearly increased with age in Virginia pine habitats, but there was considerable variation, especially at the middle seral stages. DBH curves generated by the final models (Fig. 11) were consistent among habitat types and suggest a realistic relationship between dbh and stand age.

Tree height

As expected, a strong relationship existed between stand age and height of the overstory (Table 17). Little predictive ability was gained by including mean dbh in the height model (Table 18). This may be a result of the effect of understory trees on dbh. Increasing numbers of understory trees due to understory reinitiation in maturing stands may reduce the average dbh as stands reach maturity, even though height is increasing, so dbh may not explain as much of the variation in height of the overstory as might be expected.

Tree height did not extrapolate well beyond stand age 30 for loblolly-shortleaf pine habitats (Fig. 12). The model suggests unrealistically that height growth slows and approaches a maximum at approximately 12 meters. Loblolly-shortleaf would be expected to easily reach heights in excess of 30 meters (Wernert 1982). Therefore, the height model should not be used to predict height of loblolly-shortleaf habitats beyond 30 years. Curves appeared to be realistic for the other habitats where the model was significant.

Density of woody stems

Measurement of woody stem density gives a general indication of how "dense" the understory cover is. The density of woody stems is related to the amount of light that reaches the forest floor (Oliver and Larson 1990), therefore, stem density tended to decrease with increasing stand age (Fig. 13). The relationship between stem density and age was poor in loblolly-shortleaf pine (Table 19) habitats, again probably due to variation in the early seral stages. Deliberate spacing of trees and burning to prevent competition of other species with the pines kept stem densities low in the early seral stages until understory growth of sweetgum and hercules' club temporarily increased stem densities. Plots of stem density with age in Virginia pine and non-mast hardwoods showed no pattern, and R^2_{adj} values were correspondingly low (Table 19).

Curves showing stem density response to succession (Fig. 13) suggest a realistic pattern of stems decreasing with increasing stand age. The exception is loblolly-shortleaf pine, which increased until about 20 years and then stayed constant, an unrealistic relationship and another example of where the model should not be used to predict beyond 30 years.

Percent canopy cover

Percent canopy cover of the overstory generally increased rapidly with stand age to about 100% between 15 and 30 years, then leveled off between 80 and 100%. This relationship was strong ($R^2_{adj} = 0.86$) in loblolly pine habitats where evenly spaced trees and little mortality made the degree of canopy closure predictable. The canopy cover curve for loblolly-shortleaf pine extrapolated out to 100 years (Fig. 14) shows canopy cover declining slightly as the stand matures, a biologically reasonable prediction. As trees grow taller and limbs longer, overlapping branches rub and break against each other until the canopies no longer overlap. Greater swaying caused by height growth causes more gaps in the canopy, leading to overall diminished canopy cover as a stand matures (Oliver and Larson 1990). Canopy cover was not as closely related to age in the other habitats, though regressions were significant ($\underline{P} < 0.1$) for all but non-mast hardwood habitats (Table 20). Defoliation and mortality of overstory trees caused by gypsy moths appeared to be a significant source of variation in canopy cover in hard-mast hardwood stands. The model predicts a realistic trend in canopy cover with increasing stand age out to 120 years (Fig. 14). Although the models for pine-hardwood and Virginia pine habitats were significant, the curves derived from the models did not reflect low canopy cover at the early stages as would normally be the case and therefore may be somewhat unrealistic. Mortality of large trees and wind-throw appeared to contribute to variation in the other habitats, particularly in the older seral stages.

Canopy cover of shrubs ≤ 1.5 meters tall

Modeling shrub characteristics with respect to stand age was difficult because of 2 major sources of variation: disturbance (causing changes in the light regime) and site conditions. Even minor disturbances in the forest overstory, especially in mature stands, release growing space that can allow shrubs to grow vigorously where they may not have otherwise (Oliver and Larson 1990, Miles 1979). The spatial distribution and species composition or forest floor vegetation also varies with soils and microtopography, rooting media, competition, location of seeds, and overstory conditions (Oliver and Larson 1990). Percent of shrub cover appeared to be related to stand age only in the early seral stages. Shrub cover was high in clear-cut stands up to about 7 years, then shrub cover declined, presumably as the canopy decreased the amount of light reaching the forest floor. After about 30 years, shrub cover appeared to vary greatly with site conditions and disturbance. For example, Vaccinium was nearly a solid layer or completely absent in stands of the same age depending on the site. Natural disturbances in the overstory because of wind, mortality, and gypsy moth damage also appeared to cause considerable variation in shrub cover among stands of the same age, making prediction of shrub cover from stand age difficult. The best relationship between shrub cover and stand age occurred in loblolly-shortleaf pine habitats (Table 21). Less variation in shrub cover occurred in these habitats because of the solid canopies and lack of mortality, and because no stands older than 28 years were sampled (most variation in shrub canopy occurred in stands older than 30 years in the other habitat types). The model predicted a realistic relationship between shrub cover and stand age in loblolly-shortleaf pine at least up to 30 years (Fig. 15).

When shrub height was added as a predictor of shrub cover, there was a significant relationship for hard-mast hardwood and a stronger relationship in loblolly-shortleaf pine habitats (Table 22). The amount of linear shrub coverage appears to be somewhat related to height of shrubs. Shrub growth may be closely related to amount of light reaching the forest floor (Oliver and Larson 1990). Correspondingly, tree canopy cover accounted for more variation in shrub cover in hard-mast hardwood and loblolly-shortleaf pine habitats when added to the model (Table 23), but no more so than shrub height. Adding both tree canopy cover and shrub canopy cover, however, accounted for considerably more variation in shrub cover than with either variable alone in hard-mast hardwood (R^2_{adj} = 0.22, 4,41 df, $\underline{P}$ = 0.009), loblolly-shortleaf pine (R^2_{adj} = 0.62, 4,26 df, $\underline{P}$ = 0.0001), and pine-hardwood habitats (R^2_{adj} = 0.33, 4, 24 df, $\underline{P}$ = 0.006) (Table 24).

Shrub height

There was very little relationship between shrub height and stand age, although regressions were significant ($P \leq 0.1$) for loblolly-shortleaf pine, pine-hardwood and Virginia pine (Table 25). Plots of the data suggested a slight tendency for shrub height to decrease with age, especially in the earlier seral stages. Shrubs will invade maturing stands where canopy cover is high and light is low, but may not grow very much (Oliver and Larson 1990). The same sources of variation creating large differences in shrub cover in stands of the same age probably affect shrub height, as well. Shrub height models predicted logical relationships between shrub height and stand age in pine-hardwood and loblolly-shortleaf pine habitats (Fig. 16).

Tree canopy cover accounted for additional variation when added to the shrub height model (Table 26). Adding both shrub cover and tree canopy cover improved the model further (Table 27).

Shrub density

Variation in shrub density within the same cover type and age class was affected by the same environmental variables as were discussed above for shrub canopy cover and shrub height. Plots of the data show no visible pattern in shrub density relative to stand age (Table 28). Very little additional variation was accounted for by adding percent canopy cover to the shrub density model.

Snag density and diameter

Density of snags was weakly related to stand age in hard-mast hardwood and Virginia pine habitats (Table 29). There was a clear tendency for snag density to increase with stand age, but variation was high and sample sizes small. One would expect there to be a strong relationship between tree mortality and stand age, but site conditions and natural disturbances, especially defoliation by gypsy moth and disease, cause mortality independent of age. Snag density models show density of snags increasing linearly with stand age (Fig. 17), but it is more likely that snag density would level off or even decrease before 120 years.

Snag diameter was generally more strongly related to stand age than snag density, although R^2_{adj} was still low (Table 29). The exception being hard-mast hardwood, where snag density had a slightly better relationship with age. Curves showing the response of snag diameter to increasing stand age (Fig. 18) indicate snag diameter increasing to 130 cm on average at year 120 in pine-hardwood habitats, an unlikely scenario given predictions of average live tree dbh in the same stands.

Herbaceous vegetation

Characteristics of herbaceous vegetation generally did not model well (Table 31). Herbaceous vegetation was typically very dense at the earliest seral stages (1-7 years), then declined rapidly, presumably as shade increased (Oliver and Larson 1990). As stands matured, presence of herbaceous vegetation was influenced by disturbances that created small openings in forest canopies and therefore was fairly unpredictable from stand age. An exception was loblolly-shortleaf pine habitats, where there was a relatively strong relationship ($R^2_{adj} = 0.67$) between percent herbaceous ground cover and percent bare ground with stand age. Percent grass cover and height of herbaceous vegetation in loblolly-shortleaf pine habitats also were significantly related to stand age ($\underline{P} < 0.05$), but R^2_{adj} was < 0.35. The strength of these relationships is probably again due to systematic planting leading to low mortality and consistent canopy cover that occurred in loblolly-shortleaf pine stands. Curves showing the relationship of herbaceous cover to stand age indicated by the models appeared realistic for loblolly-shortleaf pine habitats (Fig. 19).

Models for percent grass cover were significant for loblolly-shortleaf and Virginia pine habitats and curves were realistic (Fig. 20). The model for height of herbaceous cover also predicted a realistic relationship with increasing stand age (Fig. 21).

Conclusions

Windfall, fire, drought, insect infestation and senescence keep forests in a constant state of flux (Miles 1979), thereby causing variation that makes it difficult to model specific vegetation characteristics at particular time and space. Habitat parameters related to trees provided the best models. Dominant overstory and understory trees are generally slow growing and less affected than shrubs and herbaceous growth by disturbance that causes changes in the light regime (Oliver and Larson 1990). Modeling shrub and herbaceous vegetation characteristics with respect to stand age alone is difficult mainly because of the sensitivity of these variables to changes in light intensity brought about by disturbance in the forest overstory and site conditions. Additionally, herbaceous and woody plants naturally exhibit more varied growth patterns than in woody tree and shrub assemblages (Oliver and Larson 1990).

Although R^2_{adj} was low for many of the models, curves generated by the models suggest that reasonable predictions can be made, perhaps even beyond 120 years, with many of the models. In general, the best models for each variable were developed for loblolly-shortleaf pine habitats. Management for loblolly-shortleaf pine at Quantico in the form of systematic planting and burning of the undergrowth has apparently led to homogeneous pine stands and predictable characteristics with respect to even non-tree habitat parameters. Unfortunately, prediction in these habitats cannot be made with confidence with the models presented here beyond the age of 30 years since no pine stands older than that occur on Quantico.

The addition of related characteristics to models accounted for a greater amount of variation than stand age alone in some instances. The drawback to adding these variables is the compounding of errors that may occur. In a real-life scenario, the additional variables would be predicted with error (considerable in some cases) and then used to predict another value with its own associated error. Thus, no accuracy in prediction may actually be gained even though the model with more predictors originally had a better fit.

The results of this study suggest that understory habitat parameters can be predicted, especially with a more intense modeling effort. If stand specific disturbances and variation, such as overstory defoliation by gypsy moths, mortality, and site conditions, can be accounted for and included in the modeling process, some of the non-tree habitat variables that we were unable to model could be modeled with better results. Larger sample sizes would probably improve the models, as well.

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Appendix A. Mean basal area, tree density and diameter (DBH) by age and type for forest stands sampled on Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Basal Area	Se	Tree Density	SE	DBH	Se
40	30	7	HMHD	1.7	1.51	235	180.38	3.4	2.09
23	34	9	HMHD	11.4	4.61	975	178.57	9.9	1.87
35	8	9	HMHD	9.1	1.37	820	106.71	10.3	0.87
23	17	12	HMHD	12.7	1.03	1395	73.06	10.0	0.44
2	43	17	HMHD	3.4	0.74	230	24.24	12.6	1.84
7	5	17	HMHD	16.4	1.19	1510	120.05	10.8	0.28
30	21	22	HMHD	21.1	1.47	1805	101.16	11.3	0.21
39	19	28	HMHD	24.8	1.90	1368	104.88	13.7	0.40
10	13	31	HMHD	19.8	3.29	1203	184.41	12.9	0.83
39	12	31	HMHD	24.7	0.39	1080	82.69	15.5	0.46
39	16	31	HMHD	27.8	3.07	1493	100.97	13.6	0.30
39	21	31	HMHD	18.3	1.70	855	103.80	14.9	0.85
40	25	32	HMHD	15.6	2.14	895	116.30	13.0	0.63
10	50	39	HMHD	21.5	2.00	533	35.60	20.1	1.09
14	2	39	HMHD	23.9	1.56	1048	82.03	15.1	0.61
14	13	40	HMHD	26.6	2.11	838	74.65	17.8	0.88
35	23	41	HMHD	28.8	2.02	1023	92.30	17.9	1.05
14	45	43	HMHD	26.4	2.47	1072	76.88	14.9	0.66
13	2	46	HMHD	28.5	1.76	1035	93.18	15.9	0.87
48	19	52	HMHD	23.3	1.89	915	137.07	16.3	1.60
3	9	66	HMHD	34.9	1.68	790	53.52	19.1	0.74
33	7	70	HMHD	32.9	2.60	798	62.63	18.1	1.08
43	17	71	HMHD	26.5	3.06	698	72.60	18.3	0.81
16	4	78	HMHD	32.7	4.71	520	121.30	26.3	3.76
34	13	80	HMHD	29.0	2.70	788	58.36	17.5	1.02
35	16	81	HMHD	40.5	3.22	600	36.32	24.9	0.78
49	1	85	HMHD	30.1	1.82	595	26.03	22.4	0.94
4	30	86	HMHD	35.2	4.57	698	120.44	21.8	1.29
25	7	86	HMHD	30.5	1.83	438	34.21	26.4	1.88
34	5	86	HMHD	30.3	2.40	583	40.15	20.6	1.44
49	16	86	HMHD	32.4	3.53	403	29.92	26.4	1.03
26	18	101	HMHD	33.8	3.35	498	45.71	26.0	1.32
47	17	102	HMHD	26.5	2.08	533	35.76	20.8	1.03
4	5	106	HMHD	35.6	4.82	613	68.24	23.1	1.26
3	8	111	HMHD	35.8	2.59	533	95.46	26.0	1.96
45	13	112	HMHD	31.2	2.07	485	35.00	24.6	1.07
13	12	3	LSLP	0.0	0.05	25	0.00	1.7	1.67
7	18	4	LSLP	1.0	0.46	106	32.87	9.6	1.29
7	23	4	LSLP	0.3	0.22	100	46.10	3.6	1.51
7	34	4	LSLP	0.2	0.06	53	16.44	4.8	1.44
22	23	8	LSLP	0.7	0.30	195	70.00	5.6	1.52
8	45	9	LSLP	8.0	1.09	1355	113.94	8.2	0.59
18	14	17	LSLP	30.8	2.59	2165	164.96	12.5	0.26

Appendix A. (Cont.)

Comp	Stand	Age	Type	Basal Area	Se	Tree Density	Se	DBH	Se
30	8	25	LSLP	35.0	1.53	1788	113.73	14.7	0.32
39	15	26	LSLP	43.7	2.15	1333	86.93	19.5	0.77
38	7	28	LSLP	24.2	1.22	1873	103.38	12.0	0.38
43	1	28	LSLP	38.3	3.96	1010	100.81	21.1	0.49
2	3	25	NMHD	36.3	2.47	858	105.28	21.6	1.56
45	2	40	NMHD	21.0	2.95	618	64.45	18.2	1.10
41	2	41	NMHD	28.1	2.68	685	133.37	21.7	1.81
49	27	41	NMHD	21.6	5.14	290	45.14	26.4	3.68
4	37	46	NMHD	31.9	1.82	890	67.82	17.6	0.76
10	2	47	NMHD	35.2	3.41	660	44.44	20.8	1.04
44	1	53	NMHD	31.5	2.68	673	72.12	21.1	0.81
14	34	54	NMHD	39.6	4.60	640	130.50	26.1	2.17
2	4	55	NMHD	26.8	3.78	348	61.40	28.3	1.65
45	11	58	NMHD	29.1	4.43	550	97.18	24.3	2.27
49	2	62	NMHD	22.5	5.50	510	107.99	23.2	6.65
34	14	64	NMHD	43.9	2.93	1570	56.68	15.9	0.66
39	28	65	NMHD	26.2	2.12	1000	62.80	14.9	0.41
38	6	66	NMHD	23.4	3.13	713	80.56	17.0	1.37
1	1	78	NMHD	49.8	2.88	800	77.82	25.4	1.58
3	21	82	NMHD	49.0	3.85	955	144.35	20.2	1.56
2	17	86	NMHD	54.0	6.08	850	80.23	24.9	1.54
16	18	9	PHWD	10.5	1.72	2595	294.79	6.6	0.38
43	14	14	PHWD	8.5	0.62	1456	91.27	8.1	0.21
16	8	21	PHWD	20.0	1.23	1800	106.65	11.1	0.21
10	9	23	PHWD	18.8	2.36	1465	184.29	11.5	0.66
8	52	25	PHWD	24.5	1.14	2255	206.15	11.1	0.48
45	15	28	PHWD	24.4	1.80	1498	95.78	13.4	0.71
48	20	28	PHWD	26.6	1.63	1513	87.58	13.7	0.42
40	20	29	PHWD	26.7	2.43	1335	141.09	14.6	0.54
39	20	31	PHWD	14.4	1.36	633	83.92	16.2	0.68
40	17	33	PHWD	26.8	1.61	1458	80.88	13.7	0.45
45	25	34	PHWD	22.1	2.88	1108	87.88	14.2	0.68
42	32	38	PHWD	26.9	2.26	1468	128.13	14.1	0.50
2	42	41	PHWD	33.6	4.08	930	131.12	18.5	0.89
48	24	46	PHWD	29.7	3.25	1325	133.93	15.1	0.79
47	10	50	PHWD	27.3	2.09	540	70.53	21.6	2.42
39	30	55	PHWD	20.5	1.79	1145	224.00	16.0	2.41
36	13	61	PHWD	30.0	1.03	800	51.91	19.0	0.61
12	18	66	PHWD	29.4	2.43	755	50.66	17.7	1.09
20	24	66	PHWD	33.6	4.40	1240	116.50	15.1	0.79
35	17	66	PHWD	28.4	2.01	768	98.11	19.0	1.52
12	13	81	PHWD	31.5	2.86	693	46.11	20.5	1.04
2	25	86	PHWD	31.0	2.27	975	79.14	16.1	0.63
20	5	87	PHWD	26.9	2.53	1080	96.23	14.5	0.51
45	16	28	VAPI	28.3	2.48	1433	150.56	15.3	0.74

Appendix A. (Cont.)

Comp	Stand	Age	Type	Basal Area	Se	Tree Density	Se	DBH	Se
39	2	29	VAPI	30.1	1.54	1738	129.06	13.6	0.24
32	9	30	VAPI	30.5	2.00	966	58.62	18.5	0.88
41	16	30	VAPI	27.6	2.21	935	161.36	18.8	1.06
39	10	31	VAPI	32.3	1.09	2218	171.39	12.7	0.49
12	6	38	VAPI	33.6	1.77	1000	56.52	19.3	0.62
14	17	41	VAPI	33.7	1.29	1115	62.16	17.8	0.34
32	4	46	VAPI	32.0	1.63	1170	71.57	16.7	0.55
10	28	47	VAPI	28.4	1.98	920	27.84	17.4	0.78
33	8	48	VAPI	27.4	1.36	845	67.27	18.5	0.67
45	4	50	VAPI	29.8	4.80	900	117.70	17.0	0.75
44	3	52	VAPI	30.2	1.55	1193	73.41	16.3	0.44
7	21	56	VAPI	36.3	1.51	820	33.91	22.1	0.66
18	5	56	VAPI	38.3	1.62	1500	117.79	16.6	0.50
12	17	60	VAPI	29.5	1.63	800	43.46	19.8	0.73
33	17	63	VAPI	38.4	1.89	995	99.18	20.1	0.77
47	7	63	VAPI	26.2	2.44	655	77.08	21.6	1.19
25	12	70	VAPI	34.9	2.49	890	77.70	20.1	0.95
8	22	72	VAPI	30.8	2.00	1010	55.05	18.5	0.68
31	6	72	VAPI	33.6	2.68	800	89.83	21.7	1.15
33	28	72	VAPI	34.3	4.26	1215	108.22	15.7	0.70
34	6	81	VAPI	40.3	2.01	1250	86.68	17.5	0.59

Appendix B. Mean height of dominant overstory trees by compartment (comp), stand, age and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Height	Se
24	22	7	HMHD	5.3	0.34
23	34	9	HMHD	6.4	0.60
35	8	9	HMHD	5.2	0.32
3	25	10	HMHD	4.5	0.25
23	17	12	HMHD	9.3	0.50
27	7	14	HMHD	5.9	0.50
2	18	17	HMHD	14.6	1.80
2	43	17	HMHD	6.9	0.67
7	5	17	HMHD	8.5	0.87
45	7	20	HMHD	7.4	0.46
30	10	21	HMHD	9.9	0.53
10	13	31	HMHD	15.2	1.50
39	16	31	HMHD	13.4	0.45
39	21	31	HMHD	13.4	0.57
40	25	32	HMHD	17.2	0.72
10	50	38	HMHD	18.7	1.71
14	2	39	HMHD	19.7	0.69
50	10	39	HMHD	17.8	1.00
14	13	40	HMHD	25.3	0.94
23	35	41	HMHD	21.0	0.82
14	45	43	HMHD	22.7	1.44
13	2	46	HMHD	25.1	1.28
3	9	66	HMHD	26.6	0.53
33	7	70	HMHD	26.5	1.00
43	17	71	HMHD	23.3	1.00
16	4	78	HMHD	16.5	0.88
34	13	80	HMHD	24.6	1.86
35	16	81	HMHD	28.9	0.91
49	1	85	HMHD	28.0	0.75
4	30	86	HMHD	27.6	0.94
25	7	86	HMHD	17.4	0.31
34	5	86	HMHD	26.8	1.31
49	16	86	HMHD	31.3	0.66
26	18	101	HMHD	28.7	0.83
47	17	102	HMHD	17.3	0.44
4	5	106	HMHD	23.0	1.09
3	8	111	HMHD	28.4	1.01
45	13	112	HMHD	29.4	0.61
9	18	2	LSLP	0.0	0.00
12	42	2	LSLP	0.0	0.00
12	43	3	LSLP	1.5	0.11
13	12	3	LSLP	2.0	0.09
7	18	4	LSLP	3.2	0.30
7	34	4	LSLP	2.9	0.14

Appendix B. (Cont.)

Comp	Stand	Age	Type	Height	Se
25	17	7	LSLP	4.3	0.26
22	23	8	LSLP	3.8	0.34
25	5	8	LSLP	3.8	0.44
8	45	9	LSLP	6.0	0.61
8	46	9	LSLP	6.8	0.49
9	4	9	LSLP	5.5	0.22
9	24	10	LSLP	5.4	0.37
10	34	10	LSLP	5.6	0.16
39	7	10	LSLP	5.4	0.34
47	16	10	LSLP	4.7	0.15
47	19	14	LSLP	5.4	0.63
18	14	17	LSLP	11.5	0.60
30	4	17	LSLP	15.1	0.39
12	4	21	LSLP	12.4	0.47
32	27	21	LSLP	16.2	0.85
30	8	25	LSLP	16.6	0.51
39	15	26	LSLP	22.1	1.01
38	7	28	LSLP	11.4	0.59
43	1	28	LSLP	13.6	0.77
2	3	25	NMHD	22.4	1.34
45	2	40	NMHD	14.5	0.29
41	2	41	NMHD	19.1	0.92
49	27	41	NMHD	23.6	3.11
4	37	46	NMHD	22.7	1.00
10	2	47	NMHD	23.6	1.07
44	1	53	NMHD	30.6	0.52
14	34	54	NMHD	25.8	1.33
2	4	55	NMHD	27.7	0.56
45	11	58	NMHD	26.6	2.39
49	2	62	NMHD	25.7	1.43
34	14	64	NMHD	24.1	0.90
39	28	65	NMHD	21.5	1.05
38	6	66	NMHD	20.8	0.71
1	1	78	NMHD	23.0	0.35
3	21	82	NMHD	18.4	0.06
2	17	86	NMHD	30.3	0.15
25	2	7	PHWD	3.6	0.29
10	48	8	PHWD	4.6	0.21
16	18	9	PHWD	6.1	0.50
33	4	10	PHWD	8.1	1.10
36	30	10	PHWD	4.5	0.48
43	14	14	PHWD	6.6	0.56
16	8	21	PHWD	10.3	0.46
10	9	23	PHWD	12.5	0.90
8	52	25	PHWD	11.7	0.50
40	20	29	PHWD	18.7	1.53

Appendix B. (Cont.)

Comp	Stand	Age	Type	Height	Se
39	20	31	PHWD	13.4	1.07
40	17	33	PHWD	15.8	0.77
45	25	34	PHWD	11.9	0.65
42	32	38	PHWD	19.2	0.98
2	42	41	PHWD	23.7	1.35
48	24	46	PHWD	13.8	0.39
39	30	56	PHWD	16.5	0.59
14	36	60	PHWD	23.7	1.57
36	13	61	PHWD	22.1	0.37
12	18	65	PHWD	28.3	1.35
20	24	66	PHWD	24.6	1.24
35	17	66	PHWD	27.7	1.33
12	13	81	PHWD	27.3	1.27
2	25	86	PHWD	24.1	1.12
20	5	87	PHWD	26.1	1.48
21	20	87	PHWD	25.7	2.01
8	18	23	VAPI	13.1	0.48
10	12	24	VAPI	14.3	0.67
45	16	28	VAPI	16.0	0.72
39	2	29	VAPI	16.8	0.59
32	9	30	VAPI	18.7	0.38
39	10	30	VAPI	15.7	0.92
41	16	30	VAPI	12.4	0.38
12	6	38	VAPI	20.2	0.76
14	17	41	VAPI	19.9	0.29
32	4	46	VAPI	21.9	0.69
33	8	48	VAPI	17.3	0.64
45	4	50	VAPI	15.8	1.09
18	5	56	VAPI	21.1	0.76
12	17	60	VAPI	16.2	1.34
8	2	62	VAPI	20.3	0.70
33	17	63	VAPI	25.1	0.57
47	7	63	VAPI	26.2	1.07
25	12	70	VAPI	16.4	0.76
8	22	72	VAPI	20.8	1.24
31	6	72	VAPI	23.1	0.82
33	28	72	VAPI	24.0	0.86
34	6	81	VAPI	25.2	1.27

Appendix C. Density of woody stems < 5cm dbh by forest by compartment, stand, age, and type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Stem Density	Se
24	22	7	HMHD	8009.0	774.02
40	30	7	HMHD	9580.0	1409.1
23	34	9	HMHD	8252.0	559.01
35	8	9	HMHD	9657.0	1756.0
3	25	10	HMHD	3739.0	419.06
23	17	12	HMHD	7058.0	1278.3
27	7	14	HMHD	5243.0	1665.4
2	18	17	HMHD	5420.0	818.14
2	43	17	HMHD	6305.0	784.54
7	5	17	HMHD	5575.0	981.09
45	7	20	HMHD	3827.0	298.06
30	10	21	HMHD	2257.0	533.50
30	21	22	HMHD	3009.0	465.48
39	19	28	HMHD	708.0	115.67
10	13	31	HMHD	1979.0	507.74
39	12	31	HMHD	1018.0	107.25
39	16	31	HMHD	1427.0	200.92
39	21	31	HMHD	796.0	274.10
40	25	32	HMHD	2124.0	432.78
10	50	39	HMHD	22.0	22.12
14	2	39	HMHD	1825.0	296.48
14	13	40	HMHD	1416.0	251.60
23	35	41	HMHD	2301.0	248.34
14	45	43	HMHD	1475.0	184.37
13	2	46	HMHD	863.0	205.83
48	19	52	HMHD	2965.0	1002.6
3	9	66	HMHD	1040.0	194.56
33	7	70	HMHD	1615.0	143.95
43	17	71	HMHD	1637.0	261.67
16	4	78	HMHD	442.0	144.23
34	13	80	HMHD	2019.0	329.00
35	16	81	HMHD	2533.0	431.10
49	1	85	HMHD	1139.0	276.94
4	30	86	HMHD	2102.0	280.82
25	7	86	HMHD	1903.0	411.53
34	5	86	HMHD	1327.0	233.21
49	16	86	HMHD	1305.0	330.54
26	18	101	HMHD	2157.0	275.56
47	17	102	HMHD	2268.0	276.06
4	5	106	HMHD	1084.0	230.15
3	8	111	HMHD	973.0	157.13
45	13	112	HMHD	1305.0	309.73
14	54	2	LSLP	1338.0	254.64

Appendix C. (Cont.)

Comp	Stand	Age	Type	Stem Density	Se
12	43	3	LSLP	1980.0	725.46
13	12	3	LSLP	1095.0	204.27
15	29	3	LSLP	1139.0	80.87
7	18	4	LSLP	4757.0	811.38
7	23	4	LSLP	1128.0	238.28
7	34	4	LSLP	1726.0	334.39
25	17	7	LSLP	7942.0	1317.2
22	23	8	LSLP	14823	1721.2
25	5	8	LSLP	8175.0	1036.6
8	45	9	LSLP	9403.0	456.99
8	46	9	LSLP	10531	2732.0
9	4	9	LSLP	7942.0	1964.7
9	24	10	LSLP	9934.0	1909.4
10	34	10	LSLP	5398.0	424.70
39	7	10	LSLP	7898.0	793.54
47	16	10	LSLP	8186.0	778.28
9	12	12	LSLP	3650.0	181.77
47	19	14	LSLP	6084.0	920.87
18	14	17	LSLP	985.0	198.19
30	4	17	LSLP	1173.0	364.54
12	4	21	LSLP	2058.0	364.54
32	27	21	LSLP	1117.0	559.32
30	8	25	LSLP	708.0	139.14
39	15	26	LSLP	2168.0	538.45
38	7	28	LSLP	1217.0	286.57
43	1	28	LSLP	2522.0	424.70
2	3	25	NMHD	1538.0	270.18
45	2	40	NMHD	1781.0	240.36
41	2	41	NMHD	3031.0	1002.1
49	27	41	NMHD	1571.0	405.54
4	37	46	NMHD	1692.0	501.81
10	2	47	NMHD	1748.0	259.58
44	1	53	NMHD	1303.0	331.74
14	34	54	NMHD	4027.0	877.12
2	4	55	NMHD	3097.0	469.32
45	11	58	NMHD	2644.0	386.18
49	2	62	NMHD	2445.0	593.29
34	14	64	NMHD	2600.0	297.34
39	28	65	NMHD	918.0	199.29
38	6	66	NMHD	2942.0	520.21
1	1	78	NMHD	1737.0	176.88
3	21	82	NMHD	597.0	169.94
2	17	86	NMHD	1637.0	456.63
25	2	7	PHWD	12588	3264.9
33	4	10	PHWD	8097.0	1292.1

Appendix C. (Cont.)

Comp	Stand	Age	Type	Stem Density	Se
36	30	10	PHWD	4270.0	587.24
33	15	14	PHWD	4900.0	912.94
43	14	14	PHWD	7179.0	1109.4
16	8	21	PHWD	2312.0	268.67
10	9	23	PHWD	3850.0	851.41
8	52	25	PHWD	1914.0	164.12
45	15	28	PHWD	2611.0	373.20
48	20	28	PHWD	1593.0	219.51
40	20	29	PHWD	1206.0	189.78
39	20	31	PHWD	2489.0	591.18
40	17	33	PHWD	1493.0	163.45
45	25	34	PHWD	1925.0	384.68
42	32	38	PHWD	1604.0	711.80
2	42	41	PHWD	1847.0	142.86
48	24	46	PHWD	2345.0	192.87
47	10	50	PHWD	2655.0	1348.9
39	30	56	PHWD	1814.0	260.84
14	36	60	PHWD	2046.0	605.49
36	13	61	PHWD	2135.0	210.56
12	18	66	PHWD	3850.0	733.73
20	24	66	PHWD	1825.0	258.24
35	17	66	PHWD	2223.0	320.37
12	13	81	PHWD	2157.0	270.58
2	25	86	PHWD	1471.0	235.56
20	5	87	PHWD	2378.0	271.09
20	21	87	PHWD	1737.0	251.20
8	18	23	VAPI	973.0	120.95
10	12	24	VAPI	1106.0	633.85
45	16	28	VAPI	2046.0	284.31
39	2	29	VAPI	1250.0	139.00
32	9	30	VAPI	3584.0	689.58
41	16	30	VAPI	487.0	124.17
39	10	31	VAPI	1228.0	103.57
12	6	38	VAPI	1327.0	314.61
14	17	41	VAPI	553.0	106.87
32	4	46	VAPI	1925.0	363.61
10	28	47	VAPI	2721.0	550.44
33	8	48	VAPI	2898.0	382.24
45	4	50	VAPI	3816.0	317.73
44	3	52	VAPI	2854.0	499.03
7	21	56	VAPI	2854.0	617.29
18	5	56	VAPI	1991.0	266.41
12	17	60	VAPI	3308.0	456.53
8	2	62	VAPI	2301.0	403.52
25	12	70	VAPI	1084.0	169.22

Appendix C. (Cont.)

Comp	Stand	Age	Type	Stem Density	Se
8	22	72	VAPI	1814.0	412.65
31	6	72	VAPI	1154.0	376.18
33	28	72	VAPI	2611.0	738.42
34	6	81	VAPI	1527.0	123.18

Appendix D. Mean percent canopy cover of overstory by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	%Canopy Cover	Se
24	22	7	HMHD	92.0	5.61
40	30	7	HMHD	58.0	9.00
23	34	9	HMHD	90.0	2.40
35	8	9	HMHD	92.5	1.87
3	25	10	HMHD	94.2	1.49
23	17	12	HMHD	93.5	0.75
27	7	14	HMHD	95.0	0.94
2	18	17	HMHD	94.2	0.58
2	43	17	HMHD	95.3	0.39
7	5	17	HMHD	92.8	1.24
45	7	20	HMHD	94.0	0.97
30	10	21	HMHD	93.2	0.91
30	21	22	HMHD	92.3	0.90
39	19	28	HMHD	90.3	0.69
10	13	31	HMHD	93.3	0.90
39	12	31	HMHD	87.0	1.52
39	16	31	HMHD	92.5	1.05
39	21	31	HMHD	87.7	1.50
40	25	32	HMHD	92.2	1.29
10	50	39	HMHD	81.0	1.91
14	2	39	HMHD	93.0	0.72
14	13	40	HMHD	90.6	0.89
23	35	41	HMHD	95.3	0.52
14	45	44	HMHD	93.0	0.67
13	2	46	HMHD	91.9	0.99
48	19	52	HMHD	89.7	1.07
44	1	53	HMHD	91.8	0.75
3	9	66	HMHD	94.1	0.39
33	7	70	HMHD	96.1	0.26
43	17	71	HMHD	91.1	0.90
16	4	78	HMHD	80.6	5.22
34	13	80	HMHD	92.3	0.62
35	16	81	HMHD	90.8	0.57
49	1	85	HMHD	89.0	0.68
4	30	86	HMHD	94.7	0.57
25	7	86	HMHD	88.5	0.76
34	5	86	HMHD	94.2	0.60
49	16	86	HMHD	90.6	1.33
26	18	101	HMHD	95.4	0.54
47	17	102	HMHD	93.1	0.83
4	5	106	HMHD	93.5	0.56
3	8	111	HMHD	93.8	0.53
12	42	2	LSLP	0.0	0.00

Appendix D. (Cont.)

			% Canopy		
Comp	Stand	Age	Type	Cover	Se
12	43	3	LSLP	0.2	0.17
13	12	3	LSLP	7.0	4.09
15	29	3	LSLP	0.0	0.00
7	18	4	LSLP	37.8	11.57
7	23	4	LSLP	13.3	4.25
7	34	4	LSLP	15.0	4.50
25	17	7	LSLP	76.1	6.56
22	23	8	LSLP	80.7	9.18
25	5	8	LSLP	86.8	3.34
8	45	9	LSLP	93.0	1.52
8	46	9	LSLP	90.5	3.56
9	4	9	LSLP	88.2	10.47
9	24	10	LSLP	85.7	5.62
10	34	10	LSLP	88.5	1.39
39	7	10	LSLP	90.0	3.33
47	16	10	LSLP	93.7	1.43
9	12	12	LSLP	82.9	4.80
18	14	17	LSLP	90.0	0.91
30	4	17	LSLP	95.2	0.68
12	4	21	LSLP	93.0	1.09
32	27	21	LSLP	95.4	0.60
30	8	25	LSLP	93.8	0.47
39	15	26	LSLP	85.8	0.90
38	7	28	LSLP	83.7	1.92
43	1	28	LSLP	84.0	2.29
2	3	25	NMHD	95.5	0.40
45	2	40	NMHD	89.7	0.72
41	2	41	NMHD	92.3	2.28
4	37	46	NMHD	92.1	1.01
10	2	47	NMHD	95.8	0.44
44	1	53	NMHD	85.9	1.33
14	34	54	NMHD	92.6	0.56
2	4	55	NMHD	88.4	3.56
45	11	58	NMHD	92.4	0.57
49	2	62	NMHD	94.3	1.32
34	14	64	NMHD	93.3	0.71
37	28	65	NMHD	93.0	0.74
38	6	66	NMHD	95.4	0.57
1	1	78	NMHD	93.4	0.78
3	21	82	NMHD	94.2	1.13
2	17	86	NMHD	93.3	1.28
25	2	7	PHWD	62.7	6.91
10	48	8	PHWD	91.9	1.16
16	18	9	PHWD	92.0	1.87
43	14	14	PHWD	90.9	1.28

Appendix D. (Cont.)

Comp	Stand	Age	Type	% Canopy Cover	Se
16	8	21	PHWD	88.3	1.05
10	9	23	PHWD	93.4	0.81
8	52	25	PHWD	92.7	0.97
45	15	28	PHWD	86.0	4.17
48	20	28	PHWD	89.7	1.16
40	20	29	PHWD	92.4	0.81
39	20	31	PHWD	82.1	3.34
40	17	33	PHWD	93.9	0.66
45	25	34	PHWD	89.5	0.80
42	32	38	PHWD	94.4	0.75
2	42	41	PHWD	93.7	0.61
48	24	46	PHWD	90.1	1.48
47	10	50	PHWD	93.8	1.40
39	30	56	PHWD	86.9	2.03
14	36	60	PHWD	94.2	0.61
36	13	61	PHWD	93.4	0.90
12	18	65	PHWD	88.3	0.90
20	24	66	PHWD	91.8	0.68
35	17	66	PHWD	91.1	1.08
12	13	81	PHWD	95.8	0.39
2	25	86	PHWD	94.3	0.47
20	5	87	PHWD	92.7	0.68
21	20	87	PHWD	94.8	0.58
8	18	23	VAPI	81.5	5.71
10	12	24	VAPI	89.1	1.02
45	16	28	VAPI	86.4	2.38
45	46	28	VAPI	89.3	2.17
39	2	29	VAPI	93.8	0.37
32	9	30	VAPI	89.7	0.81
41	16	30	VAPI	82.1	2.15
39	10	31	VAPI	92.5	0.64
12	6	38	VAPI	95.9	0.48
14	17	41	VAPI	89.9	0.84
32	4	46	VAPI	92.0	1.01
10	28	47	VAPI	93.8	1.31
33	8	48	VAPI	89.2	3.61
45	4	50	VAPI	94.7	1.24
44	3	52	VAPI	85.3	2.22
7	21	56	VAPI	87.6	1.83
18	5	56	VAPI	88.2	1.13
12	17	60	VAPI	89.0	1.06
8	2	62	VAPI	93.3	2.06
33	17	63	VAPI	91.2	1.07
47	7	63	VAPI	95.8	0.80
8	22	72	VAPI	88.8	1.08

APPENDIX E. Mean shrub canopy cover and shrub height by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	%Shrub cover	Se	Shrub height	Se
10	14	2	HMHD	6.9	1.30	0.4	0.02
12	44	3	HMHD	20.5	2.25	0.6	0.01
24	22	7	HMHD	23.9	3.98	1.0	0.03
40	30	7	HMHD	34.5	4.60	0.9	0.02
23	34	9	HMHD	11.4	3.11	0.7	0.02
35	8	9	HMHD	25.0	1.52	0.7	0.02
3	25	10	HMHD	9.7	2.35	0.6	0.02
23	17	12	HMHD	16.4	4.53	0.6	0.03
27	7	14	HMHD	20.0	3.09	0.5	0.02
2	18	17	HMHD	3.6	0.42	0.5	0.05
2	43	17	HMHD	15.4	4.23	0.6	0.04
7	5	17	HMHD	4.4	0.61	0.8	0.24
45	7	20	HMHD	5.0	0.80	0.5	0.05
30	10	21	HMHD	2.8	0.64	0.3	0.02
30	21	22	HMHD	6.6	0.95	0.4	0.02
39	19	28	HMHD	10.8	1.76	0.4	0.01
10	13	31	HMHD	14.1	2.19	0.6	0.02
39	12	31	HMHD	9.3	2.41	0.4	0.03
39	16	31	HMHD	3.4	0.80	0.3	0.02
39	21	31	HMHD	12.5	1.13	0.4	0.02
40	25	32	HMHD	12.5	1.42	0.5	0.03
10	50	39	HMHD	21.1	2.29	0.4	0.01
14	2	39	HMHD	13.2	2.05	0.4	0.01
14	13	40	HMHD	9.7	3.25	0.5	0.02
23	35	41	HMHD	6.7	1.15	0.5	0.03
12	45	43	HMHD	10.0	2.58	0.3	0.03
48	19	52	HMHD	7.2	0.59	0.6	0.05
3	9	66	HMHD	7.8	1.23	0.6	0.04
33	7	70	HMHD	7.6	1.93	0.6	0.04
43	17	71	HMHD	18.5	2.26	0.5	0.02
16	4	78	HMHD	14.1	3.76	0.7	0.03
35	16	80	HMHD	22.7	3.81	0.5	0.02
49	1	85	HMHD	11.1	2.08	0.3	0.01
4	30	86	HMHD	11.1	1.11	0.5	0.03
25	7	86	HMHD	23.1	3.60	0.5	0.01
34	5	86	HMHD	12.0	2.56	0.5	0.02
49	16	86	HMHD	17.0	3.75	0.4	0.01
26	18	101	HMHD	10.3	2.06	0.6	0.02
47	17	102	HMHD	11.5	1.85	0.4	0.02
4	5	106	HMHD	15.5	3.22	0.4	0.01
3	8	111	HMHD	9.8	3.57	0.7	0.03
45	13	112	HMHD	8.6	1.63	0.4	0.02
9	18	2	LSLP	41.1	3.30	0.8	0.02

Appendix E. (Cont.)

Comp	Stand	Age	Type	%Shrub cover	Se	Shrub height	Se
12	24	2	LSLP	12.4	1.26	0.5	0.01
14	54	2	LSLP	13.7	0.03	0.6	0.02
7	33	3	LSLP	25.7	3.63	0.7	0.02
12	43	3	LSLP	27.2	2.24	0.8	0.02
13	12	3	LSLP	38.3	8.37	0.8	0.02
15	29	3	LSLP	20.2	3.13	0.6	0.02
7	23	4	LSLP	36.8	2.93	0.8	0.03
7	34	4	LSLP	18.5	3.32	0.8	0.02
18	7	4	LSLP	28.7	3.23	0.9	0.03
25	17	7	LSLP	19.6	2.80	0.8	0.02
22	23	8	LSLP	32.0	1.12	0.9	0.03
25	5	8	LSLP	18.6	2.79	0.6	0.02
9	4	9	LSLP	13.0	1.85	0.6	0.04
9	24	10	LSLP	13.5	1.42	0.6	0.03
10	34	10	LSLP	4.3	0.83	0.5	0.04
39	7	10	LSLP	9.6	2.01	0.5	0.03
47	16	10	LSLP	9.3	2.59	0.6	0.04
9	12	12	LSLP	16.3	1.06	0.5	0.02
47	19	14	LSLP	5.6	0.71	0.6	0.04
18	14	17	LSLP	24.8	2.72	0.5	0.01
30	4	17	LSLP	1.1	0.29	0.4	0.04
12	4	21	LSLP	17.7	3.25	0.5	0.02
32	27	21	LSLP	4.8	1.47	0.6	0.04
39	15	26	LSLP	8.6	1.69	0.4	0.03
38	7	28	LSLP	6.9	1.47	0.4	0.03
43	1	28	LSLP	20.8	3.06	0.5	0.02
2	3	25	NMHD	5.7	1.34	0.7	0.03
45	2	40	NMHD	13.6	1.96	0.5	0.02
2	41	41	NMHD	27.0	1.91	0.6	0.03
49	27	41	NMHD	5.9	2.22	0.7	0.05
4	37	46	NMHD	4.5	1.01	0.7	0.05
10	2	47	NMHD	8.5	1.18	0.7	0.03
44	1	53	NMHD	10.3	2.39	0.4	0.02
14	34	54	NMHD	20.9	4.31	0.8	0.02
2	4	55	NMHD	2.1	0.71	0.7	0.05
45	11	58	NMHD	15.0	2.48	0.7	0.03
49	2	62	NMHD	9.4	2.97	0.7	0.03
34	14	64	NMHD	9.9	1.56	0.5	0.02
39	28	65	NMHD	9.8	1.55	0.5	0.02
38	6	66	NMHD	16.1	2.31	0.9	0.03
1	1	78	NMHD	11.7	2.16	0.6	0.03
3	21	82	NMHD	9.3	2.08	0.5	0.02
2	17	86	NMHD	10.5	4.90	0.7	0.04

Appendix E. (Cont.)

Comp	Stand	Age	Type	%Shrub cover	Se	Shrub height	Se
10	48	8	PHWD	16.8	3.81	0.7	0.02
33	4	10	PHWD	9.8	2.28	0.6	0.03
36	30	10	PHWD	20.0	2.86	0.7	0.03
33	15	14	PHWD	18.7	2.72	0.6	0.02
43	14	14	PHWD	15.8	2.08	0.6	0.02
16	8	21	PHWD	2.4	0.56	0.4	0.03
10	9	23	PHWD	19.5	3.86	0.7	0.02
8	52	25	PHWD	4.3	0.80	0.5	0.03
45	15	28	PHWD	8.5	1.29	0.4	0.02
48	20	28	PHWD	5.0	0.96	0.3	0.02
40	20	29	PHWD	12.4	1.73	0.6	0.03
39	20	31	PHWD	17.7	1.49	0.6	0.02
40	17	33	PHWD	5.9	2.21	0.5	0.04
45	25	34	PHWD	12.6	1.95	0.5	0.02
42	32	38	PHWD	10.7	2.69	0.5	0.02
2	42	41	PHWD	17.0	4.39	0.6	0.02
48	24	46	PHWD	4.4	1.31	0.4	0.04
47	10	50	PHWD	9.1	3.30	0.5	0.04
39	30	56	PHWD	30.9	4.34	0.6	0.02
14	36	60	PHWD	14.2	3.28	0.7	0.02
36	13	61	PHWD	25.1	12.23	0.4	0.01
12	18	66	PHWD	19.9	2.46	0.6	0.02
20	24	66	PHWD	6.6	1.66	0.5	0.03
35	17	66	PHWD	30.1	3.72	0.5	0.01
12	13	81	PHWD	7.2	1.23	0.6	0.04
2	25	86	PHWD	9.5	1.11	0.7	0.03
20	5	87	PHWD	24.7	4.82	0.6	0.02
20	21	87	PHWD	20.4	8.23	0.4	0.02
8	18	23	VAPI	11.7	0.68	0.5	0.02
10	12	24	VAPI	20.2	3.36	0.5	0.03
45	16	28	VAPI	17.5	1.60	0.6	0.02
39	2	29	VAPI	9.0	1.33	0.4	0.02
32	9	30	VAPI	13.9	3.89	0.7	0.03
41	16	30	VAPI	18.7	4.26	0.5	0.02
39	10	31	VAPI	9.1	1.10	0.5	0.02
12	6	38	VAPI	7.1	1.87	0.6	0.03
14	17	41	VAPI	14.8	2.98	0.6	0.02
10	28	47	VAPI	10.3	2.01	0.7	0.04
33	8	48	VAPI	12.6	3.56	0.7	0.04
45	4	50	VAPI	10.6	1.51	0.6	0.04
44	3	52	VAPI	27.7	2.17	0.5	0.01
17	21	56	VAPI	16.4	4.38	0.7	0.03
18	5	56	VAPI	29.9	3.66	0.6	0.02
12	17	60	VAPI	18.8	2.19	0.6	0.02
8	2	62	VAPI	10.7	2.15	0.7	0.03

Appendix E. (Cont.)

Comp	Stand	Age	Type	%Shrub cover	Se	Shrub height	Se
33	17	63	VAPI	8.3	1.74	0.6	0.04
47	7	63	VAPI	8.0	1.76	0.7	0.04
25	12	70	VAPI	7.6	1.49	0.5	0.04
8	22	72	VAPI	11.4	2.30	0.6	0.03
31	6	72	VAPI	15.0	3.13	0.5	0.02
34	6	81	VAPI	8.0	1.37	0.6	0.04

Appendix F. Mean density of shrubs by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Shrub density	Se
10	14	2	HMHD	15875	1387.28
12	44	3	HMHD	19875	2533.61
24	22	7	HMHD	14375	2208.46
40	30	7	HMHD	25975	3470.44
23	34	9	HMHD	17150	1087.92
35	8	9	HMHD	19150	2783.43
3	25	10	HMHD	35100	2748.94
23	17	12	HMHD	13200	1701.47
27	7	14	HMHD	21350	1682.01
2	18	17	HMHD	5725	898.49
2	43	17	HMHD	7825	1478.39
7	5	17	HMHD	3400	1057.51
45	7	20	HMHD	11650	427.20
30	10	21	HMHD	8100	778.89
30	21	22	HMHD	7938	871.97
39	19	28	HMHD	16775	1907.39
10	13	31	HMHD	12525	3001.35
39	12	31	HMHD	8775	1643.36
39	16	31	HMHD	7913	1278.17
39	21	31	HMHD	10800	1196.52
40	25	32	HMHD	21125	1646.40
10	50	39	HMHD	15614	1892.27
14	2	39	HMHD	13725	1818.63
14	13	40	HMHD	10775	1046.55
23	35	41	HMHD	20475	1534.80
14	45	44	HMHD	24400	2900.00
13	2	46	HMHD	16288	1690.88
48	19	52	HMHD	8625	423.03
3	9	66	HMHD	8888	950.46
33	7	70	HMHD	8650	1522.33
43	17	71	HMHD	25838	2580.97
16	4	78	HMHD	17550	4087.48
13	34	80	HMHD	15350	1623.52
34	13	80	HMHD	13975	780.36
35	16	81	HMHD	17888	2017.20
49	1	85	HMHD	12000	1684.81
4	30	86	HMHD	15438	2888.33
25	7	86	HMHD	22175	1130.38
34	5	86	HMHD	13625	1343.74
49	16	86	HMHD	16150	3221.02
18	26	101	HMHD	19025	1453.04
47	17	102	HMHD	20888	2073.60
9	18	2	LSLP	12963	1018.74

Appendix F. (Cont.)

Comp	Stand	Age	Type	Shrub density	Se
12	24	2	LSLP	10988	1184.64
12	42	2	LSLP	7613	992.19
14	54	2	LSLP	9200	1108.30
54	14	2	LSLP	10300	794.77
7	33	3	LSLP	11550	1000.71
12	43	3	LSLP	20813	3606.66
13	12	3	LSLP	19525	1442.93
15	29	3	LSLP	17588	756.98
7	18	4	LSLP	18800	3036.72
7	23	4	LSLP	23025	7359.05
7	34	4	LSLP	15013	2603.12
25	17	7	LSLP	14013	789.31
22	23	8	LSLP	26150	1919.42
25	5	8	LSLP	19625	2326.46
8	45	9	LSLP	8263	816.34
8	46	9	LSLP	4525	601.91
9	4	9	LSLP	13850	997.08
9	24	10	LSLP	22275	2076.61
10	34	10	LSLP	15075	1713.37
39	7	10	LSLP	16950	739.93
47	16	10	LSLP	9975	1344.36
9	12	12	LSLP	19725	1095.73
47	19	14	LSLP	12600	1515.48
18	14	17	LSLP	20788	1608.95
30	4	17	LSLP	3975	836.61
12	4	21	LSLP	11000	646.79
32	27	21	LSLP	15025	1554.80
30	8	25	LSLP	7200	657.01
39	15	26	LSLP	16350	3245.64
38	7	28	LSLP	17625	2603.89
43	1	28	LSLP	33300	4762.18
2	3	25	NMHD	6525	1527.18
3	2	25	NMHD	15050	3689.06
45	2	40	NMHD	21300	2385.97
2	41	41	NMHD	19100	3997.08
49	27	41	NMHD	4800	1530.25
4	37	46	NMHD	6775	1055.56
10	2	47	NMHD	18838	2812.47
44	1	53	NMHD	13488	3997.70
14	34	54	NMHD	24888	3349.33
4	2	55	NMHD	4813	1119.06
45	11	58	NMHD	9513	469.97
49	2	62	NMHD	12838	1815.80
34	14	64	NMHD	15325	2385.20
39	28	65	NMHD	14825	2246.41
3	21	82	NMHD	21825	2777.40

Appendix F. (Cont.)

Comp	Stand	Age	Type	Shrub density	Se
2	17	86	NMHD	7850	1270.50
25	2	7	PHWD	31963	3179.73
10	48	8	PHWD	19925	2490.18
16	18	9	PHWD	19613	3495.79
33	4	10	PHWD	9725	1880.33
36	30	10	PHWD	19700	1769.18
33	15	14	PHWD	19500	1290.35
43	14	14	PHWD	17775	1366.66
16	8	21	PHWD	7275	1747.63
10	9	23	PHWD	21525	3188.92
8	52	25	PHWD	10013	1099.26
45	15	28	PHWD	9975	1284.49
48	20	28	PHWD	12225	1953.82
40	20	29	PHWD	36150	2855.55
39	20	31	PHWD	12300	1589.14
40	17	33	PHWD	15275	1734.19
45	25	34	PHWD	10700	1049.66
42	32	38	PHWD	21288	3224.54
2	42	41	PHWD	14338	2062.93
48	24	46	PHWD	10400	1302.56
47	10	50	PHWD	9050	1742.84
39	30	56	PHWD	28150	2600.69
14	36	60	PHWD	15050	2695.96
36	13	61	PHWD	31050	1150.00
12	18	66	PHWD	19900	1939.62
20	24	66	PHWD	11213	1330.20
35	17	66	PHWD	30013	2801.62
12	13	81	PHWD	14725	927.51
2	25	86	PHWD	7900	513.04
20	5	87	PHWD	21313	2163.70
20	21	87	PHWD	20775	2880.89
8	18	23	VAPI	14113	732.28
10	12	24	VAPI	21867	4920.82
45	16	28	VAPI	12425	1098.98
39	2	29	VAPI	13863	1114.83
32	9	30	VAPI	13367	2316.56
41	16	30	VAPI	29750	7031.54
39	10	31	VAPI	11200	1153.26
12	6	38	VAPI	20250	3174.68
14	17	41	VAPI	17588	2023.47
32	4	46	VAPI	9963	1190.73
10	28	47	VAPI	10000	959.17
33	8	48	VAPI	13825	2463.53
45	4	50	VAPI	10375	1259.88
44	3	52	VAPI	29788	3602.60
12	17	60	VAPI	14238	1093.15

Appendix F. (Cont.)

Comp	Stand	Age	Type	Shrub density	Se
8	2	62	VAPI	17475	1511.59
33	17	63	VAPI	11100	1247.00
47	7	63	VAPI	16625	1500.68
25	12	70	VAPI	11400	1192.34
8	22	72	VAPI	10813	1308.68
31	6	72	VAPI	21425	2195.51
33	28	72	VAPI	15600	2973.03
34	6	81	VAPI	10088	1477.02

Appendix G. Mean snag density/ha and snag diameter (cm) by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Snag density	Se[1]	Snag diameter	Se[1]
24	22	7	HMHD	2.5	.	0	.
23	17	12	HMHD	22.5	.	13	.
27	7	14	HMHD	2.5	.	16	.
2	18	17	HMHD	32.5	.	22	.
2	43	17	HMHD	25.0	.	16	.
17	5	17	HMHD	7.5	.	22	.
45	7	20	HMHD	22.5	.	9	.
30	10	21	HMHD	32.5	.	12	.
30	21	22	HMHD	17.5	15.00	6	5.46
39	19	28	HMHD	53.8	11.25	10	0.90
39	12	31	HMHD	60.0	.	14	.
39	16	31	HMHD	72.5	20.00	11	0.59
39	21	31	HMHD	70.0	.	13	.
30	19	52	HMHD	60.0	.	13	.
16	4	78	HMHD	25.0	.	29	.
35	16	81	HMHD	37.5	5.00	27	0.34
49	1	85	HMHD	68.8	23.75	19	0.25
25	7	86	HMHD	53.8	13.75	23	1.22
49	16	86	HMHD	22.5	2.50	36	10.09
47	17	102	HMHD	52.5	12.50	20	0.39
45	13	112	HMHD	37.5	2.50	28	2.55
13	12	3	LSLP	2.5	0.00	0	0.00
39	7	10	LSLP	15.0	.	12	.
19	4	19	LSLP	5.0	.	18	.
12	4	21	LSLP	15.0	.	9	.
39	15	26	LSLP	23.8	1.25	14	0.23
38	7	28	LSLP	118.8	28.75	9	1.23
43	1	28	LSLP	72.5	.	15	.
45	2	40	NMHD	32.5	7.50	43	18.68
41	2	41	NMHD	32.5	.	18	.
49	27	41	NMHD	37.5	.	17	.
45	11	58	NMHD	45.0	15.00	25	4.08
1	1	78	NMHD	41.3	11.25	20	0.41
3	21	82	NMHD	25.0	.	21	.
2	17	86	NMHD	55.0	.	18	.
10	48	8	PHWD	7.5	.	17	.
33	4	10	PHWD	22.5	.	15	.
16	8	21	PHWD	136.3	1.25	10	0.30
8	52	25	PHWD	33.8	3.75	10	1.45
45	15	28	PHWD	21.3	6.25	10	1.03
48	20	28	PHWD	92.5	22.50	12	0.77
39	20	31	PHWD	53.8	3.75	11	1.18
20	21	87	PHWD	122.5	10.00	17	0.14

Appendix G. (Cont.)

Comp	Stand	Age	Type	Snag density	Se[1]	Snag diameter	Se[1]
8	18	23	VAPI	26.3	1.25	14	3.06
45	16	28	VAPI	38.8	3.75	11	0.86
32	9	30	VAPI	90.0	22.50	14	1.58
41	16	30	VAPI	10.0	.	13	.
10	28	47	VAPI	70.0	.	15	.
33	8	48	VAPI	87.5	.	18	.
45	4	50	VAPI	37.5	.	15	.
44	3	52	VAPI	33.8	8.75	14	0.93
7	21	56	VAPI	92.5	.	16	.
12	17	60	VAPI	70.0	15.00	17	0.50
33	17	63	VAPI	110.0	.	18	.
25	12	70	VAPI	115.0	.	16	.
8	22	72	VAPI	97.5	42.50	13	0.81

[1] Missing standard errors (Se) a result of calculating the means from a single 15 x 200m plot. Se reported when means calculated from 4-15 x 50m plots.

Appendix H. Mean percent herbaceous ground cover and percent grass cover by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	%Herbaceous cover	Se	%Grass cover	Se
10	14	2	HMHD	14.1	4.57	1.7	1.10
12	44	3	HMHD	34.7	7.55	16.9	4.40
24	22	7	HMHD	5.8	3.44	2.8	1.15
23	34	9	HMHD	14.5	3.85	3.4	1.97
3	25	10	HMHD	2.9	2.74	2.1	2.13
23	17	12	HMHD	3.3	2.95	0.3	0.25
27	7	14	HMHD	0.0	0.00	0.0	0.00
2	18	17	HMHD	4.8	3.41	0.0	0.00
2	43	17	HMHD	0.4	0.40	0.0	0.00
7	5	17	HMHD	1.0	1.00	0.8	0.75
30	10	21	HMHD	0.8	0.75	0.5	0.50
30	21	22	HMHD	0.0	0.00	0.0	0.00
39	19	28	HMHD	0.0	0.00	0.0	0.00
10	13	31	HMHD	0.0	0.00	0.0	0.00
39	12	31	HMHD	5.3	2.26	4.3	2.15
39	16	31	HMHD	1.0	1.00	0.0	0.00
39	21	31	HMHD	5.1	3.62	4.9	3.69
23	35	41	HMHD	3.7	3.68	0.1	0.05
14	45	44	HMHD	3.6	3.57	0.5	0.54
48	19	52	HMHD	32.6	7.48	0.0	0.00
43	17	71	HMHD	32.1	12.39	13.2	6.72
16	4	78	HMHD	56.0	13.72	15.5	6.83
35	16	81	HMHD	2.5	2.01	1.8	1.29
49	1	85	HMHD	11.3	3.94	3.1	1.18
49	16	86	HMHD	0.6	0.38	0.2	0.13
26	18	101	HMHD	15.9	6.77	0.1	0.05
47	17	102	HMHD	0.0	0.00	0.0	0.00
45	13	112	HMHD	0.1	0.05	0.1	0.05
9	18	2	LSLP	43.1	7.00	25.6	5.17
12	24	2	LSLP	62.5	5.67	16.2	4.57
12	42	2	LSLP	42.6	9.55	12.6	3.41
14	54	2	LSLP	82.5	5.87	41.1	5.87
7	33	3	LSLP	63.9	7.03	31.1	7.64
12	43	3	LSLP	39.9	10.33	37.8	10.60
13	12	3	LSLP	54.3	7.70	37.6	5.95
15	29	3	LSLP	60.0	7.55	52.2	7.33
7	18	4	LSLP	46.0	8.73	36.8	12.82
7	23	4	LSLP	37.8	17.19	31.3	12.36
7	34	4	LSLP	63.9	4.92	56.9	6.23
25	17	7	LSLP	46.8	4.77	33.3	6.03
25	5	8	LSLP	13.4	5.86	12.1	6.02
8	45	9	LSLP	0.0	0.00	0.0	0.00
39	7	10	LSLP	22.5	8.05	14.0	8.13

Appendix H. (Cont.)

Comp	Stand	Age	Type	%Herbaceous cover	Se	%Grass cover	Se
47	16	10	LSLP	0.0	0.00	0.0	0.00
30	4	17	LSLP	7.8	3.71	4.4	2.59
12	4	21	LSLP	0.0	0.00	0.0	0.00
32	27	21	LSLP	24.6	6.29	16.9	5.24
39	15	26	LSLP	4.2	1.12	0.1	0.05
38	7	28	LSLP	3.8	1.46	0.3	0.13
43	1	28	LSLP	1.7	1.21	1.0	1.00
2	3	25	NMHD	24.5	5.48	8.7	3.71
45	2	40	NMHD	27.5	5.21	18.6	4.81
41	2	41	NMHD	30.8	2.95	21.8	4.02
49	27	41	NMHD	55.8	6.66	27.0	5.37
10	2	47	NMHD	30.2	5.26	11.7	5.04
44	1	53	NMHD	33.0	5.04	5.3	3.11
14	34	54	NMHD	19.4	5.27	6.5	2.58
2	4	55	NMHD	53.1	11.69	29.8	9.98
45	11	58	NMHD	37.5	4.27	18.0	4.33
49	2	62	NMHD	22.7	3.22	2.5	1.01
38	6	66	NMHD	37.0	7.11	11.2	3.76
1	1	78	NMHD	7.1	3.79	2.7	1.57
3	21	82	NMHD	35.8	17.63	0.0	0.00
2	17	86	NMHD	29.9	16.43	1.9	1.62
25	2	7	PHWD	22.7	8.63	11.2	7.19
10	8	8	PHWD	0.4	0.42	0.3	0.33
10	48	8	PHWD	1.7	1.66	1.7	1.66
39	1	9	PHWD	14.8	3.84	3.5	1.81
33	4	10	PHWD	20.1	9.37	2.0	1.70
36	30	10	PHWD	32.7	8.25	29.9	7.92
33	15	14	PHWD	1.5	1.23	1.5	1.24
16	8	21	PHWD	0.2	0.15	0.0	0.00
8	52	25	PHWD	12.9	4.10	7.9	2.76
45	15	28	PHWD	13.9	6.63	10.4	5.05
48	20	28	PHWD	2.0	1.63	0.0	0.00
39	20	31	PHWD	13.0	5.86	10.5	5.08
45	25	34	PHWD	11.8	3.71	7.5	2.99
48	24	46	PHWD	1.3	1.25	0.0	0.00
47	10	50	PHWD	0.0	0.00	0.0	0.00
39	30	56	PHWD	2.6	1.35	0.6	0.34
36	13	61	PHWD	15.7	3.76	1.4	1.24
12	13	81	PHWD	7.5	3.54	1.3	0.97
8	18	23	VAPI	6.8	2.52	3.4	1.78
45	16	28	VAPI	10.8	4.08	8.1	3.72
32	9	30	VAPI	10.5	4.85	0.3	0.17
41	16	30	VAPI	7.8	4.58	5.0	3.14
12	6	38	VAPI	37.4	9.14	2.6	2.63
10	28	47	VAPI	18.3	7.81	0.1	0.10

Appendix H. (Cont.)

Comp	Stand	Age	Type	%Herbaceous cover	Se	%Grass cover	Se
45	4	50	VAPI	3.8	1.13	0.7	0.53
44	3	52	VAPI	11.2	2.97	1.7	0.62
7	21	56	VAPI	1.8	1.46	0.0	0.00
12	17	60	VAPI	5.0	1.35	0.7	0.29
8	2	62	VAPI	12.3	6.19	0.9	0.63
33	17	63	VAPI	44.8	15.29	2.9	2.85
47	7	63	VAPI	7.3	2.46	0.1	0.13
30	12	70	VAPI	0.0	0.00	0.0	0.00
8	22	72	VAPI	2.8	1.53	1.9	1.21
31	6	72	VAPI	10.3	2.31	1.8	1.75

Appendix J. Mean height (meters) of herbaceous ground cover by forest compartment (comp), stand, age, and cover type at Quantico Marine Corps Base, Virginia.

Comp	Stand	Age	Type	Height	Se
1	1	78	NMHD	0.05	0.01
2	3	25	NMHD	0.20	0.04
2	4	55	NMHD	0.39	0.11
2	17	86	NMHD	0.11	0.05
2	18	17	HMHD	0.02	0.01
2	43	17	HMHD	0.01	0.01
3	21	82	NMHD	0.14	0.07
3	25	10	HMHD	0.02	0.02
7	5	17	HMHD	0.01	0.01
7	18	4	LSLP	0.18	0.05
7	21	56	VAPI	0.01	0.01
7	23	4	LSLP	0.16	0.06
7	33	3	LSLP	0.25	0.05
7	34	4	LSLP	0.26	0.03
8	2	62	VAPI	0.07	0.02
8	18	23	VAPI	0.05	0.02
8	22	72	VAPI	0.03	0.01
8	45	9	LSLP	0.00	0.00
8	46	9	LSLP	0.04	0.02
8	52	25	PHWD	0.11	0.02
9	4	9	LSLP	0.01	0.01
9	18	2	LSLP	0.19	0.04
10	2	47	NMHD	0.18	0.02
10	8	8	PHWD	0.01	0.01
10	13	31	HMHD	0.00	0.00
10	14	2	HMHD	0.13	0.03
10	28	47	VAPI	0.06	0.02
10	34	10	LSLP	0.02	0.01
10	48	8	PHWD	0.01	0.01
12	4	21	LSLP	0.00	0.00
12	6	38	VAPI	0.10	0.02
12	13	81	PHWD	0.06	0.02
12	17	60	VAPI	0.07	0.01
12	24	2	LSLP	0.25	0.04
12	42	2	LSLP	0.15	0.03
12	43	3	LSLP	0.24	0.05
12	44	3	HMHD	0.21	0.03
13	12	3	LSLP	0.29	0.07
14	17	41	VAPI	0.10	0.04
14	34	54	NMHD	0.09	0.02
14	45	44	HMHD	0.00	0.00
14	54	2	LSLP	0.19	0.03
15	29	3	LSLP	0.30	0.06
23	17	12	HMHD	0.02	0.01

Appendix J. (Cont.)

Comp	Stand	Age	Type	Height	Se
23	34	9	HMHD	1.36	1.26
23	35	41	HMHD	0.02	0.02
24	22	7	HMHD	0.05	0.03
25	2	7	PHWD	0.14	0.05
25	5	8	LSLP	0.06	0.02
25	17	7	LSLP	0.21	0.04
26	18	101	HMHD	0.09	0.03
27	7	14	HMHD	0.00	0.00
30	4	17	LSLP	0.06	0.01
30	10	21	HMHD	0.02	0.02
30	12	70	VAPI	0.00	0.00
30	21	22	HMHD	0.00	0.00
31	6	72	VAPI	0.06	0.01
32	4	46	VAPI	0.08	0.02
32	9	30	VAPI	0.04	0.01
32	27	21	LSLP	0.11	0.02
33	4	10	PHWD	0.28	0.21
33	15	14	PHWD	0.05	0.03
33	17	63	VAPI	0.08	0.03
35	16	81	HMHD	0.02	0.01
36	13	61	PHWD	0.00	0.00
36	30	10	PHWD	1.19	1.00
38	6	66	NMHD	0.15	0.03
38	7	28	LSLP	0.06	0.02
39	7	10	LSLP	0.08	0.02
39	12	31	HMHD	0.07	0.03
39	15	26	LSLP	0.56	0.50
39	16	31	HMHD	0.01	0.01
39	19	28	HMHD	0.00	0.00
39	20	31	PHWD	0.10	0.02
39	21	31	HMHD	0.07	0.03
39	30	56	PHWD	0.03	0.01
41	2	41	NMHD	0.24	0.06
41	16	30	VAPI	0.04	0.02
43	1	28	LSLP	0.02	0.01
43	17	71	HMHD	0.12	0.04
44	1	53	NMHD	0.22	0.03
44	3	52	VAPI	0.10	0.01
45	2	40	NMHD	0.24	0.03
45	4	50	VAPI	0.07	0.02
45	11	58	NMHD	0.21	0.04
45	13	112	HMHD	0.00	0.00
45	15	28	PHWD	0.08	0.02
45	16	28	VAPI	0.07	0.02
45	25	34	PHWD	0.06	0.01
47	7	63	VAPI	0.04	0.02

Appendix J. (Cont.)

Comp	Stand	Age	Type	Height	Se
47	17	102	HMHD	0.00	0.00
48	19	52	HMHD	0.10	0.00
48	20	28	PHWD	0.01	0.00
48	24	46	PHWD	0.01	0.01
49	1	85	HMHD	0.07	0.02
49	2	62	NMHD	0.13	0.02
49	16	86	HMHD	0.01	0.00
49	27	41	NMHD	0.50	0.10

Appendix K. Correlation matrix (Spearman's r) comparing measures of deer condition with model output and estimates of deer quality and quantity.

	HSIM2	HSI3M1	HSIMIN	HSIMIN1	MWT	PIS	BL	BD	HIAREA	OCA13	OCA16	NDF	NDS	LIG	DDM
HSIM2	1.00000 0.0	0.91744 0.0001	0.61329 0.0448	0.70940 0.0145	-0.49429 0.1222	-0.25987 0.4403	0.39770 0.2258	-0.01848 0.9570	0.32953 0.3224	0.86959 0.0005	-0.19680 0.5619	-0.69109 0.0185	0.62244 0.0408	-0.36343 0.2719	0.52874 0.0945
HSI3M1	0.91744 0.0001	1.00000 0.0	0.49658 0.1202	0.61504 0.0440	-0.40091 0.2217	-0.24251 0.4725	0.36842 0.2649	0.06437 0.8509	0.24146 0.4744	0.92028 0.0001	0.11845 0.7287	-0.49203 0.1242	0.42825 0.1888	-0.34103 0.3047	0.35240 0.2878
HSIMIN	0.61329 0.0448	0.49658 0.1202	1.00000 0.0	0.54545 0.0827	-0.34545 0.2981	0.15209 0.6553	0.61644 0.0434	0.07340 0.8302	0.13636 0.6893	0.40000 0.2229	-0.62727 0.0388	-0.46364 0.1509	0.40909 0.2115	0.00460 0.9893	0.19178 0.5721
HSIMIN1	0.70940 0.0145	0.61504 0.0440	0.54545 0.0827	1.00000 0.0	-0.83636 0.0013	-0.26270 0.4351	0.15982 0.6388	-0.09175 0.7885	0.25455 0.4500	0.59091 0.0556	-0.44545 0.1697	-0.87273 0.0005	0.86364 0.0006	-0.54256 0.0846	0.76713 0.0059
MWT	-0.49429 0.1222	-0.40091 0.2217	-0.34545 0.2981	-0.83636 0.0013	1.00000 0.0	0.61296 0.0449	0.12786 0.7079	0.44956 0.1654	-0.05455 0.8734	-0.24545 0.4669	0.43636 0.1797	0.70909 0.0146	-0.69091 0.0186	0.21611 0.5233	-0.59818 0.0519
PIS	-0.25987 0.4403	-0.24251 0.4725	0.15209 0.6553	-0.26270 0.4351	0.61296 0.0449	1.00000 0.0	0.63892 0.0343	0.75350 0.0074	0.20278 0.5498	-0.05991 0.8611	-0.11983 0.7256	0.21200 0.5314	-0.16131 0.6356	0.02797 0.9349	-0.21529 0.5249
BL	0.39770 0.2258	0.36842 0.2649	0.61644 0.0434	0.15982 0.6388	0.12786 0.7079	0.63892 0.0343	1.00000 0.0	0.52074 0.1005	0.47946 0.1356	0.39270 0.2322	-0.30594 0.3602	-0.09589 0.7791	0.07306 0.8310	0.14550 0.6695	-0.09862 0.7730
BD	-0.01848 0.9570	0.06437 0.8509	0.07340 0.8302	-0.09175 0.7885	0.44956 0.1654	0.75350 0.0074	0.52074 0.1005	1.00000 0.0	0.48626 0.1294	0.15597 0.6470	0.20184 0.5517	0.01835 0.9573	0.02752 0.9360	-0.32019 0.3371	-0.01843 0.9571
HIAREA	0.32953 0.3224	0.24146 0.4744	0.13636 0.6893	0.25455 0.4500	-0.05455 0.8734	0.20278 0.5498	0.47946 0.1356	0.48626 0.1294	1.00000 0.0	0.26364 0.4334	-0.09091 0.7904	-0.33636 0.3118	0.32727 0.3259	-0.41842 0.2003	0.31507 0.3453
OCA13	0.86959 0.0005	0.92028 0.0001	0.40000 0.2229	0.59091 0.0556	-0.24545 0.4669	-0.05991 0.8611	0.39270 0.2322	0.15597 0.6470	0.26364 0.4334	1.00000 0.0	0.11818 0.7293	-0.49091 0.1252	0.43636 0.1797	-0.42761 0.1896	0.38813 0.2382
OCA16	-0.19680 0.5619	0.11845 0.7287	-0.62727 0.0388	-0.44545 0.1697	0.43636 0.1797	-0.11983 0.7256	-0.30594 0.3602	0.20184 0.5517	-0.09091 0.7904	0.11818 0.7293	1.00000 0.0	0.54545 0.0827	-0.53636 0.0890	-0.06897 0.8403	0.39270 0.2322
NDF	-0.69109 0.0185	-0.49203 0.1242	-0.46364 0.1509	-0.87273 0.0005	0.70909 0.0146	0.21200 0.5314	-0.09589 0.7791	0.01835 0.9573	-0.33636 0.3118	-0.49091 0.1252	0.54545 0.0827	1.00000 0.0	-0.99091 0.0001	0.64832 0.0310	-0.93608 0.0001
NDS	0.62244 0.0408	0.42825 0.1888	0.40909 0.2115	0.86364 0.0006	-0.69091 0.0186	-0.16131 0.6356	0.07306 0.8310	0.02752 0.9360	0.32727 0.3259	0.43636 0.1797	-0.53636 0.0890	-0.99091 0.0001	1.00000 0.0	-0.68970 0.0189	0.95891 0.0001
LIG	-0.36343 0.2719	-0.34103 0.3047	0.00460 0.9893	-0.54256 0.0846	0.21611 0.5233	0.02797 0.9349	0.14550 0.6695	-0.32019 0.3371	-0.41842 0.2003	-0.4276 0.189	-0.06897 0.8403	0.64832 0.0310	-0.68970 0.0189	1.00000 0.0	-0.80140 0.0030
DDM	0.52874 0.0945	0.35240 0.2878	0.19178 0.5721	0.76713 0.0059	-0.59818 0.0519	-0.21529 0.5249	-0.09862 0.7730	-0.01843 0.9571	0.31507 0.3453	0.3881 0.238	-0.39270 0.2322	-0.93608 0.0001	0.95891 0.0001	-0.80140 0.0030	1.00000 0.0

Appendix K. (Cont.)

Variable Definitions

HSIM2 = HSI estimates from sub-model 2 of white-tailed deer HSI model for 11 deer management units.

HSI3M1 = HSI estimates from sub-model 1 of white-tailed deer HSI model.

HSIMIN = HSI estimates from sub-model 1 with fallen leaves excluded.

HSIMIN1 = HSI estimates from sub-model 1 with fallen leaves, twigs and needles, and ground pine excluded.

MWT = Mean dressed weight of 1.5 year-old male deer.

PTS = Mean number of antler points for 1.5 year-old males.

BL = Mean beam length of 1.5 year-old males.

BD = Mean beam diameter of 1.5 year-old males.

HIAREA = Total area of each deer management unit with HSI > 0.5.

QCAT3 = Amount of forage (g/ha) contributed by forage category 3, leafy browse.

QCAT6 = Amount of forage (g/ha) contributed by forage category 6, grasses and forbs.

NDF = Mean percent neutral detergent fiber (All forages and habitats combined).

NDS = Mean percent neutral detergent solubles (All forages and habitats combined).

LIG = Mean percent lignin content (All forages and habitats combined).

DDM = Mean percent digestible dry matter (All forages and habitats combined).

VITA

Mark Eugene Banker was born the youngest of 4 children in Huntingdon, Pennsylvania, on November 15, 1969. By the time that he reached high school, he knew he would pursue a career in the natural sciences. Mark earned his B.S. in Wildlife Science from Penn State University in the spring of 1991. While at Penn State, he worked for the U.S Fish and Wildlife Service in the summer of 1989 and assisted with research intended to facilitate river otter reintroduction in Pennsylvania. In the fall of 1991, he began graduate work at Virginia Tech University and received his M.S. in Wildlife Science on April 28, 1994.

Mark E. Banker