LONGLEAF PINE CHARACTERISTICS ASSOCIATED WITH ARTHROPODS AVAILABLE FOR RED-COCKADED WOODPECKERS

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Abstract: Red-cockaded woodpeckers (*Picoides* borealis) forage on the boles of living pine trees for a variety of arthropods. To assess the availability of prey under differing stand conditions, we sampled arthropods that crawled up the boles of 300 living longleaf pine trees (*Pinus palustris*) ranging in age from 20-100 years with passive traps over a l-year period. We identified, counted, ovendried, and weighed >50,000 arthropods in 22 orders and 470 genera. The most diverse orders were the Coleoptera (beetles), Araneae (spiders), and Hymenoptera (ants, wasps and bees). The most abundant orders were the Homoptera with large numbers of aphids (Aphididae) and the Hymenoptera with large numbers of ants (Formicidae). The Coleoptera and Araneae accounted for the greatest available biomass. Overall, arthropod biomass/tree increased with increasing stand age up to approximately 65-70 years, but arthropod biomass/ha was highest in the youngest stands. Abundance and biomass of arthropods on each tree bole were positively correlated with bark thickness and tree diameter, and negatively correlated with basal area (m^2/ha). Arthropod biomass differed among seasons, with the highest arthropod biomass occurring in winter and spring. We found no correlation of diversity, abundance, or biomass of arthropods on the tree bole with site index, the numbers of herbaceous plant genera in the understory, the number of herbaceous plant stems, or the percentage of ground covered by herbs. Stand characteristics, such as average bark thickness and diameter, associated with increased arthropod abundance and biomass on the bark are positively correlated to tree age, but these relationships would change with management practices that either accelerated or slowed tree growth.

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Key words: arthropods, bark thickness, basal area, foraging habitat, longleaf pine, ***Picoides borealis,*** red-cockaded woodpecker, site quality stand age, tree diameter.

Longleaf pine forests may have covered >24 million ha in the southern United States before European settlement. Today, <1.3 million ha remain as small isolated parcels (Outcalt and Sheffield 1996). The reduction in longleaf pine forests and the exclusion of fire, which allowed hardwood midstories to develop beneath the pine overstories, are considered the primary reasons for the red-cockaded woodpecker's (RCW) decline to its current endangered status (U.S. Forest Service 1995).

Because many of the remaining RCW populations are on National Forests, those lands are expected to support 80% of the existing and new populations needed for recovery of this species (U.S. Forest Service 1995). Habitat management for RCW recovery on those lands will include restoration of native pine communities (U.S. Forest Service 1995), especially longleaf pine. It is important that we understand how forest conditions and forest management practices affect the crawling arthropod fauna that RCW rely on for food in those communities (Hanula and Franzreb 1995, Hess and James 1998).

The boles of living longleaf pine trees, the primary foraging substrate of RCWs, are not the exclusive habitats of the arthropod prey of these woodpeckers. Instead, a large proportion of the arthropods crawl onto the bole from the soil or litter layer. In addition, the amount of arthropod biomass captured at any given location on the bole below the crown is the same regardless of trap height (Hanula and Franzreb 1998). This information coupled with knowledge of RCW prey selection (Hanula and Franzreb 1995, Hanula et al. 2000) was used to design an experiment to determine how arthropod abundance and biomass on the boles of longleaf pine trees are affected by stand characteristics such as age, tree density, site quality, and abundance and diversity of understory vegetation.

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METHODS

The study was conducted on the Escambia Experimental Forest in Escambia County, Alabama and the northwestern portion of the Blackwater State Forest in Santa Rosa County, Florida. The 2 locations, situated within 16 km of each other, were selected because they contained continuous stands of longleaf pine ranging in age from 20 to 90 years.

We chose 4 stands of longleaf pine from each of the following age classes: 20-25, 3035, 40-45, 50-55, 60-65, 70-75, 80-85, and 90-95 years old. Stand age was based on stand establishment data and was the primary criterion for stand selection. However, when >4 stands of the same age were available we selected the 4 that were most similar in tree density and understory composition to minimize the variation in arthropod communities between plots. We selected a total of 30 stands because only 2 stands were available in the 70-75 year age class. Ten dominant or codominant longleaf pine trees were randomly selected per stand.

Because a large portion of RCW prey crawls onto the bark from the soil (Hanula and Franzreb 1998), we used crawl traps to sample prey availability. We fitted each tree with a crawl trap and drift fence (Hanula and New 1996). The crawl trap consisted of an inverted metal funnel painted black. The side of the funnel was cut so it could be attached to the tree with the spout pointing directly upward. The inside of the funnel was coated with sand to provide secure footing for arthropods crawling through the funnel spout into the collection container mounted on top. Traps were attached to the trees at a height of 2 m. A drift fence, consisting of a 10-cm wide aluminum sheet metal band, was added to force arthropods into the trap and collection container. The sheet metal band was wrapped around the tree directly below the trap and sealed to the bark with silicone caulk to prevent arthropods from crawling under it. A gap in the drift fence at the opening of the trap allowed arthropods into the trap. Arthropods that entered the traps were preserved in a saturated NaCl solution containing 1% formaldehyde. This preservative was used because we felt it was least likely to attract or repel arthropods and was not attractive or toxic to mammals. Therefore, the traps were passive, because they only caught arthropods that would normally be on the boles of trees.

The traps, installed in April 1994, were operated continuously for 1 year. Samples were collected monthly and stored in 70% ethyl alcohol. Samples were sorted to morphologically similar groups and stored in separate vials of 70% alcohol until identification. Because the number of specimens collected was large, we only identified, ovendried, and weighed arthropods from every other month, or 6 of the 12 months. Specimens were identified to genus or to the lowest taxonomic level possible. Biomass estimates were obtained by ovendrying (40°C for 72 hr) and weighing at least 20-30 specimens of each taxon. The average weight of these specimens was multiplied by the number of individuals within a sample to estimate sample biomass.

The number (abundance) and biomass of each arthropod taxon were calculated for each tree for a given time period. Mean biomass/tree/year or season for each stand was calculated by averaging across the 10 sample trees in the stand. We calculated the number and biomass of arthropods crawling up the boles of trees on an area basis for each stand by multiplying the estimated number of trees/ha (described later in this section) and the average number or biomass of arthropods/tree.

Seasonal trends in arthropod biomass were determined using data from samples collected in May (spring), July (summer), October (fall) and February (winter). The October and February samples were processed in addition to the 6 bimonthly samples.

Although we were primarily interested in how arthropod abundance and biomass varied with stand age, we also measured a variety of other stand characteristics in August 1995: individual tree age, diameter at breast height (dbh), tree height, bark thickness (measured from the outer-most bark to cambium), tree density, percent herbaceous ground cover, herb and shrub abundance, and diversity.

Tree age was determined by removing an increment core from each tree and counting the number of rings. Because longleaf pines remain in the grass stage for a number of years before height growth begins, we added 5 years to the core age to estimate actual tree age. Bark thickness was measured with a bark thickness gauge. Two thickness measurements were taken per tree at a height of 1.4 m and averaged to estimate bark thickness for the tree. Tree dbh was also measured at a height of 1.4 m using a standard diameter tape. Stand basal area was estimated with a 10-factor prism at a point 5 m from each sample tree. The 10 basal area estimates per stand were averaged to get an overall estimate for each stand. Trees/ha were estimated by dividing the stand basal area estimate by the cross-sectional area of the bole of the average tree in the stand.

We were interested in determining if site quality was related to or could be used to predict the abundance of arthropods. Site index is a measure of the quality of a site for growing trees using tree height at given ages as indicators (Avery 1975). Tree height was measured with a clinometer and used in conjunction with tree age to estimate site index using Farrar's (1981) equation when age was ≥30 years. When age was <30 we used Schumacher and Coile's (1960) equation for longleaf pine.

Five of the 10 trees used for arthropod sampling in each stand were randomly selected for understory vegetation analysis. Shrubs and understory trees were identified and counted within a circular 0.04-ha plot surrounding each tree. In addition, a sample point was located by selecting a random compass direction and distance (1-20 m) from each tree. At each point, percent herbaceous ground cover was estimated using a modification of the Daubenmire cover scale (Mueller-Dombois and Ellenberg 1974), and overstory canopy cover was recorded as present or absent by sighting through a cardboard tube to a point directly above each sample point (James and Shugart 1970). A 1-m^2 plot was also established at each sample point, and all herbaceous plants in the plot were identified to genus and counted.

Since stands >20 years were thinned at least once, we were interested in determining how arthropod abundance and biomass might differ in normal or fully stocked stands. Therefore, we conducted an additional analysis of arthropod biomass/ha using our arthropod biomass/tree estimates and the number of dominant trees expected in a fully stocked second-growth stand of longleaf pine (U.S. Forest Service 1929) on a moderately good site (site index = 21.3 m).

Statistical analyses were performed with SAS General Linear Models procedure (SAS Institute 1987). In univariate analyses, dependent variables were arthropod biomass, arthropod abundance, and arthropod diversity. Independent variables used separately or in combination were stand age, mean tree attributes per stand, site index, and abundance or diversity of herbaceous plants. Second-degree polynomials and linear equations were used to approximate a number of relationships.

RESULTS

We captured and identified' >50,000 arthropods in 22 orders and 470 genera (Table 1). The most diverse orders were Coleoptera (beetles), Araneae (spiders), and Hymenoptera (ants, wasps, and bees). The most abundant orders were Homoptera with large numbers of aphids, and Hymenoptera with large numbers of ants. Coleoptera and Araneae accounted for the greatest available biomass. Arthropod biomass differed among seasons across all age classes (Fig. 1). In winter and spring, similar arthropod biomass was captured crawling up tree boles. Summer and fall catches were also similar but lower in arthropod biomass than other seasons.

The number and biomass of arthropods captured on the boles of living longleaf pine trees were significantly correlated with stand age (Fig. 2). A second degree polynomial regression equation provided the best fit for modelling the relationship of arthropod biomass to stand age. The model revealed that biomass of arthropods/tree increased with increasing stand age to approximately 60 years after which the biomass began to decline. The number of arthropods captured per tree increased linearly with stand age. Arthropod numbers and biomass exhibited a significant negative linear relationship to pine basal area (Fig. 3).

The relationship of arthropod number and biomass to bark thickness was more similar to the relationships of those variables to stand age (Fig. 4). As bark thickness increased, the number and biomass of arthropods/tree increased to bark thicknesses of 1.75-2.0 cm, after which arthropod number and biomass began to declined.

Tree diameter was also correlated with arthropod numbers and biomass (Fig. 5). The number of arthropods/tree bole exhibited a positive linear relationship to diameter while arthropod biomass increased with increasing diameter to approximately 32 cm, after which it began to decline. When we included only trees ≥25 cm dbh in the analyses, there was no significant correlation with arthropod biomass ($P = 0.26$) or number ($P = 0.77$). Basal area, bark thickness, and diameter were correlated with stand age (Fig. 6). Basal area declined with in-

Table 1. Total number of genera and individuals, and biomass (ovendried weight) of arthropod orders captured in funnel traps on 300 longleaf pine trees of varying ages over a l-year period. Traps were operated from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

Arthropod order	Genera	Individuals	Total weight (g)
Araneae	97	6,508	29.1
Blattaria	3	1,416	9.6
Coleoptera	105	1,471	40.6
Diptera	69	1,296	0.4
Geophilomorpha	1	7	0.02
Hemiptera	28	925	34.7
Homoptera	23	23,330	9.9
Hymenoptera	90	13,001	18.7
Isopoda	1	24	0.1
Isoptera	1	235	0.1
Lepidoptera	17	33	7.9
Lithobiomorpha	1	2	0.02
Mantodea	2	2	0.05
Mecoptera	1	1	0.004
Neuroptera	6	167	5.06
Opiliones	4	300	1.2
Orthoptera	14	1,061	14.4
Phasmida	1	83	11.4
Plecoptera	1	8	0.004
Psocoptera	2	517	0.1
Scolopendromorpha	2	19	1.6
Thysanura	1	29	0.07

creasing stand age to 70 years after which it began to increase after 80 years of age. Bark thickness and diameter increased with increasing stand age until stand age 60 years and then remained relatively constant.

Because RCWs prefer to forage on trees ≥25 cm (Hooper and Lennartz 1981, Hooper and Harlow 1986, Engstrom and Sanders 1997), we wanted to determine if arthropod abundance and biomass were correlated with basal area when we included only stands that had trees in the size classes preferred by RCW. We found no significant relationship of pine basal area to arthropod abundance (P = 0.245) or biomass (P = 0.33) in stands with trees having diameters ≥25 cm even though such stands exhibited a broad range of basal areas (10–25 m^2/ha). A similar analysis with diameter also showed no significant correlations (P = 0.77 for abundance; P = 0.26 for biomass) when stands of smaller trees were excluded.

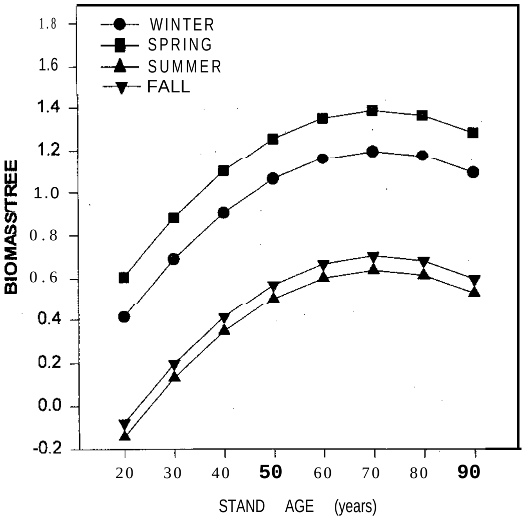

Fig. 1. Second degree polynomial regressions of arthropod biomass on longleaf pine tree boles and stand age based on month-long samples taken in each season during the period from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

Estimates of the number and biomass of arthropods/ha in stands were negatively correlated with stand age, with the youngest stands having the highest biomass/ha and number/ha (Fig. 7). Although the average biomass/tree was less in younger stands, trees/ha was much higher, resulting in more biomass/ha. When we estimated arthropod biomass for fully stocked second-growth stands, we found that although the shape of the graph in Fig. 8 differed from Fig. 7, it showed a similar trend.

Our results showed site quality, as measured by site index, had no effect on diversity (P = 0.43), abundance (P = 0.51), or biomass (P =

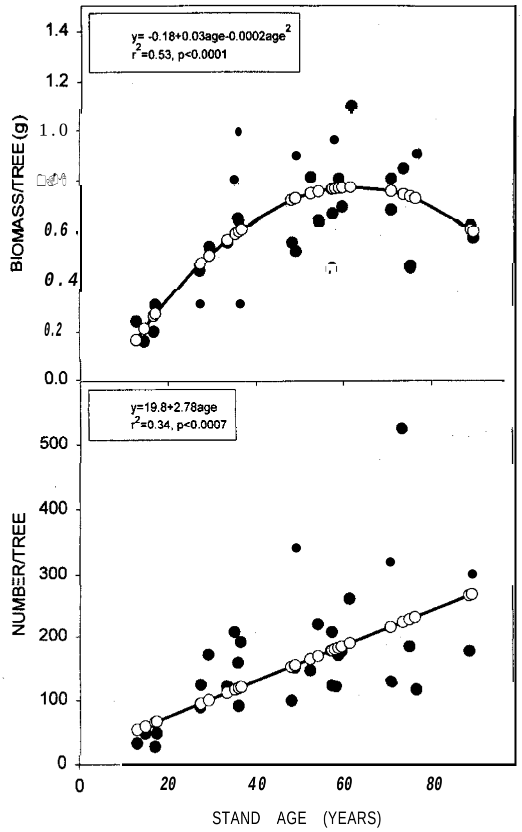

Fig. 2. Relationship of the average age of longleaf pines in a stand to the mean number/tree and biomass/tree of arthropods on boles from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

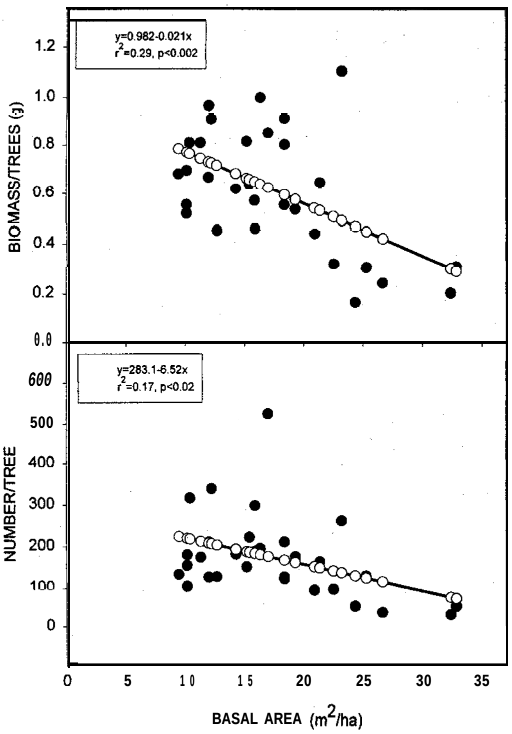

Fig. 3. Relationship between the average basal area for longleaf pine stands and the mean number/tree and biomass/tree of arthropods on boles from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

0.35) of arthropods on trees. Percent ground cover of herbaceous plants, number of herbaceous stems/m^2, and the number of herbaceous genera were correlated with stand age (Fig. 9). As age increased, herbaceous plant diversity, numbers, and percent ground covered also increased to stand age 60-70 years after which they began to decline. We did not detect any correlations between abundance or biomass of arthropods and the number of herbaceous plant genera (P = 0.12 and 0.14 for arthropod abundance and biomass, respectively), herbaceous stems/m^2 (P = 0.6 and 0.34), or percent herbaceous ground cover (P = 0.14 and 0.15).

DISCUSSION

Several key tree and stand characteristics correlated to arthropod availability for RCW. Number and biomass of arthropods per tree was related to stand age, diameter, bark thickness, and basal area. Bark thickness, tree diameter, and stand age were the best predictors of arthropod biomass on tree boles. Because the 3 variables were almost equal in their predictive value, we selected stand age for use in subsequent analyses. Information on stand age is readily available for most forests and, therefore, can be easily used as a management criterion. In addition, basal area, bark thickness, and tree diameter were closely correlated with stand age. The relationships of bark thickness and tree diameter with tree age were similar to those reported by Wahlenberg (1946). Mariani and Manuwal (1990) also reported that bark furrow depth and tree diameter were closely correlated for Douglas fir (*Pseudotsuga menziesii*).

Although we believe tree age is an easier management criterion to use in even-age forests, bark thickness is probably a more important characteristic in determining arthropod abundance on tree boles. For example, Nicolai (1986) reported that tree boles of European hardwoods with fissured bark contained more arthropods than those with smooth bark. He

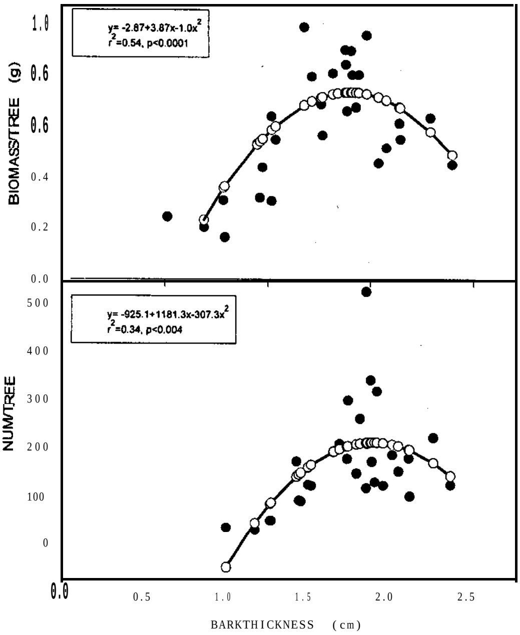

Fig. 4. Relationship between average bark thickness of longleaf pine trees in a stand and the mean biomass/tree and number/tree of arthropods on boles from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

found deeper furrows moderated temperature extremes providing a more stable habitat for arthropods. Additionally, Mariani and Manuwal (1990) reported spider abundance was greater for all size classes of spiders on bark with deeper furrows.

We observed a positive correlation between the number and biomass of arthropods and bark thickness. However, second degree polynomial equations provided the best fit, which suggests arthropod abundance and biomass decline on trees with bark thicknesses >2 cm. We suspect this result is an artifact of the model and that arthropod number and biomass are approximately equal on trees with bark thicknesses >1.5 cm.

Our data represent captures of arthropods crawling up the tree bole 24 hrs/day but give no indication of residence time on the bole. By providing better refuge, thicker bark may result in arthropods remaining on the tree for a longer time. Thick bark may be particularly important for arthropods active at night, because it allows them to use the bark crevices for refuge during daylight hours. For example, Hanula and Franzreb (1998) found the number of wood roaches under bark flakes and in crevices at different heights was similar over the tree bole, but roach biomass decreased with height in the tree (i.e. the roaches were smaller higher up in the tree). Larger roaches were only found high on the tree in dead branches where they could hide under the loose, sloughing bark. Wahlenberg (1946) observed that bark thickness declined with height above ground on longleaf pines. He also found thicker bark higher up the tree bole of larger diameter trees. If bark thickness is important to arthropods that use tree surfaces, bigger arthropods may remain higher on larger, thick-barked trees during the daylight hours when RCW are foraging. The presence of larger arthropods higher on these boles may help explain why RCWs prefer to forage on large trees (Skorupa 1979, Hooper and Lennartz 1981,

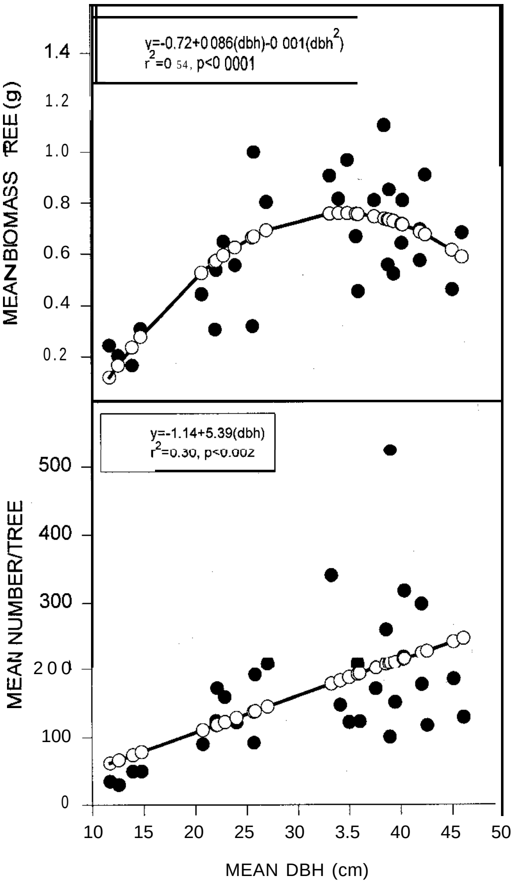

Fig. 5. Relationship between average longleaf pine tree diameter (dbh) in a stand and the mean number/tree and biomass of arthropods on boles during April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

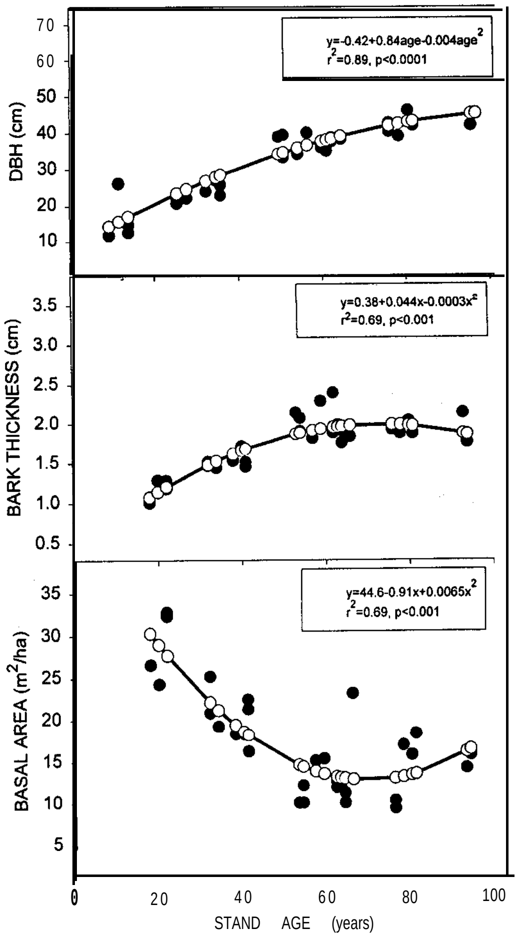

Fig. 6. Relationship of longleaf pine stand age to stand basal area, average bark thickness, and tree diameter (dbh) on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida in August 1995.

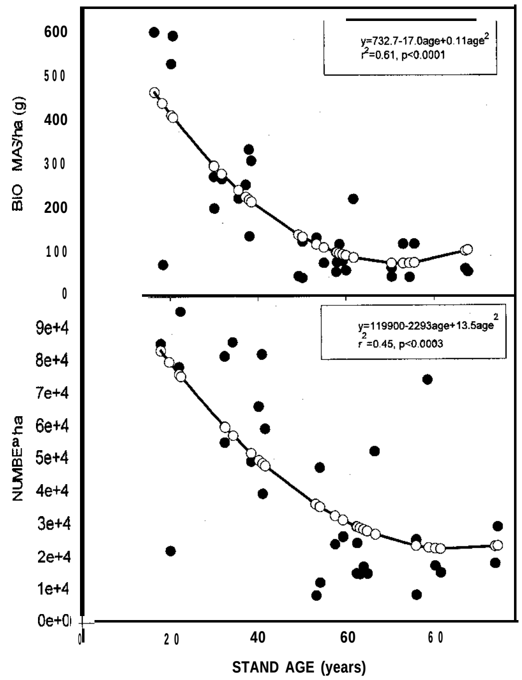

Fig. 7. Relationship between stand age and the mean number/ha and biomass/ha of arthropods. Arthropods were collected from April 1994 to April 1995 on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida.

DeLotelle et al. 1983, Porter and Labisky 1986, Engstrom and Sanders 1997).

Hooper (1996) and Hanula and Franzreb (1998) demonstrated the importance of dead branches as a resource for arthropods in live pine tree canopies. In both studies, arthropod biomass was higher in dead branches than in live branches or in nearby sample positions on the bole. Hooper (1996) reported dead branches harbored more arthropod biomass than any other portion of the tree, regardless of tree age. Hanula and Franzreb (1998) found that bark 1 m above the ground and dead branches in the canopy contained similar arthropod biomass and both contained significantly more than other sample positions. Hooper (1996) suggested large dead branches would harbor more arthropods than small ones and demonstrated dead branch diameters were positively correlated with tree age. Because natural pruning occurs more rapidly in denser stands and results in small dead branches (Smith 1962), large, open grown trees are more likely to have large dead

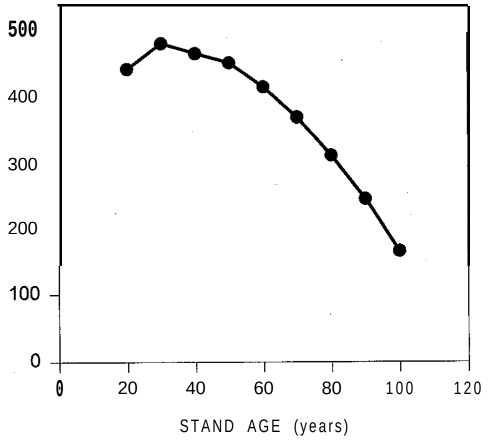

Fig. 8. Estimated arthropod biomass/ha in fully stocked second-growth longleaf pine stands of various ages with a site index of 21 m (U.S. Forest Service 1929).

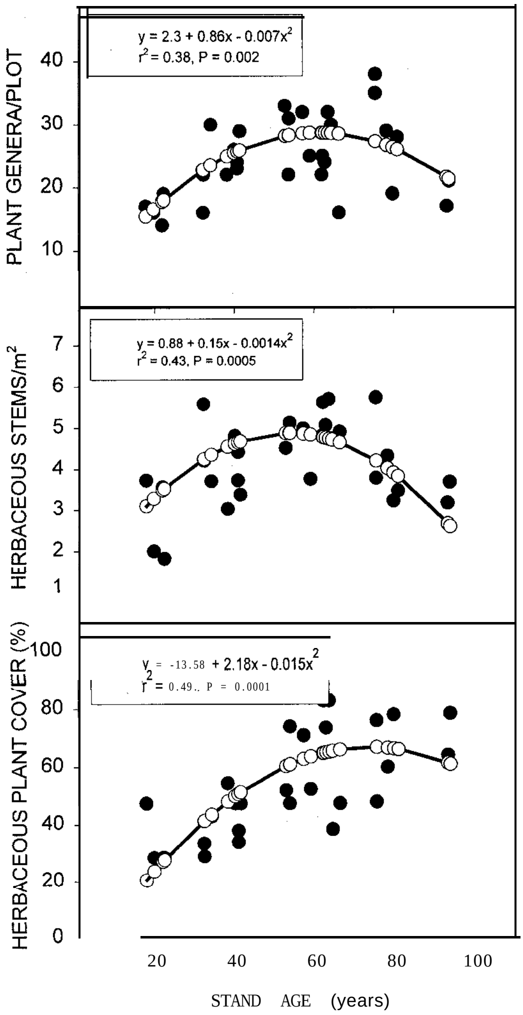

Fig. 9. Relationship between herbaceous understory plant characteristics and age of the overstory longleaf pine stand on the Escambia Experimental Forest, Alabama and the Blackwater State Forest, Florida in August 1995.

branches. Thus, older, open stands may retain more arthropods during the day because their thick bark and large dead branches provide better arthropod habitat.

Stand basal area declined with age to age 60-70 years, after which it remained relatively constant or increased slightly in older stands. However, stand tables that represent projections of normal or fully stocked stands with complete crown closure for second-growth longleaf pine (U.S. Forest Service 1929) show basal area of dominant trees increases with increasing age. In contrast, all but the 20-year-age class stands in our study had been thinned and only a few would fit the definition of normal or fully stocked stands. Thus, the basal area-age relationship we observed may not represent a similar distribution of age classes in another location. For example, when we projected arthropod biomass/ha using our arthropod biomass/tree estimates and the number of dominant trees expected in a fully stocked second-growth stand (U.S. Forest Service 1929), the shape of the graph (Fig. 8) differed from our stands (Fig. 7). However, the 2 graphs show a similar trend (i.e., young stands have high arthropod biomass/ha and biomass declines with age as the number of trees/unit area declines). Although estimates for second-growth stands (Fig. 8) suggest that arthropod biomass/ha might decline to near zero, that is unlikely For example, Wahlenberg (1946) presented data for old-growth longleaf pine showing that stands lose approximately 4–5 trees/O.4 ha/decade from 100 to 150 years of age, 2-3 trees/O.4 ha/decade from 160 to 200 years of age, and l-2 trees/O.4 ha/decade thereafter in even-aged stands up to 320 years old. Therefore, it is likely that the curve in Fig. 8 would level off or decline slowly over a long period of time. In addition, trees >100 years old may have attributes that favor retention of arthropods such as crown structure and branch size that would not be measured in traps at the base of trees.

Despite the higher arthropod biomasses in young stands, RCWs prefer foraging on larger diameter and presumably older trees (Skorupa 1979, Hooper and Lennartz 1981, DeLotelle et al. 1983, Porter and Labisky 1986, Engstrom and Sanders 1997). This may be a result of the higher energy required to forage on younger trees, as suggested by Hooper and Lennartz (1981), or possibly fewer arthropods remain on smaller trees during the day.

Seasonal trends in arthropod availability on the bark are important for identifying times when food is most limited. Hooper (1996) speculated winter would be a time of limited arthropod abundance for the RCW. However, we found summer and fall samples had the least arthropod biomass while winter and spring had the most. In a previous study, crawling arthropod biomass on mature longleaf pines was low during summer and high during fall (Hanula and Franzreb 1998). The difference between these observations may be the result of timing and duration of sampling. In this study we used data from a single l-month fall sample in October while the previous study used data from

3 monthly samples. The 2 studies do agree that summer is a time of low arthropod availability.

In general discussions about arthropod availability for RCWs, the question is often raised about the relationship between understory composition and arthropod abundance on the bark. We found stand age was positively correlated with understory characteristics. Although the models suggest that herbaceous understory characteristics begin to decline in older stands, we see no biological reason for this and suspect that this is an artifact of the models. We did not find any correlations of understory plant characteristics and arthropod abundance or biomass on the tree bole. These findings are consistent with a previous study that found that herbivores make up only 25% of arthropod biomass on the lower bole of mature longleaf pine trees (Hanula and Franzreb 1998). In addition, RCW diets consist primarily of omnivores, predators, and detritivores (Beal 1911, Harlow and Lennartz 1977, Hanula and Franzreb 1995, Hanula et al. 2000, Hess and James 1997). Therefore, understory vegetation may not be an important part of the food chain that supports RCWs.

Our results were in agreement with Hooper (1996) who revealed that total arthropod biomass/tree increased with increasing tree age to 76–96 years, depending on sample position. Hooper (1996) showed arthropod biomass/m^2 of bark surface decreased with increasing tree age and decreasing radial growth. Using very different techniques, we found arthropod biomass/tree increased with increasing stand ages up to approximately 65–70 years and arthropod biomass/ha was highest in younger stands. In both studies, models suggested that arthropod biomass declines in older trees. Because we see no biological reason for arthropod biomass to decline on older trees, we believe these declines are artifacts of the models and that arthropod numbers and biomass remain relatively constant over time after trees reach the 50–70-year class.

Current management guidelines for RCW foraging areas require (1) >789 m^2 basal area in pine stems >12.7 cm diameter, (2) >6,350 pine stems ≥25.4 cm diameter and ≥30 years old, (3) habitat must be <800 m from the geometric center of the cluster (group of roosting or nesting cavity trees) and continuous and contiguous with the cluster, and (4) it must include only pine and pine–hardwood stands (excluding white and sand pines; U.S. Fish and Wildlife Service 1985). Our data support the idea, expressed in the management guidelines, that more trees in the vicinity of a cluster of cavity trees results in more arthropod biomass. Basal area in older age-class stands ranged from 9–24 m^2/ha, but arthropod biomass/tree was not correlated with basal area or number of trees/ha when we excluded younger stands. This suggests that maintaining older stands at higher densities would mean more arthropods/ha because arthropod abundance and biomass per tree were similar regardless of tree densities in older stands. However, even fully stocked stands will experience a decline with time in arthropod biomass as the number of trees declines (Figs. 7 and 8).

A number of studies have shown that RCW do not need the amount of foraging habitat required by the recovery plan to maintain high density populations (Wood et al. 1985, Conner and Rudolph 1991, Hooper and Lennartz 1995, Beyer et al. 1996). For example, Conner and Rudolph (1991) reported large populations were not affected by the habitat loss they measured but small populations were affected. Wood et al. (1985) removed 37% of the foraging habitat from the home ranges of RCW groups without adverse effects on the birds. Likewise, Hooper and Lennartz (1995) removed 43% of the foraging habitat of a high density population, but were unable to detect any negative effects on group sizes or reproductive rates. One reason for these findings may be that trees, the foraging substrate of RCWs, are not the only habitat of their arthropod prey (Hanula and Franzreb 1998). For example, despite trapping continuously for 1 year, we did not observe any reduction in arthropod numbers or biomass in the vicinity of our trees. We started the study in the spring and 9 months later we caught a similar number and biomass of arthropods. It is unlikely that RCWs could deplete the available arthropod resources in reasonably stocked foraging areas. In addition, because RCWs are opportunistic and take advantage of available arthropods (Beal **1911, Harlow** and Lennartz 1977, Hanula and Franzreb 1995, Hanula et al. 2000, Hess and James 1998), depletion of one prey is unlikely to be detrimental.

MANAGEMENT IMPLICATIONS

Stand and tree characteristics such as bark thickness and diameter that are associated with increased abundance and biomass of arthropods on bark are positively correlated to tree age, but these relationships would change with different management practices. Arthropod biomass was highest on trees with a diameter of 30–35 cm and a bark thickness of 1.5-2.0 cm. Management that favors growth and retention of such trees in reasonably stocked stands should favor a sustainable supply of arthropods for bark foraging birds. Since most arthropods are not exclusively residents on the trees, other stand characteristics are also likely to influence them. However, our data suggest that site quality, herbaceous understory conditions, and overstory tree densities can vary considerably without affecting arthropod biomass. We see no evidence in our data or that of Hooper (1996) that trees older than 60–80 years are inherently better as foraging substrates in terms of arthropod availability on the bole.

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