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Arthropod biomass in winter and the age of longleaf pines

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Abstract

The endangered red-cockaded woodpecker (*Picoides borealis*) satisfies its nutrient requirements by capturing arthropods from live pine trees. Age of pine stands has been used as a guide for providing suitable habitat for the species, however, little is known about the relationship of arthropods to age of pines. The relationship on longleaf pines (*Pinus palustris*) 22–127 years old was examined in winter. Arthropod biomass m^{-2} on the bole, live limbs and dead limbs was related to tree age, radial growth 6–10 years before sampling and ambient temperature. Arthropod biomass m^{-2} declined with increasing tree age on the lower, mid- and upper bole; increased with tree age on dead limbs; and increased with tree age on live limbs until 80 years when it declined with increasing age. Slower growing trees had higher arthropod biomass m^{-2} for a given age than faster growing trees. Total arthropod biomass for the whole tree increased with tree age up to 86 years, when it declined with increasing tree age. However, the older the tree, the greater the arthropod biomass on dead limbs.

Keywords: Pinus palustris; *Picoides borealis*; Tree age; Prey base

1. Introduction

An important factor in the recovery of the red-cockaded woodpecker is the provisioning of suitable foraging habitat over extensive areas (Lennartz and Henry, 1985). Each family of woodpeckers requires more than 40 ha of foraging habitat. To provide foraging habitat for recovery of the species directly affects more than 1 000 000 ha of public lands in the southern United States.

Red-cockaded woodpeckers spend up to 95% of their foraging time capturing arthropods on live pine trees (Ligon, 1968; Morse, 1972; Wood, 1977; Miller, 1978; Nesbitt et al., 1978; Skorupa, 1979; Ramey, 1980; Hooper and Lennartz, 1981; Patterson and Robertson, 1981; DeLotelle et al., 1983; Repasky, 1984; Porter and Labisky, 1986). Among the questions that must be addressed when managing foraging habitat for the woodpecker is what age and size of pine trees to provide (Lennartz and Henry, 1985; Henry, 1989). Considerable work has been done on the size and age of trees selected by foraging red-cockaded woodpeckers. Little, however, is known about the arthropod prey base on pines or its relationship to tree age and size.

Red-cockaded woodpeckers forage on pines greater than 5 cm diameter at breast height (DBH), particularly those pines greater than 25 cm DBH (Skorupa, 1979; Hooper and Lennartz, 1981; DeLotelle et al., 1983; Repasky, 1984; Porter and Labisky, 1986). However, these studies did not indicate an increase in preference as DBH increased beyond 25 cm. Compelling evidence has not been presented that indicates, for example, that a tree of 48 cm DBH is more sought after as a foraging site than a tree of 25 cm DBH. Hooper and Harlow

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(1986) examined selection of forest stands by foraging red-cockaded woodpeckers and concluded that use of pine stands 30-115 years old was independent of stand age. They also found that the abundance of pines greater than either 36 or 48 cm DBH did not influence selection of pine stands for foraging any more than pines 24–35 cm DBH. While woodpeckers prefer pine stands more than 30 years old for foraging, preferences beyond this age are not clear (Lennartz, 1988; Walters, 1990).

If we assume that foraging red-cockaded woodpeckers select trees that support the higher densities of prey, then arthropod densities do not appear to be a function of tree age or size once a threshold of about 25 cm DBH has been obtained. Yet, arthropod biomass may increase as southern pines age for several reasons. Older pines may have more arthropods than younger pines because older pines either have or are thought to have: (1) thicker and more rugose bark, (2) more epiphytes, (3) larger live limbs and (4) more dead limbs (Jackson, 1979; Skorupa, 1979; Hooper and Lennartz, 1981; Jackson and Jackson, 1986).

To explore the relationship between tree age and arthropod biomass, I sampled arthropods on longleaf pines 22-127 years old. Specifically, I tested the following null hypotheses: (1) arthropod biomass m^{-2} on longleaf pines in winter was equal among trees of different ages and (2) total arthropod biomass on longleaf pines in winter was equal among trees of different ages.

2. Methods

2.1. Study area

The study was conducted in the Francis Marion National Forest (FMNF) in the Coastal Plain of South Carolina. The 101 200 ha area is forested with stands of longleaf and loblolly pines interspersed with wetland forests (Hooper et al., 1991). The foraging behavior of the red-cockaded woodpeckers in this area was reported by Hooper and Lennartz (1981) and Hooper and Harlow (1986). The red-cockaded woodpecker population was large and expanding (Hooper et al., 1991), thus the foraging habitat was thought to be good.

2.2. Study design

Arthropods were collected from 33 longleaf pines ranging in age from 22 to 127 years old. Trees were aged by counting annuli from an increment core taken at breast height (1.4 m) and adding 7 years. Three trees were sampled in each 10-year age class. One tree from each of the 11 age classes was considered a series. A series was completed before sampling in another series began. Trees were processed randomly within a series. Sampling arthropods on the 33 trees took 77 days (4 December 1985 to 18 February 1986). This design prevented confounding age class with time.

I chose winter for the study because I thought arthropods would be less active and their populations more stable than during other seasons, and thus, they would be easier to sample. Also, if prey populations are lower in winter, arthropod–tree age relationships may be more important than in other seasons.

2.3. Tree selection

Longleaf pine stands were selected at random from a FMNF data base. Stands had been prescribed burned on a 2–5 year cycle for several decades, but trees were selected from stands that had not been burned within the last year. Only one tree was processed for arthropods per stand. Only dominant trees in even-aged stands greater than 1.0 ha were considered. To lessen the likelihood of red-cockaded woodpeckers having depleted a tree of arthropods, all selected trees were more than 400 m from an active red-cockaded woodpecker cavity tree, but all were within woodpecker territories. Trees recently scaled by foraging red-cockaded woodpeckers (Jackson, 1977) were not selected.

2.4. Foraging positions sampled

Arthropods were collected at the five foraging positions used by Hooper and Lennartz (1981) to study foraging behavior:

1. Lower bole: area of the bole from the ground to half the distance to the base of the live crown.
2. Mid-bole: area of the bole from the base of the live crown halfway to the ground.

3. Upper bole: the bole from the base of the live crown to where the bole diameter tapered to 10.0 cm.
4. Live Limbs: live primary limbs.
5. Dead Limbs: dead primary limbs.

2.5. Collection of arthropods

2.5.1. Weather

Arthropods were not collected from trees on windy days or when the bark was wet. Strong winds blew bark away from the collecting pans and escaping arthropods were difficult to see. Arthropods stuck to the wet bark and were difficult to detect.

2.5.2. Bole

At each of the three bole positions, arthropods were collected from a plot measuring 2.13 × 0.25 m. The 2.13 m corresponded to seven rungs of a Swedish ladder and the 0.25 m was the width of a rectangular plastic container that fit tightly between the tree and the ladder. The flexible container conformed to the curvature of the bole, and the plot width was measured to ensure the same area was sampled on each tree and position. The plot for the lower bole was centered 2.0 m from the ground. The centers of the plots for the mid-bole and upper bole coincided with the centers of their respective positions on the trees.

The bark was examined within the plot boundary for arthropods on the surface and in fissures. Larger arthropods were captured with forceps and smaller ones with a small brush wetted with ethanol. To capture arthropods beneath the bark, the container was fitted with its mouth at the bottom of the 2.13 × 0.25 plot. Just forward of the container, a knife was used to remove the outer bark within the sides of the plot boundary. One hand was used to guide the loosened bark into the container, and the other operated the knife as the container was moved up the plot. The outer bark was removed to within 2–6 mm of the cambium within the plot boundary and run through a gang of sieves with 9.5, 6.4, 3.4 and 2.0 mm screens. Arthropods were retained by the various screens. Each piece of bark passed through a given sieve, was broken to enable passage through that sieve, or passed a rigorous visual inspection for arthropods. Bark was oven dried and weighed.

Table 1
Frequency of occurrence and mean biomass m^{-2} of arthropods on 33 longleaf pines 22–127 years old from 4 December 1985 to 18 February 1986 in the Francis Marion National Forest, South Carolina

Taxon [a]	Frequency of occurrence (%)					Mean biomass m^{-2} (mg)				
	Lower bole	Mid-bole	Upper bole	Live limbs	Dead limbs	Lower bole	Mid-bole	Upper bole	Live limbs	Dead limbs
Chilopoda (Centipedes)	63.6	60.6	72.7	42.4	42.4	6.2	5.6	7.4	2.8	6.3
Pseudoscorpiones (Pseudoscorpions)	39.4	72.7	72.7	48.5	30.3	0.4	0.9	0.6	0.1	0.4
Opiliones (Daddy longlegs)	3.0	0	6.1	0	3.0	0.9	0	0.2	0	t [b]
Araneae (Spiders)	100.0	100.0	100.0	100.0	81.8	21.1	27.7	23.3	7.7	2.3
Acari (Mites)	42.4	30.3	63.6	15.2	3.0	0.1	0.1	0.2	t [b]	t [b]
Thysanura (Silverfish)	51.5	42.4	15.2	6.1	3.0	4.1	3.5	0.7	t [b]	t [b]
Embioptera (Webspinners)	0	3.0	6.1	6.1	0	0	t [b]	0.1	t [b]	0
Dictyoptera (Cockroaches)	72.7	78.8	100.0	84.9	42.4	18.9	10.7	36.2	10.3	4.8
Hemiptera (Bugs)	39.4	24.2	30.3	9.1	3.0	33.6	104.1	24.1	0.8	0.9
Homoptera (Hoppers)a,p	9.1	0	9.1	12.1	18.2	t [b]	0	0.8	t [b]	0.5
Neuroptera (Lacewings)	0	9.1	6.1	3.0	0	0	t [b]	0.2	0.1	0
Coleoptera (Beetles)a	72.7	84.9	93.9	60.6	57.6	14.4	12.2	14.8	6.7	13.2
(Beetles)l,p	72.7	30.3	51.5	36.4	87.9	3.9	1.2	3.6	0.3	48.9
Hymemoptera (Ants)a	39.4	30.3	45.5	36.4	69.7	14.9	7.5	8.9	3.3	172.8
(Wasps)a,l	6.1	6.1	12.1	18.1	12.1	0.1	t [b]	1.2	0.1	0.9
Lepidoptera (Moths)a,l,p	39.4	12.1	42.4	27.3	18.2	8.7	13.3	17.6	1.0	0.5
Diptera (Flies)a,l,p	54.6	12.1	15.2	36.4	36.4	0.9	0.1	0.1	0.1	3.9

[a] a, adults; l, larvae; p, pupae. [b] $t = < 0.1$ mg.

2.5.3. Live limbs

The looser outer bark was scraped from five randomly selected live limbs within the crown of each of the trees sampled. A plastic container 35.8 × 31.4 cm was hung directly beneath the portion of the limb being scraped. Before scraping, the diameter of each limb sampled was measured 5 m from the bole and at the distal point where scraping ended. The distance that each limb had been scraped was recorded, and the surface area of the scraped portion was approximated as the curved surface of the frustrum of a right cone. Scraping began proximal to the bole and proceeded distally as far as the climber could reach. The collected bark was processed through sieves as described earlier.

2.5.4. Dead limbs

Five dead limbs were removed at random from each tree sampled. Bark, if any, was removed and run through sieves. The limbs were sawn into 30 cm lengths and split into small pieces to expose arthropods.

2.5.5. Handling of arthropods

Arthropods that were dropped or escaped during the collection process were recorded by order and relative size for the order (small to extra large). A mean weight was obtained within each order for each size and the final biomass for the position was adjusted by the estimated weight of the escaped arthropods. On average, escaped arthropods accounted for 1.3-5.3% of the final biomass, depending upon foraging position.

Collected arthropods (Table 1) were stored in 70% ethanol by tree, position and order. They were oven dried at 70°C for 24 h and weighed to 0.1 mg. Members of the same order were generally weighed together, for example, all centipedes from the same tree and position.

2.6. Aspect

Only one face of the bole on each tree could be sampled. That face was determined by the arrangement of limbs in the crown that allowed the extension of ladders into the crown. Trees representing all quadrants were sampled: for 0°–90° ($n = 6$), 91°–180° ($n = 6$), 181°–270° ($n = 14$), and 271°–360° ($n = 7$). Because of the problems inherent to a circular scale (Zar, 1984:422), a transformed azimuth (T) was calculated: if $0° \leq \text{Azimuth} \leq 225°$, $T = |\text{Azimuth} - 45°|$, otherwise, $T = |\text{Azimuth} - 360°| + 45°$.

While not a perfect solution to the problems of circular scale, the transformation did allow much closer approximation of azimuth to heat loading of the bark from insolation. The highest values were nearest the warmest part of the bole, and the lowest values were nearest the coldest part of the bole. Moreover, the discontinuity between 0° and 360° was eliminated.

2.7. Surface area

2.7.1. Bole

The surface area of the lower, mid-bole, and upper bole was approximated by assuming each section was the curved surface of the frustum of a right cone. The surface area for the whole tree was approximated by the sum of surface areas of the lower, mid-, and upper boles and dead and live limbs.

2.7.2. Live limbs

The surface area of primary live limbs from the bole out to a limb diameter of 15 mm was approximated by the formula for the curved surface of the frustum of a right cone. The length of the live limbs sampled for arthropods was measured with a calibrated pole from the bole to where limb diameter measured 15 mm (same diameter as the distal end of the pole).

A regression equation was developed from these data so limb diameter could be used to estimate the surface area of the other primary live limbs on each tree. The diameter of all primary live limbs on each tree was measured 5 cm from the bole for use in the regression equation: $LA = -0.2559 + 10.9071\,LD$ where LA is the surface area (m^2) of the primary limb from the bole to where its diameter is 15 mm, and LD is the diameter (m) of the primary live limb measured 5 cm from the bole. For the regression model: df = 1, 163; $R^2 = 0.88$; probability of a larger value of t if $b^1 = 0$ was 0.0001.

2.7.3. Dead limbs

The surface area of all dead limbs was approximated by assuming each was a frustum of a right

cone. Proximal and distal diameters and length of all dead limbs on each tree were measured. On dead limbs that still retained their terminal branch, the distal diameter was set at 15 mm, and length was measured to that diameter.

2.8. Analyses

The REG procedure (SAS Institute Inc., 1987) was used for linear regression analyses. Regression coefficients were considered significant if $P < 0.05$. Arthropod biomass m^{-2} and the total arthropod biomass for each foraging position and for the whole tree on average were used as dependent variables in regressions (Table 2). Arthropod biomass m^{-2} for the whole tree was a weighted average of the five foraging positions. Total arthropod biomass for each foraging position was a projection of its arthropod biomass m^{-2} over its surface area. Whole tree biomass was the sum of the biomass for all foraging positions.

Table 2
Mean, range, and standard deviation for variables used in study of arthropod biomass m^{-2} and total arthropod biomass on longleaf pines in winter

Variable	Minimum	Maximum	Mean	Standard Deviation
Arthropod biomass m^{-2} (mg) [a]				
Lower bole	16.9	390.0	142.1 (136.1)	102.0 (99.6)
Mid-bole	10.5	1824.6 (444.1)	205.7 (109.5)	341.5 (94.0)
Upper bole	19.7	494.8 (422.9)	170.8 (164.8)	120.7 (108.4)
Live limbs	0.2	83.9	35.1	24.8
Dead limbs	2.1	1586.5	270.0	327.6
Whole tree	28.1	478.6 (196.2)	124.6 (104.2)	80.2
Total arthropod biomass (g) [a]				
Lower bole	0.14	3.10	1.00 (0.99)	0.77 (0.77)
Mid-bole	0.02	12.92 (2.50)	1.37 (0.66)	2.52 (0.58)
Upper bole	0.05	2.53	0.94 (0.92)	0.70 (0.69)
Live limbs	0.01	1.50	0.49	0.45
Dead limbs	0.01	1.71	0.35	0.41
Whole tree	0.24	17.85 (7.32)	4.16 (3.40)	3.13
Tree age (years)	22	127	75.2	32.1
Diameter breast height (cm)	18.1	52.0	38.7	10.5
Radial growth (mm)				
1–5 years before study	2.9	16.2	8.7	3.53
6–10 years before study	4.6	21.1	9.8	4.65
Bark weight (kg m^{-2})				
Lower bole	1.5	6.3	3.4	1.02
Mid-bole	1.1	3.7	2.3	0.67
Upper bole	0.9	3.1	1.8	0.51
Live limbs	0.5	1.2	0.8	0.16
Ambient temperature (c)				
Minimum 24 h	−11	17	3.2	5.74
Maximum 24 h	−2	24	14.4	6.32
Aspect of bole samples [b]	15	203	107.5	55.2
Elapsed sampling days	1	77	38.6	24.2

[a] Parentheses indicate biomass excluding hemiptera greater than 60 mg. [b] Transformed azimuths. See Aspect Section.

Independent variables were tree age; minimum, maximum and mean temperatures during the 24 h prior to sampling; number of days since the study began; aspect of the sample plots on the bole; bark weight m^{-2}; and radial growth 1–10, 1–5, and 6–10 years before the study (Table 2).

It took 77 days to sample all trees in the study. To control for population changes over time, data were collected in three series. One tree from each age class was sampled at random before the second tree from each age class was sampled, etc (see Section 2.2). To test for a series effect, two-way ANOVA's were performed using age class X series (SAS Institute Inc., 1987). To test for first order autocorrelation, I calculated a lag variable for each dependent variable. The data were sorted in the order trees were sampled for arthropods, and the lag variable for a given observation of a dependent variable was the value for that variable in the preceding observation. The dependent variables were then regressed on the lag variables. If a lag variable and the corresponding dependent variable were not significantly related, then evidence of autocorrelation did not exist. In addition, the number of elapsed days at the time of arthropod sampling (DAY) was tested for inclusion in regression models.

3. Results

3.1. Series effects and autocorrelation

The order in which each subset of the data was collected (series) was not a significant factor affecting arthropod biomass m^{-2} or total biomass. Only one ANOVA out of 12 was significant. Series had a significant effect on arthropod biomass m^{-2} on live limbs ($F_{2,10}$; $P = 0.02$). However, the Duncan's test indicated that the second series was smaller than the first series but not the third series and that the first and third series were similar (44.5, 20.7 and 39.9 mg m^{-2} for the first, second and third series, respectively). The ANOVA testing series effect on total arthropod biomass on live limbs was not significant ($F_{2,10}$; $P = 0.11$). The other ANOVA's testing series effect on either arthropod biomass m^{-2} or total biomass at the other four foraging positions or the entire tree were not significant ($F_{2,10}$; $P > 0.05$).

Regressions of the dependent variables on the corresponding lag variables did not support existence of first order autocorrelation for the dependent variables. R^2 values were less than 0.01 for all dependent variables ($P > 0.60$) except arthropod biomass m^{-2} on live limbs, where $R^2 = 0.09$ ($P = 0.096$).

3.2. Arthropod biomass m^{-2}

3.2.1. Regression models

Only three unweighted regressions involving arthropod biomass m^{-2} on the whole tree, five foraging positions, and the ten independent variables were significant. Because standard deviation of arthropod biomass m^{-2} increased as tree age increased weighted regression analysis with a weight value of $1/\text{tree age}^2$ was used (Neter et al., 1985, pp. 167–170). Weighted regressions resulted in 17 significant regressions with arthropod biomass m^{-2} and the independent variables (Tables 3–5).

Table 3
Summary of regression analyses of arthropod biomass m^{-2} (mg) on longleaf pines in winter when hemiptera greater than 60 mg (dry weight) were ignored

Regression model [a]	R_2	(R_2) [c]	P [b]		
			b^1	b^2	b^3
(1) $y_{tree} = -9.598 + 4.288\text{Age} - 0.0314\text{Age}^2$	.27	(.24)	.002	.004	-
(2) $y_{tree} = 161.7 - 4.336\text{Growth}$	.25	(.20)	.003	-	-
(3) $y_{tree} = 168.6 - 1.794\text{Temp.}$	.35	(.18)	.0003	-	-
(4) $y_{tree} = 232.9 - 4.411\text{Growth} - 1.815\text{Temp.}$	.60	(.39)	.0001	.0001	-
(5) $y_{tree} = 357.9 - 8.952\text{Growth} - 1.965\text{Temp.} - 1.204\text{Age}$	.76	(NS)	.0001	.0001	.0002

[a] y_{tree} = Arthropod biomass m^{-2} (mg) exclusive of hemiptera greater than 60 mg (dry weight) averaged over entire tree. Regressions weighted using $1/\text{Age}^2$ as the weighting value. Age, age of longleaf pines; Growth, radial growth (mm) measured at 1.4 m for 6–10 years before sampling arthropods; Temp., minimum temperature during the 24 h before sampling. [b] Probability of larger value of t if coefficient is equal to zero. [c] R^2 values for weighted regressions that included hemiptera greater than 60 mg (dry weight). NS, non-significant regression.

Table 4
Summary of regression analyses of arthropod biomass m^{-2} (mg) on the lower bole (y_{LS}), mid-bole (y_{MB}), and upper bole (y_{UB}) of longleaf pine in winter when hemiptera greater than 60 mg (dry weight) were ignored

Regression model [a]	R^2	(R^2) [c]	P [b]		
			b^1	b^2	b^3
(1) $y_{LB} = 500.8 - 15.24\text{Growth} - 2.885\text{Age}$	.29	(NS)	.002	.004	
(2) $y_{LB} = 606.8 - 16.29\text{Growth} - 3.141\text{Age} - 2.056\text{Temp.}$	.40	(.25)	.0005	.001	.027
(3) $y_{MB} = 263.0 - 3.814\text{Temp.}$	.40	(NS)	.0001		
(4) $y_{MB} = 481.4 - 4.037\text{Temp.} - 9.324\text{Growth} - 1.669\text{Age}$	.51	(NS)	.0001	.018	.041
(5) $y_{UB} = -93.72 + 9.49\text{Age} - 0.0625\text{Age}^2$	.18	(NS)	.022	.041	
(6) $y_{UB} = 318.4 - 12.01\text{Growth}$	.25	(.25)	.003		
(7) $y_{UB} = 423.8 - 12.11\text{Growth} - 2.685\text{Temp.}$	.36	(.36)	.002	.035	
(8) $y_{UB} = 677.3 - 21.32\text{Growth} - 2.990\text{Temp.} - 2.442\text{Age}$	.44	(NS)	.0005	.015	.043

[a] y_{LB}, y_{MB} and y_{UB} are equal to arthropod biomass m^{-2} (mg) exclusive of hemiptera greater than 60 mg (dry weight). Regressions were weighted using $1/\text{Age}^2$ as the weighting value. Age, age of longleaf pines. Growth, radial growth (mm) measured at 1.4 m, 6–10 years before sampling. Temp., minimum temperature during the 24 h before sampling.[b] P, Probability of larger value of t if coefficient is equal to zero.[c] R^2 values for weighted regressions that included hemiptera greater than 60 mg (dry weight). NS, non-significant regressions.

Five of the 33 trees (6 of 165 foraging positions sampled) had large hemiptera of apparently the same species, that individually weighed more than 60 mg (dry weight). These trees had 1488, 632, 583, 471, 299 and 161 mg m^{-2} of large hemiptera on either their lower or mid-bole. All other arthropods for these respective trees and positions totaled 337, 179, 196, 68, 17, and 79 mg m^{-2}. Ages of the trees were 62, 104, 48, 48, 125 and 45 years, respectively. The 48 year old tree had large hemiptera on both its mid- and upper bole. I redefined the response variable to exclude these large hemiptera.

Ignoring large hempitera greatly improved the fit of weighted regression models for the whole tree and three bole positions. These improved models allowed a better evaluation of the relationship between tree age and arthropod biomass m^{-2} (Tables 3 and 4). Because weighted regression models with and without large hemiptera were similar, the same conclusions about the relationship would have been made if both sets of regressions had been significant.

Unless otherwise noted, weighted regression models that ignored large hemiptera are the models reported in the applicable text and tables (Tables 3 and

Table 5
Summary of regression analyses of arthropod biomass m^{-2} (mg) on live limbs (y_{LL}) and dead limbs (y_{DL}) of longleaf in winter

Regression model [a]	R^2	P [b]			
		b^1	b^2	b^3	b^4
(1) $y_{LL} = 5.834 + 0.4383\text{Age}$	.18	.013			
(2) $y_{LL} = 54.89 - 2.047\text{Growth}$	.18	.015	–	–	–
(3) $y_{LL} = -36.41 + 1.113\text{Temp.}$	.20	.009	–	–	–
(4) $y_{LL} = -31.14 + 0.0833\text{Bark weight}$	.30	.001	–	–	–
(5) $y_{LL} = -49.60 + 2.792\text{Age} - 0.0189\text{Age}^2$	.46	.0001	.0005	–	–
(6) $y_{LL} = -42.41 + 3.199\text{Age} - .0215\text{Age}^2 - 1.605\text{Day} + 0.0205\text{Day}^2$	.62	.0001	.0001	.002	.004
(7) $y_{DL} = -71.07 + 4.572\text{Age}$	.33	.0004	–	–	–
(8) $y_{DL} = -202.1 + 82.85\text{Mean diameter}$ [c]	.34	.0004	–	–	–

[a] y_{LL} = arthropod biomass m^{-2} (mg) of all arthropods on live limbs. y_{DL} = arthropod biomass m^{-2} (mg) of all arthropods on dead limbs. Regressions were weighted using $1/\text{Age}^2$ as the weighting value. Growth, radial growth (mm) measured at 1.4 m, 6–10 years before sampling. Temp., maximum temperature during the 24 h period before sampling.[b] P is equal to the probability of large value of t if coefficient is equal to zero.[c] Mean proximal diameter of dead primary limbs (cm).

4). The R^2 values for the weighted regressions that included large hemiptera are presented for comparison. Weighted regressions are reported for live and dead limbs (Table 5). No large hemiptera were found on limbs.

3.2.2. Whole tree

Arthropod biomass m^{-2} averaged over the whole tree was significantly related to tree age in a polynomial regression using tree age and tree age^2 (Table 3, Model 1). Arthropod biomass m^{-2} peaked at about 70 years and then declined with increasing tree age. Arthropod density on trees 50 years old was predicted to be greater than that on trees more than 100 years old.

In single variable regressions, arthropod biomass m^{-2} was significantly related to radial growth 6–10 years before the study and to the minimum tempera-

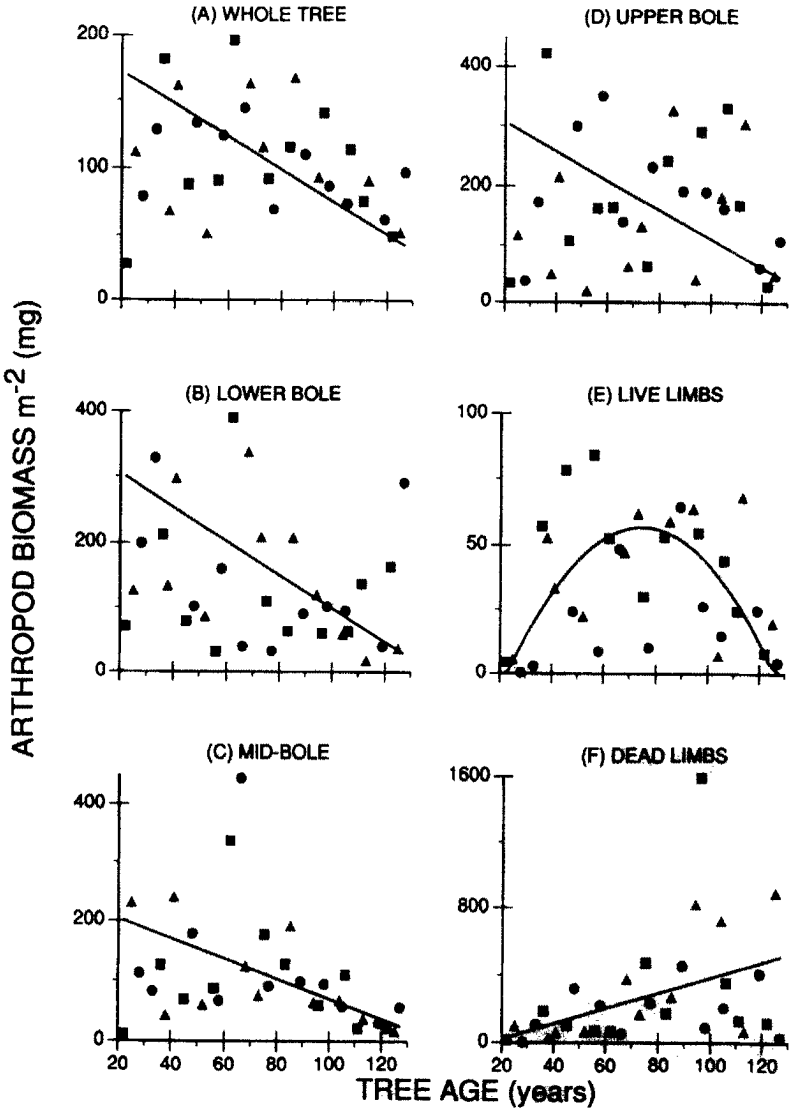

Fig. 1. Relationship between tree age and arthropod biomass m^{-2} on longleaf pines when tree age is allowed to vary and other independent variables in the regressions are held constant at their mean value. Regressions for the plots are: (A) Table 2, Model 5; (B) Table 3, Model 2; (C) Table 3, Model 4; (D) Table 3, Model 8; (E) Table 4, Model 6; (F) Table 4, Model 7. Symbols indicate the order in which observations were made: first series, ■; second series, ●; third series, ▲.

ture during the 24 h before sampling arthropods (Table 3, Models 2 and 3). Together in the same regression, radial growth and temperature accounted for 60% of the variation in arthropod biomass m^{-2} (Table 3, Model 4). Tree age, in the presence of radial growth and minimum temperature, accounted for an additional 16% of the variation in arthropod biomass m^{-2} (Table 3, Model 5). In the presence of radial growth and minimum temperature, arthropod biomass m^{-2} decreased as tree age increased (Fig. 1(A)). Bark weight and aspect did not make significant contributions to regressions.

Radial growth 6–10 years prior to the study appeared to have a major influence on arthropod biomass m^{-2}. When tree age and radial growth are allowed to vary together in the presence of minimum temperature (Fig. 2(A)), the relationship between tree age and arthropod biomass m^{-2} is somewhat different than implied in Fig. 1(A). The greatest arthropod biomass m^{-2} values were found on slow

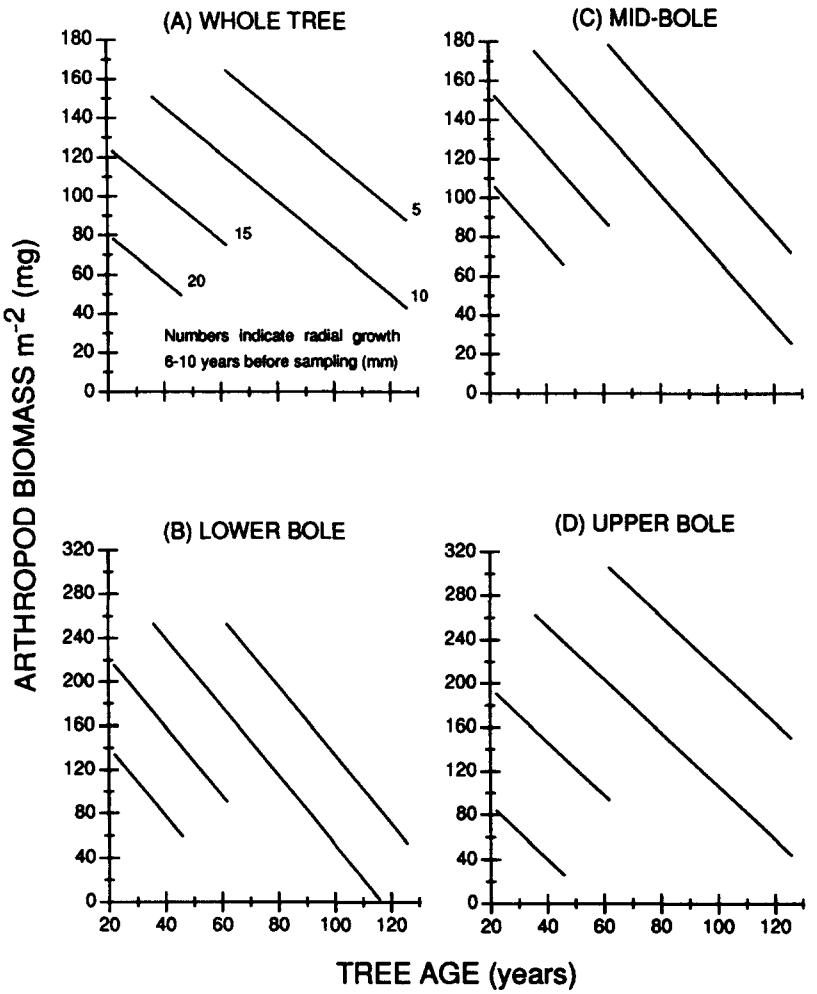

Fig. 2. Relationship between tree age, radial growth 6–10 years prior to sampling, and arthropod biomass m^{-2} (mg) on longleaf pines in winter. Minimum temperature during the 24 h prior to sampling was held constant at its mean value. Regressions for the plots are: (A) Table 2, Model (5); (B) Table 3, Model 2; (C) Table 3, Model 4; (D) Table 3, Model 8.

growing trees 40–80 years old (Fig. 2(A)), not the youngest trees (as implied in Fig. 1(A)): trees less than 30 years old had arthropod biomass m^{-2} similar to that on trees more than 110 years old, rather than substantially more.

I rejected the null hypothesis that arthropod biomass m^{-2} at the whole tree level was equal on trees of different ages. Results supported the alternate hypothesis that when averaged over the whole tree, arthropod biomass m^{-2} decreased as tree age and radial growth increased.

3.2.3. Lower bole

Tree age in combination with radial growth 6–10 years before the study was significantly related to arthropod biomass m^{-2} on the lower bole (Table 4, Model 1). The addition of minimum temperature during the 24 h before sampling to this model resulted in a significant regression that accounted for 40% of the variation in arthropod biomass m^{-2} (Table 4, Model 2). In this model, 26% of the variation in arthropod biomass m^{-2} was attributable to tree age. As tree age increased, arthropod biomass m^{-2} decreased (Fig. 1(B)). Inclusion of bark weight and aspect did not result in significant regressions.

Radial growth modified the effect of tree age on arthropod biomass m^{-2} on the lower bole (Fig. 2(B)). Slow growing trees 40–70 years old had the highest arthropod biomass m^{-2}, and trees less than 30 years old had a higher arthropod biomass m^{-2} than trees more than 110 years old.

I rejected the null hypothesis that arthropod biomass m^{-2} on the lower bole on longleaf pines was equal on trees of different ages. The results supported the alternate hypothesis that arthropod biomass m^{-2} decreased as tree age and radial growth increased.

3.2.4. Mid-bole

A three-variable regression using tree age, minimum temperature during the 24 h before sampling arthropods, and radial growth 6–10 years before the study as independent variables accounted for 51% of the variation in arthropod biomass m^{-2} (Table 4, Model 4). However, only 8% of the variation in arthropod biomass m^{-2} was attributable to tree age. As tree age increased, arthropod biomass m^{-2} decreased (Fig. 1(C)). Bark weight and aspect did not make significant contributions to regressions.

The highest values for arthropod biomass m^{-2} were found on the slowest growing trees 40–70 years old (Fig. 2(C)). Trees less than 40 years old had higher arthropod biomass m^{-2} than those more than 110 years old.

I rejected the null hypothesis that arthropod biomass m^{-2} was equal on the mid-boles of longleaf pines of different ages. The results supported the alternate hypothesis that arthropod biomass m^{-2} decreased as tree age and radial growth increased.

3.2.5. Upper bole

Tree age and tree age^2 in combination were significantly related to arthropod biomass m^{-2} on the upper bole (Table 4, Model 5). In Model (5), arthropod biomass m^{-2} increased with increasing tree age in trees less than 70 years old and decreased with increasing age in older trees. This regression only accounted for 18% of the variation in arthropod biomass m^{-2} on the upper bole.

Radial growth 6–10 years before the study, alone and in combination with minimum temperature during the 24 h before sampling arthropods, was significantly related to arthropod biomass m^{-2} (Table 4, Models 6 and 7). The addition of tree age to the growth and temperature model was significant (Table 4, Model 8). In Model 8, as tree age increased, arthropod biomass m^{-2} decreased (Fig. 1(D)). In the presence of temperature and radial growth, tree age only accounted for an additional 8% of the variation in arthropod biomass m^{-2}. Use of bark weight or aspect did not result in significant regressions.

Arthropod biomass m^{-2} on the upper bole decreased as radial growth increased (Fig. 2(D)). The greatest arthropod biomass m^{-2} was found on the slowest growing trees 40–80 years old. Trees less than 40 years old had arthropod biomass m^{-2} similar to trees more than 110 years old.

I rejected the null hypothesis that arthropod biomass m^{-2} on the upper bole of longleaf pines was equal on trees of different ages. The results supported the alternate hypothesis that arthropod biomass m^{-2} decreased as tree age and radial growth increased.

3.2.6. Live limbs

Tree age alone accounted for 18% of the variation in arthropod biomass m^{-2} on live limbs, and the

polynomial regression with age and age^2 accounted for 46% of the variation (Table 5, Models 1 and 5, respectively). Arthropod biomass m^{-2} on live limbs was significantly related to radial growth 6–10 years before the study, bark weight, and the maximum temperature during the 24 h before sampling (Table 5, Models 2, 3 and 4), but these variables did not make a significant contribution to multiple variable models.

A four-variable regression using tree age, tree age^2, elapsed days in sampling sequence and the square of elapsed days accounted for 62% of the variation in arthropod biomass m^{-2} on live limbs (Table 5, Model 6; Fig. 1(E)). In the model, arthropod biomass m^{-2} on live limbs decreased from the beginning of the sampling period to the middle and then increased back to original levels towards the end of the sampling period. This effect was similar to that detected by ANOVA's on sampling series for live limbs: Series 1 and 3 were similar, but Series 2 was lower that Series 1.

Arthropod biomass m^{-2} on live limbs increased as tree age increased (Table 5, Model 1). In Models 5 and 6 (Table 5) where considerably more variation was accounted for, arthropod biomass m^{-2} increased with tree age up to about 75 years of age and then decreased with increasing tree age (Fig. 1(E)). In all three models, trees 30 years old had as high an arthropod biomass m^{-2} on live limbs as did 120 year old trees.

I rejected the null hypothesis that arthropod biomass m^{-2} was equal on the live limbs of longleaf pines of different ages. The results supported the alternate hypothesis that arthropod biomass m^{-2} initially increased as tree age increased but then decreased in older trees.

3.2.7. Dead limbs

Arthropod biomass m^{-2} on dead limbs was significantly related to tree age (Table 5, Model 7). Biomass m^{-2} increased as tree age increased (Fig. 1(F)). No two-variable regressions were significant including polynomial models using tree age and tree age^2.

The relationship of arthropod biomass m^{-2} to tree age appeared to be caused by the increased diameter of dead limbs as tree age increased. Arthropod biomass m^{-2} was significantly related to both dead limb diameter and tree age (Table 5, Models 7 and 8). However, together in the same regression, neither mean diameter of dead limbs nor tree age was significantly related to arthropod biomass m^{-2} ($R^2 = 0.35$; df = 2, 30; probability regression coefficients = 0 was 0.38 and 0.43 for dead limb diameter and tree age, respectively). Mean diameter of dead

Table 6
Summary of regression analyses of total arthropod biomass (mg) on longleaf pines in winter

Regression model [a]	R^2	(R^2) [c]	P [b]	
			b^1	b^2
(1) $BIOMASS_{tree} = -45.66 + 48.60Age$	.55	(.31)	.0001	–
(2) $BIOMASS_{tree} = -3138.0 + 179.9Age - 1.051Age^2$	.75	(.43)	.0001	.0001
(3) $BIOMASS_{LB} = 167.4 + 11.52Age$	.22	(.21)	.006	–
(4) $BIOMASS_{LB} = -653.1 + 46.36Age - 0.2788Age^2$	.32	(.34)	.009	.040
(5) $BIOMASS_{MB} = 67.21 + 8.692Age$	.19	(NS)	.011	–
(6) $BIOMASS_{MB} = -869.9 + 48.48Age - 0.3184Age^2$	.40	(NS)	.001	.003
(7) $BIOMASS_{UB} = -90.86 + 14.05Age$	.44	(.39)	.0001	–
(8) $BIOMASS_{UB} = -721.4 + 40.82Age - 0.2142Age^2$	.52	(.48)	.002	.031
(9) $BIOMASS_{LL} = -95.27 + 8.382Age$	.25	–	.003	–
(10) $BIOMASS_{LL} = -762.3 + 36.70Age - 0.2266Age^2$	.40	–	.002	.011
(11) $BIOMASS_{DL} = -94.07 + 5.953Age$	.36	–	.0002	–

[a] $BIOMASS_{\cdot}$ is equal to arthropod biomass (mg dry weight) exclusive of hemiptera geater than 60 mg, except Models 9–11 where all arthropods were included. Subscripts: tree, entire tree; LB, lower bole, MB, mid-bole, UB, upper bole; LL, live limbs; DL, dead limbs. Age, age of longleaf pines. All regressions were weighted using $1/Age^2$ as the weighting value.[b] Probability of larger value of t if coefficient is equal to zero.[c] R^2 values for weighted regressions that included hemiptera greater than 60 (dry weight). NS, non-significant regressions.

limbs was highly correlated to tree age ($R^2 = 0.83$; df = 1, 31; $P = .0001$).

I rejected the null hypothesis that arthropod biomass m^{-2} was equal on dead limbs of longleaf pine of different ages. The results supported the alternative hypothesis that arthropod biomass m^{-2} increased as tree age increased.

3.3. Total arthropod biomass

3.3.1. Regression models

For all foraging positions and the whole tree, weighted regressions using 1/tree age^2 as the weighting value substantially increased the percentage of variation in total arthropod biomass at-

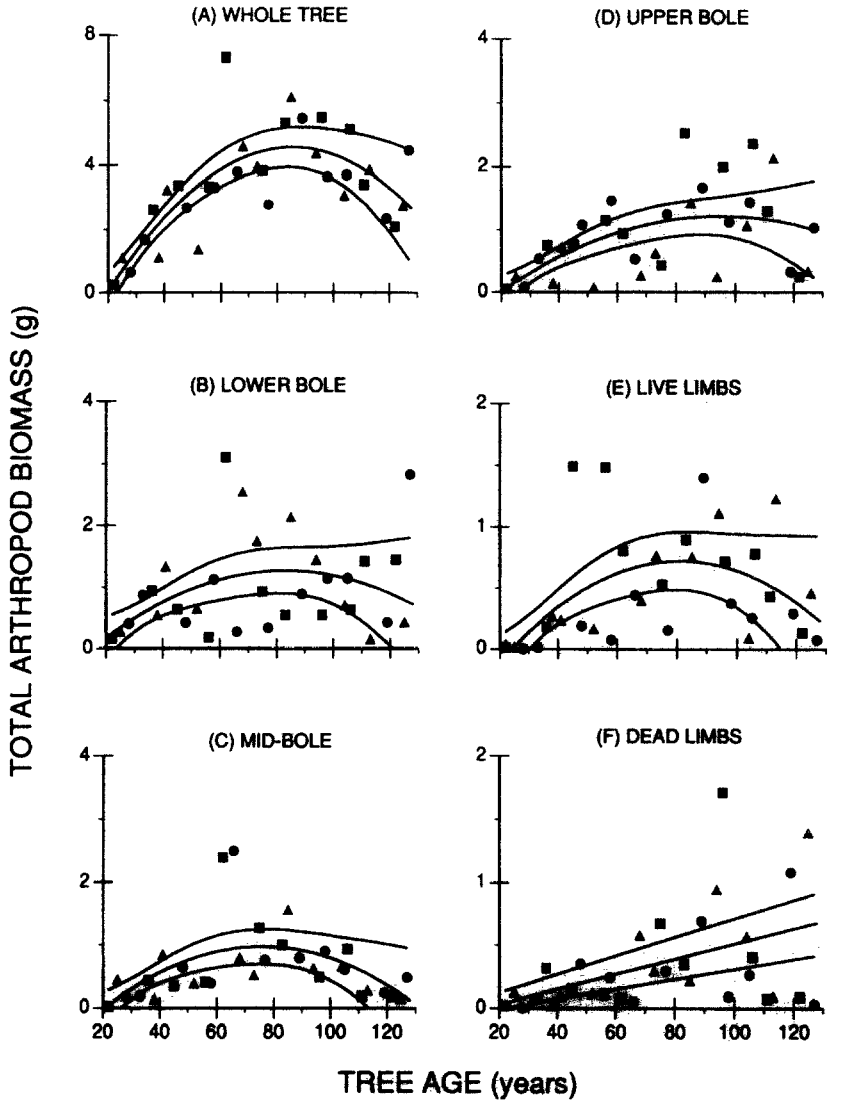

Fig. 3. Predicted total arthropod biomass (g) on longleaf pines. (A) – (E) are polynomial regressions using tree age and tree age^2. (F) is a 1-variable model using tree age. Regressions for the plots are from Table 5: (A) Model 2; (B) Model 4; (C) Model 6; (D) Model 8; (E) Model 10; (F) Model 11. Symbols indicate the order in which observations were made: first series, ■; second series ●; third series, ▲. Confidence intervals (95%) are for the mean value of the dependent variable for a given tree age.

tributable to tree age. Redefining the response variable to exclude hemiptera greater than 60 mg substantially improved the fit of regressions of total arthropod biomass on the whole tree and mid-bole. Regressions for the lower and upper bole were only slightly affected by ignoring large hemiptera. No large hemiptera were found on live and dead limbs. For simplicity, only the weighted regressions with large hemiptera ignored are presented (Table 6). In all cases, these regressions accounted for the most variation in total arthropod biomass. For comparison, R^2 values are presented for weighted regressions that include large hemiptera.

3.3.2. Effects of tree age

For the whole tree and all foraging positions, total arthropod biomass increased significantly in single variable models as tree age increased (Table 6, Models 1, 3, 5, 7, 9, and 11). Recall that for most comparisons, arthropod biomass m^{-2} decreased as tree age increased (Fig. 1(A)–1(D), Fig. 2(A)–2(D)). Thus, increasing tree surface area with tree age had a greater effect on the total arthropod biomass than decreasing arthropod biomass m^{-2} as trees grew older.

Older trees had more total arthropod biomass in dead limbs than younger trees (Fig. 3(F)) even though the surface area of dead limbs was similar across tree age classes (ANOVA: $F_{1,10}$; $P = 0.81$). The increase in total arthropod biomass in dead limbs (Fig. 3(F)) was driven by the increase in arthropod biomass m^{-2} in dead limbs as tree age increased (Fig. 1(F)).

With the exception of dead limbs, the addition of tree age^2 in polynomial regressions substantially increased the variation in total arthropod biomass attributable to tree age (Table 6, Models 2, 4, 6, 8, and 10). In the polynomial regressions, total arthropod biomass initially increased as tree age increased but then decreased with increasing tree age (Fig. 3(A)–3(E)). This response resulted primarily from the decreasing rate of surface area increases and the decline in total arthropod biomass m^{-2} as trees aged (Fig. 1(A)–1(D); 2(A)–2(D)).

I rejected the null hypothesis that total arthropod biomass was equal on longleaf pines of different ages in winter. Results supported the alternate hypothesis that total arthropod biomass increased initially with tree age up to 76-96 years (depending upon foraging position) and then declined as trees aged. An additional alternate hypothesis was needed for dead limbs where total arthropod biomass continued to increase as tree age increased.

4. Discussion

I rejected the null hypotheses that arthropod biomass m^{-2} and total arthropod biomass were equal on longleaf pines of different ages in winter. The results suggested several alternative hypotheses about the relationship of tree age to arthropod biomass m^{-2} and total arthropod biomass. These hypotheses differed among different areas on the tree. Arthropod biomass m^{-2} on the bole and averaged over the whole tree tended to decrease with increasing tree age and tree growth rate (Tables 3 and 4; Fig. 1(A)–1(D)). On live limbs, arthropod biomass m^{-2} increased with tree age up to 75 years and then declined as trees aged (Table 5; Fig. 1(E)). Arthropod biomass m^{-2} on dead limbs tended to increase as trees aged (Table 5; Fig. 1(F)).

Except on dead limbs, total arthropod biomass tended to increase with tree age up to 76–96 years depending upon area of the tree, but then decrease in older trees (Table 6; Fig. 3(A)–3(E)). Dead limbs on the other hand had increasingly greater total arthropod biomass as trees grew older (Table 6; Fig. 3F).

Excluding large arthropods from the reported regressions did not bias the conclusions of the study. Regressions without large hemiptera had slopes similar in shape and direction to regressions that included large hemiptera. Had the latter set of regressions been statistically significant, conclusions regarding tree age and arthropods would have been the same as those made from the regressions that excluded large hemiptera. Large hemiptera were found on only five of 33 trees (six of 165 foraging positions sampled) and a much larger sampling effort would be required to adequately determine their abundance. The data at hand suggests no relationship between tree age and the abundance of large hemiptera.

Negative relationships between tree age and arthropod biomass m^{-2} and biomass did not result from using weighted regressions. All the regression lines in Figs. 1 and 2 were similar to curves produced by unweighted regressions that used the same

variables, although in several cases the unweighted regressions were not significant. Use of weighted regressions improved the fit of most regression models. In several cases, the addition of variables to some weighted models were significant. These improvements in the regression models allowed an examination of the relationship of tree age to arthropod biomass, while no significant relationship had been previously found when using unweighted regressions.

Male red-cockaded woodpeckers forage substantially on dead limbs (Skorupa, 1979; Ramey, 1980; Hooper and Lennartz, 1981; Repasky, 1984), and this study suggests dead limbs are a concentrated source of prey (Table 1). Dead limbs on the oldest trees had more arthropod biomass than dead limbs on younger trees, however, more arthropod biomass was found on both the lower and upper bole of the oldest trees than on their dead limbs (Fig. 4). More arthropod biomass was also found on every foraging position except dead limbs on trees 60–100 years old, than on dead limbs of the oldest trees (Fig. 4). In addition, the increase in the diameter of dead limbs associated with increased arthropod biomass could mean an increased cost of obtaining prey from dead limbs as trees ` Older trees with their greater arthropod biomass m^{-2} and biomass on dead limbs are a valuable resource for foraging red-cockaded woodpeckers, however, the potential for older trees to meet the nutrient demands of the woodpeckers in winter does not equal the overall potential of younger trees.

Radial growth 6–10 years before the study appeared to be as important a factor in regard to arthropod biomass m^{-2} as tree age (Tables 3 and 4. Fig. 2(A)). In several cases, tree age was only significant in the presence of radial growth. Moreover, the regressions accounting for the most variation in arthropod biomass m^{-2} usually included radial growth. As expected, radial growth and tree age were inversely related (radial growth = 21.85 − 0.1669 × Tree Age; $R^2 = 0.63$; df = 1, 32; $P = 0.0001$). However, the relationship of arthropod biomass m^{-2} to growth rate and tree age was opposite that of tree age and radial growth. While younger trees were faster growing and had more arthropod biomass m^{-2} than older trees, slower growing trees tended to have more biomass m^{-2} than faster growing trees for a given tree age (Fig. 2(A)). Thus, effects of radial growth and tree age on arthropod biomass m^{-2} appear to be independent of one another.

All arthropods collected were living on or in the outer bark, except for those in dead limbs. Therefore,

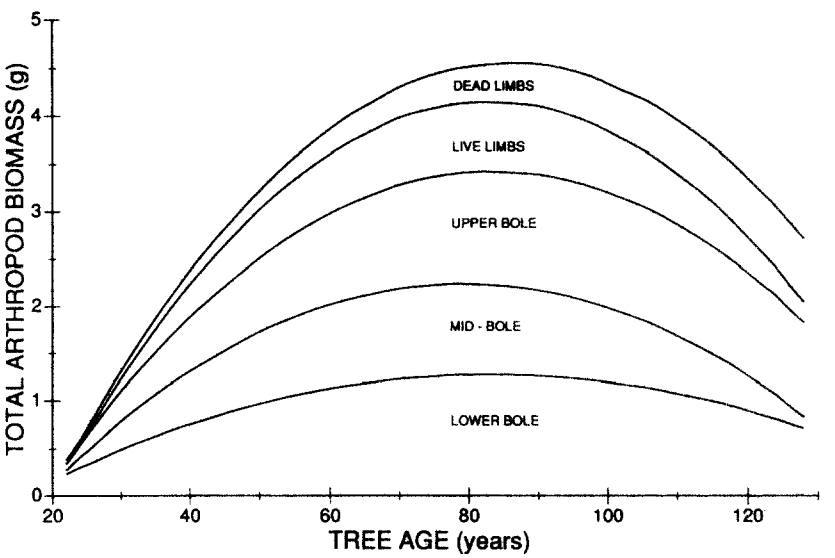

Fig. 4. The contribution of different foraging positions to the total arthropod biomass found on longleaf pines of various ages in winter. Regressions for curves are from Table 5 (Models 2,4,6,8,10, and 11).

the relationship between tree age, radial growth and arthropod biomass m^{-2} may be driven by the effect of tree age and radial growth on the physical and chemical characteristics of the outer bark because tree age and growth rate affect bark characteristics (Koch, 1972, p. 483). Older trees frequently had slick, tight bark that was difficult to remove, while younger trees more often had exfoliate bark that provided cover for arthropods. Considerable variation in the degree of exfoliation in bark existed among trees of similar ages. Exfoliation is determined by periderm formation (Kramer and Kozlowski, 1979, p. 41), which could be age related and genetically determined, as has been suggested for other characteristics on other tree species (Strong et al., 1984, p. 188). Differences in exfoliation among trees may have accounted for a significant proportion of the variation in arthropod biomass m^{-2}. However, I was unable to devise a method of quantifying this characteristic. Bark weight alone was not a significant factor associated with arthropod biomass m^{-2} except on live limbs. Other physical properties of bark related to growth rate, and perhaps tree age, include specific gravity and specific heat (Koch, 1972, pp. 502, 509). These factors could possibly influence the microclimate of bark which in turn could affect arthropods (Nicolai, 1986).

The outer bark contains an abundance of deposited materials such as tannins, phlobaphenes, and other phenolic substances (Koch, 1972, p. 477). Some of these compounds affect some insects under certain conditions (Strong et al., 1984, pp. 197–200, Harborne, 1988, pp. 82–119). To what extent bark serves as a nutrient source for resident arthropods and to what extent growth rate affects the chemical composition of bark, is unknown. Radial growth 6–10 years before the study was significantly related to arthropod density (Tables 3–5), but radial growth 1–5 years before the study was not. The outermost bark layer is the oldest, and its chemical content and physical characteristics were determined when it was living inner bark. I could not determine the age of the outermost layers of bark, but they were obviously closer to 6–10 years old than to 1–5 years old.

Arthropod biomass m^{-2} decreased on the bole as minimum temperature within the 24 h before sampling increased (Tables 3 and 4), but the reason is not clear. Arthropods are more active in warmer weather, but no evidence suggested that more arthropod were escaping capture in warmer weather. The biomass of escaped arthropods was not correlated to minimum temperature (Pearson correlation coefficients equal 0.14, 0.04, and −0.03 for the lower, mid- and upper bole and $P = 0.43$, $0.81 \wedge 0.86$, respectively). In addition, the arthropod biomass m^{-2} on live limbs increased as temperature increased (Table 5). Thus, higher temperatures probably did not bias results. Arthropods may have been moving out of sample plots ahead of the bark removal in warmer weather or more arthropods may have been seeking shelter on the bole in colder weather, but no evidence exists to support either hypothesis.

The methods used to sample arthropods mimicked the foraging techniques of red-cockaded woodpeckers, i.e. scaling and excavation of bark and the excavation of dead limbs (Hooper and Lennartz, 1981). Although bark removal was an effective method of collecting relatively inactive arthropods in winter, the use of ladders and safety belts made it impossible to control for variation within foraging positions on the bole. This weakness probably contributed to some of the unexplained variation in the regression models.

Except on dead limbs, different or additional sampling methods might be necessary in other seasons when arthropods are more active. Sampling considerations were a primary reason this study was conducted in winter. Studies in other seasons would likely be more difficult. The other reason for the winter study was that food resources may be more critical in winter than in other seasons, and thus, arthropod-tree age relationships potentially more important.

When selecting trees for foraging sites, red-cockaded woodpeckers must deal with the variation in arthropod biomass m^{-2} and total yield of arthropod biomass among trees of different ages. Although the red-cockaded woodpecker may theoretically have the most specialized foraging behavior of the extant woodpecker species in the Southern United States (Skorupa, 1979), it is clearly plastic in its selection of the sizes and ages of pine trees used for foraging (Skorupa, 1979; Ramey, 1980; Hooper and Lennartz, 1981; DeLotelle et al., 1983; Repasky, 1984; Hooper and Harlow, 1986; Porter and Labisky, 1986; DeLotelle et al., 1987). This plasticity would enable the

red-cockaded woodpecker to exploit the greater biomass m^{-2} of arthropods found on the boles of younger trees, the greater total biomass of arthropods found on the bole and live limbs of pines 70–100 years old, and the greater total biomass of arthropods found on the larger dead limbs of older pines. That longleaf pines of various ages appear to offer different advantages to foraging woodpeckers may account for the failure of past studies to demonstrate an increasing preference for trees more than 30 years old and greater than 25 cm dbh.

Because this study was limited to one season, it is important to point out that arthropod-tree age relationships may be different at other seasons when arthropods are more active and in different stages of their life cycles. Also, because of the yearly variation in the abundance of arthropods, arthropod–tree age relationships may be different across years.

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