

RELATION OF RAMET SIZE TO ACORN PRODUCTION IN FIVE OAK SPECIES OF XERIC UPLAND HABITATS IN SOUTH-CENTRAL FLORIDA¹

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This study examined variation in two components of acorn production. Percentage of bearing ramets (stems) and number of acorns per bearing ramet were examined in five clonal oaks in three xeric habitats of south-central peninsular Florida in relation to ramet size within and between species and vegetative associations. Counts of acorns on two white oaks (*Quercus chapmanii* and *Q. geminata*) and three red oaks (*Q. inopina*, *Q. laevis*, and *Q. myrtifolia*) were conducted annually from 1969 to 1996 (except in 1991) on permanent grids in southern ridge sandhill, sand pine scrub, and scrubby flatwoods associations at the Archbold Biological Station, Florida, USA. Percentage of bearing individuals and mean number of acorns per bearing individual increased with increasing ramet size for all species across all vegetation associations. However, in *Q. geminata* and *Q. myrtifolia*, acorn production declined in the largest size class (>3.2 m), implying that larger individuals of these clonal species may become senescent. All oak species in sand pine scrub, which had a nearly closed overstory, had lower frequencies of bearing oaks and mean numbers of acorns compared with similar-sized individuals of the same species in the more open-canopied southern ridge sandhill and scrubby flatwoods associations, suggesting light limitation. The annual production of acorns by a given oak species was correlated across vegetative associations and annual acorn production of oak species was correlated for species within the same section. Intermediate-size class oaks contributed the most acorns per unit area, suggesting that stands managed with short fire-return times will provide fewer acorns to wildlife than stands managed to produce more variable distributions of oak size classes. However, our study suggests that long-unburned stands, such as those studied here, will maintain relatively constant levels of acorn production as a consequence of ramet replacement within the clones of these shrubby oaks to create a variable distribution of size classes. Of the oak species studied, *Q. myrtifolia* had the highest acorn production and the smallest acorns, while *Q. laevis* had the lowest acorn production and the largest acorns, suggesting an allocation trade-off between acorn numbers and size.

Key words: acorn; fire ecology; mast; *Quercus*; ramet; size-specific reproduction.

The number of seeds produced by an individual long-lived plant can vary markedly according to climatic and site conditions, species, genotype, and size (e.g., Harper and White, 1974; Klinkhamer et al., 1992). While an individual's production of seed often is related to its life-history strategy (Harper and Ogden, 1970; Stearns, 1977; Caswell, 1982), a specific individual's annual seed production typically is dependent on the resources that it has accumulated. Hence reproduction can be correlated with the individual's size or age (Harper and White, 1974; Schmid, Bazzaz, and Weiner, 1995; Mendoza and Franco, 1998; Reekie, 1998). In oaks, for example, acorn yields and the frequency of individuals bearing acorns generally increase with size (Goodrum, Reid, and Boyd, 1971; Moody, 1985; but see Downs and McQuilkin, 1944; Beck and Olson, 1968). Similarly, the number of seeds produced per individual can vary from site to site (Crawley and Long, 1995). For example, individual plants growing in resource-limited sites would be expected to produce smaller numbers of seeds compared with individuals of the same species and

size in more optimal sites (e.g., Abrahamson, 1979). Furthermore, because resource availability affects growth rates, the time required to accumulate sufficient resources to enable reproduction can be increased in resource-limited environments.

The objectives of this study were to assess the relative effects of species, site (vegetation association), and ramet size on two components of acorn production. The frequency of individual stems bearing acorns and the mean number of acorns per bearing individual were measured in five species of oaks occurring in three xeric upland vegetation associations in south-central peninsular Florida.

Two of the five oak species studied, *Quercus chapmanii* Sargent (Chapman oak) and *Q. geminata* Small (sand live oak), are representatives of the white oak group (*Quercus* section *Quercus*), while three species, *Q. myrtifolia* Willdenow (myrtle oak), *Q. inopina* Ashe (Archbold oak), and *Q. laevis* Walter (turkey oak), are members of the red/black oak group (*Quercus* section *Lobatae*) (Jensen, 1997; Nixon and Muller, 1997). This mix of representatives from two sections of *Quercus* provides an opportunity for comparison of acorn production patterns among congeners differing in reproductive biology, specifically the length of time (2 vs. 3 yr) from flower initiation to development of mature acorns.

Quercus chapmanii and *Q. geminata* are common in southern ridge sandhill, sand pine scrub, and scrubby flatwoods, while *Q. myrtifolia* is generally abundant in southern ridge sandhill and sand pine scrub but uncommon in scrubby flatwoods. The central Florida endemic *Q. inopina*, a highly clonal shrub, is dominant only in scrubby flatwoods, while *Q. laevis* is characteristic of only southern ridge sandhill and is in-

¹ Manuscript received 2 March 2001; revision accepted 3 July 2001.

The authors thank F. E. Lohrer and C. E. Winegarner for their long-term support of annual field surveys and J. F. Douglass, L. C. Layne, M. McCauley (Connor), A. Stinchfield, R. D. Jennings, C. W. Harris, S. Craft, A. F. Johnson, C. R. Abrahamson, D. R. Smith, D. Fleck, P. A. Frank, K. R. Lips, N. Stotz, S. Denton, L. K. Harb, C. C. Smith, and I. A. Kralick for providing additional field assistance or helpful comments. The Archbold Biological Station and the Burpee Chair endowment of Bucknell University supported this work.

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frequent or absent in other vegetative associations (Abrahamson et al., 1984; Givens et al., 1984; Menges et al., 1993).

Four of the five oaks examined in our study possess evergreen leaves and have a shrub- rather than a tree-growth form. Only *Q. laevis* has deciduous leaves and a tree-growth form. Although a number of acorn production data sets exist for deciduous oaks with tree-growth forms (e.g., Sork, Bramble, and Sexton, 1993; Koenig et al., 1996), our study is apparently the first to include shrubby evergreen oaks and compare acorn production of multiple species across different vegetation associations.

The species of xeric uplands in peninsular Florida have experienced recurrent and relatively frequent fire during their evolutionary history (Abrahamson and Hartnett, 1990; Myers, 1990). Our study sites last experienced fire in 1927, which, based on early photographs and records, punctuated a period of more frequent fire (Abrahamson et al., 1984; Abrahamson and Abrahamson, 1996). Such lengthy fire-free periods are uncommon for at least southern ridge sandhill and scrubby flatwoods. The prolonged fire-free interval in these associations raises the additional question of how long-term absence of fire affects acorn production in fire-adapted oak species.

MATERIALS AND METHODS

Description of study area—The study area, Archbold Biological Station (ABS), is characterized by residual sandhills, relic beach ridges, and paleo-sand dunes (Brooks, 1981), with elevations ranging from 38 to 65 m above mean sea level (United States Geological Survey, Childs, Florida, 7.5' quadrangle). Archbold Biological Station is located 12 km south of the town of Lake Placid (27°11' N, 81°21' W), near the southern terminus of the Florida peninsula's Lake Wales Ridge.

The oaks of scrubby flatwoods occur at elevations of 41–44 m on well-drained sandy soils, whereas oaks at the highest elevations (59–65 m) occur in southern ridge sandhill on excessively well-drained sands. Intermediate elevations (42–50 m) occupied by oaks occur in sand pine scrub (Abrahamson et al., 1984).

Scrubby flatwoods are a low (1–2 m) shrubby association dominated by evergreen, xeromorphic oaks including *Q. inopina*, *Q. chapmanii*, and *Q. geminata*, as well as abundant dwarf palms, *Serenoa repens* (saw palmetto) and *Sabal etonia* (scrub palmetto). The pines, *Pinus elliotii* var. *densa* (south Florida slash pine) and *P. clausa* (sand pine), are typically widely scattered and occur at variable densities. In contrast, sand pine scrub is characterized by a tree overstory of nearly even-aged *P. clausa*, an intermediate canopy of shrubby trees including *Carya floridana* (scrub hickory), *Q. myrtifolia*, *Q. geminata*, and *Q. chapmanii*, and an understory of *Serenoa* and *Sabal* palmettos. Also a multilayered community, southern ridge sandhill has an overstory of *Pinus elliotii* var. *densa*, an intermediate deciduous canopy of *Q. laevis* and *C. floridana*, and a shrub and understory layer of *Q. myrtifolia*, *Q. geminata*, *Q. chapmanii*, *Serenoa*, *Sabal*, *Aristida stricta* (wiregrass) and forbs. Southern Lake Wales Ridge *Q. laevis* exhibit a stunted growth form compared with their more northerly counterparts. More detailed descriptions of these vegetation associations are given by Abrahamson et al. (1984), Abrahamson and Hartnett (1990), and Myers (1990).

The climate of the study area is characterized by hot, rainy summers and mild, dry winters. Highest monthly mean temperature occurs in August (27.5°C) and the lowest in January (16°C). Approximately 60% of the annual precipitation (1351 mm, 67-yr mean) falls during the 4-mo period of June through September (ABS weather records).

Sampling of acorn production—Annual counts of acorns for each species were conducted on three 2.7-ha grids from 1969 to 1996, with the exception of 1991 (counts for *Q. inopina* and *Q. myrtifolia* were combined from 1969–1971, and separate counts for these oaks began in 1972). The grids were

placed in representative stands of each vegetation association and consisted of 12 × 12 arrays of permanently marked stations at 15-m intervals.

Because of annual variation in the timing of development of acorns, the dates of counts ranged from early August to early October, with most falling in September. In all census years, counts were conducted when the acorns were well enough developed to distinguish between normal and aborted acorns but before they were ripe enough to be harvested in appreciable numbers by birds and rodents.

Each year, 60 ramets (stems) of each species (except for *Q. laevis*, see below) were sampled on each grid. Acorns were counted on one ramet in each of the four quadrants at 15 stations evenly distributed over the grid. Sample stations were placed 30 m from one another within the same row and 60 m from one another within the same column. All sampling stations were at least 15 m from any boundary of the grid. The acorn-sampling stations were the same as those used in three vegetation surveys conducted in 1969, 1979, and 1989 (Givens et al., 1984; Menges et al., 1993). These surveys provide mean density (number of ramets per square meter) estimates for each oak species in southern ridge sandhill, sand pine scrub, and scrubby flatwoods, respectively, as follows: *Q. myrtifolia*, 35.1, 52.1, 6.7; *Q. chapmanii*, 10.3, 6.0, 11.6; *Q. geminata*, 41.0, 20.5, 25.8; *Q. laevis*, 5.5, 0.2, 0; *Q. inopina*, 0, 0, 24.4 ramets/m².

At each station, the nearest ramet of each species in each quadrant was selected subject to the following qualifications: (1) Ramets within 1 m of the path between stations were not sampled to exclude individuals that might have been damaged by foot traffic or trimming and obviously damaged and abnormal individuals away from paths also were avoided. (2) Only one ramet of a given clone was sampled at a given station. (3) No more than five individuals of the same species in the smallest size class (0.3–0.8 m) were sampled, as only very rarely did oaks of that size produce acorns. Other than for this adjustment, size classes of samples reflect the actual size distributions. (4) Because *Q. laevis* ramets on the sand pine scrub grid were rare and restricted to one portion of the grid, only 30 randomly selected ramets of this species were counted and without reference to stations.

The sizes of ramets were characterized by heights that were recorded to the nearest 0.3 m, and all acorns, including fresh caps, on bearing individuals were counted. The highly variable distribution of acorns on these shrubby oaks necessitated that a total be calculated for all acorns on a given ramet because most or all of the nuts often occurred on only one or a few branches. Acorns on *Q. myrtifolia*, *Q. chapmanii*, and *Q. geminata* tended to be on the upper branches. Counts of acorns on the occasional taller individuals (>4 m) were difficult and undoubtedly less accurate than for smaller individuals. Because of the sparse and nonrandom distribution of acorns on individual stems, we believe that visual surveys and total counts of acorns on individual ramets were more efficient and produced more accurate estimates of acorn production than ground-level acorn traps. Admittedly, absolute counts of acorns on individual ramets were possible because of the small stature of these oaks.

For purposes of analysis, ramets were broken down into size classes as follows: class 1 = 0.3–0.8 m, 2 = 0.9–1.4 m, 3 = 1.5–2.0 m, 4 = 2.1–2.6 m, 5 = 2.7–3.2 m, and 6 = >3.2 m. Arcsine-transformed percentages of ramets bearing acorns were used for all statistical analyses, but we report only the untransformed percentages for ease of interpretation. Two-way analyses of variance (ANOVA) using the general linear model (GLM) univariate procedure with Tukey honestly significant difference (HSD) posthoc tests were used to test for differences among size classes, species, and vegetation associations. Pearson correlations were utilized to explore the synchrony of acorn production across vegetation associations by species. Statistical analyses were performed using the SPSS statistical package for Windows (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Acorn production by species and vegetation association—When data were pooled for all years, size classes, and vegetation associations, oak species differed significantly in their overall mean numbers of acorns per bearing ramet ($F_{4, 67} = 3.47$, $P = 0.01$) and the overall mean percentage of bearing

TABLE 1. Overall species means (± 1 SE) and rank (in parentheses) for percentages of ramets bearing acorns and the numbers of acorns per bearing ramet across size classes and vegetation associations.

Species	Ramets bearing acorns (%)		No. of acorns per bearing ramet	
	Means ± 1 SE	Rank	Means ± 1 SE	Rank
White oaks				
<i>Quercus chapmanii</i>	59.1 \pm 5.3	1	18.9 \pm 4.1	2
<i>Quercus geminata</i>	40.3 \pm 4.8	3	12.6 \pm 2.3	3
Red oaks				
<i>Quercus myrtifolia</i>	45.9 \pm 6.8	2	28.5 \pm 6.6	1
<i>Quercus inopina</i>	38.9 \pm 9.8	4	9.6 \pm 2.6	4
<i>Quercus laevis</i>	34.1 \pm 6.8	5	7.3 \pm 1.1	5

ramets ($F_{4,67} = 2.45, P = 0.05$) (Table 1). *Quercus chapmanii* and *Q. myrtifolia* exhibited the highest acorn production, while *Q. inopina* and *Q. laevis* were low producers. *Quercus geminata* was intermediate in both the frequency with which ramets produced acorns and the numbers of acorns borne per reproductive ramet.

Acorn production also varied according to vegetation as-

sociation. Overall, the oak species of sand pine scrub bore significantly fewer acorns per bearing ramet (7.7 ± 1.2 , mean ± 1 SE) than oaks in southern ridge sandhill (22.2 ± 4.1) or scrubby flatwoods (21.2 ± 4.6) (two-way ANOVA: vegetative association $F_{2,60} = 5.96, P = 0.004$ and species $F_{4,60} = 3.98, P = 0.006$). The interaction term was not significant. The highest producer, *Q. myrtifolia*, averaged 38.9 ± 12.1 and 35.2 ± 14.2 acorns per bearing ramet in southern ridge sandhill and scrubby flatwoods, respectively, but only 11.3 ± 3.2 in sand pine scrub. Comparable figures for *Q. geminata* were $19.1 \pm 4.4, 14.3 \pm 3.3,$ and 4.5 ± 0.9 acorns per bearing ramet for southern ridge sandhill, scrubby flatwoods, and sand pine scrub, respectively. Even though the number of acorns per bearing ramet varied across vegetative associations, the percentage of ramets bearing acorns did not vary significantly among vegetative associations.

Oaks of sand pine scrub also showed lower acorn production levels within comparable size classes of the same species in other associations (Fig. 1). For example, the >3.2 m size class of *Q. myrtifolia* averaged 98.3 ± 12.9 acorns per bearing ramet in open-canopied scrubby flatwoods, however this mean

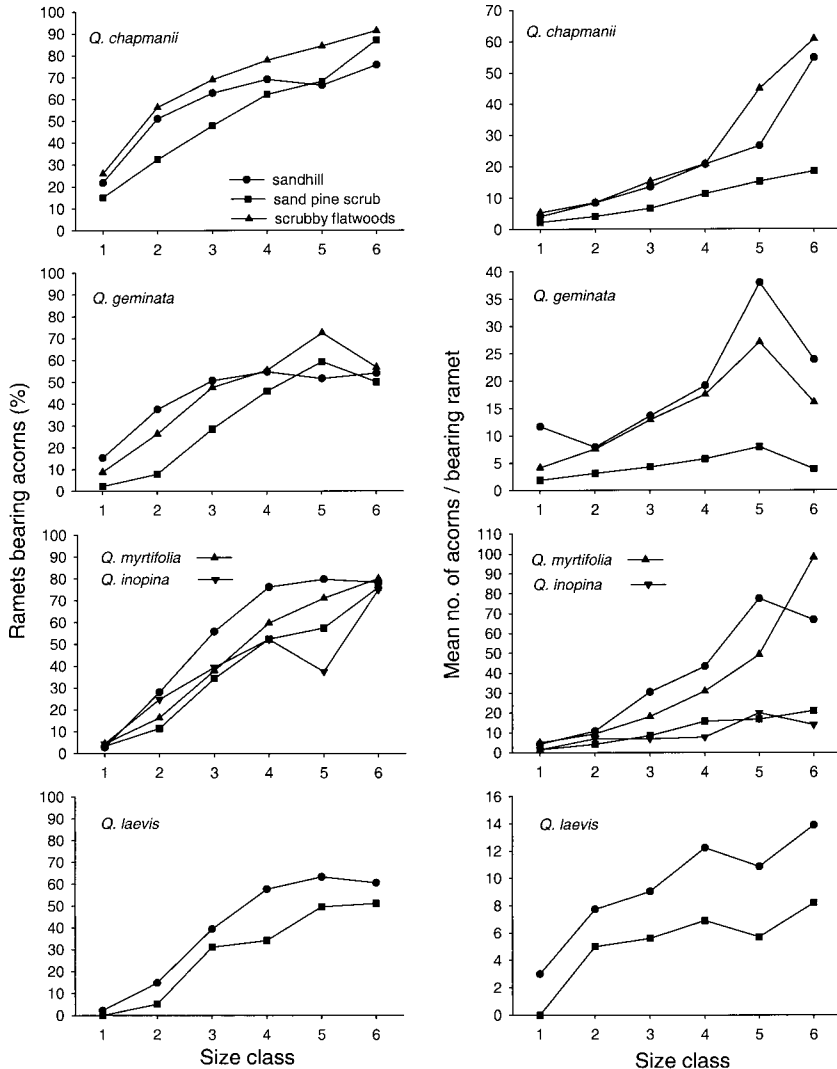


Fig. 1. Percentage of ramets bearing acorns and mean number of acorns per bearing ramet in different size classes of five oak species in three xeric upland vegetative associations in south-central Florida. Size classes: 1 = 0.3–0.8 m, 2 = 0.9–1.4 m, 3 = 1.5–2.0 m, 4 = 2.1–2.6 m, 5 = 2.7–3.2 m, 6 = >3.2 m.

TABLE 2. Coefficients of variation (CV) and CV rank (in parentheses) for mean number of acorns per bearing ramet for oak species by vegetation association. *Quercus inopina* does not occur in southern ridge sandhill or sand pine scrub and *Q. laevis* does not occur in scrubby flatwoods.

Species	Association					
	Southern ridge sandhill		Sand pine scrub		Scrubby flatwoods	
	CV	Rank	CV	Rank	CV	Rank
White oaks						
<i>Quercus chapmanii</i>	169.6	4	161.5	2	175.4	4
<i>Quercus geminata</i>	202.0	2	138.5	3	189.7	2
Red oaks						
<i>Quercus myrtifolia</i>	204.3	1	179.0	1	207.5	1
<i>Quercus inopina</i>	—	—	—	—	176.4	3
<i>Quercus laevis</i>	171.0	3	138.3	4	—	—
Mean	186.7		154.3		187.3	

dropped to 66.9 ± 15.5 acorns per in the partial-canopied southern ridge sandhill and to only 21.1 ± 3.8 acorns per in the nearly closed-canopied sand pine scrub. Mean photosynthetically active radiation (PAR) light levels during January at midday increased from 61 800 ergs·cm⁻²·s⁻¹ in sand pine scrub to 119 000 in southern ridge sandhill to 154 000 in scrubby flatwoods (Abrahamson and Rubinstein, 1976).

The reduced level of acorn production of all oaks in sand pine scrub was also reflected in reduced variability (Table 2). The mean coefficient of variation (CV) for numbers of acorns per bearing ramet for the four species on the sand pine scrub grid was 154.3 compared to 186.7 for the same four species growing in southern ridge sandhill. Similarly, the mean CV for the three oak species shared by sand pine scrub and scrubby flatwoods was 159.7 vs. 190.9, respectively.

Ramet-size effects on acorn production—Data from pooled counts for all years analyzed by size class within oak species across vegetative associations showed that the smallest ramets of all species infrequently bore acorns and that those small ramets that did become reproductive produced few acorns. Furthermore, acorn production generally increased with ramet size (Fig. 1). A two-way ANOVA found that the frequency with which ramets bore acorns increased with size class ($F_{5,42} = 65.7$, $P < 0.001$) and differed by oak species ($F_{4,42} = 16.9$, $P < 0.001$). There was no interaction of size class and species. A Tukey HSD posthoc test performed on the transformed frequencies found four subsets among the six size classes. Subset A included only size class 1 (mean percentage ± 1 SE of 8.9 ± 8.6) and subset B was composed of only size class 2 (26.0 ± 16.3). Subset C contained size classes 3 and 4 (45.4 ± 12.6 and 58.1 ± 12.3 , respectively) and subset D again included size class 4, as well as size classes 5 and 6 (63.4 ± 13.3 and 69.6 ± 14.4 , respectively). The Tukey HSD posthoc test showed three subsets among oak species. Subset A was composed of *Q. laevis*, *Q. inopina*, and *Q. geminata*; subset B included *Q. inopina*, *Q. geminata*, and *Q. myrtifolia*; and subset C included only *Q. chapmanii* (Table 1).

Similarly, a two-way ANOVA on the mean number of acorns per bearing ramet found a significant effect of ramet size class ($F_{5,42} = 5.6$, $P < 0.001$) and species ($F_{4,42} = 5.5$, $P = 0.001$). Again, there was no interaction of size class and species. A Tukey HSD posthoc test found three subsets among the six size classes. The four smallest size classes of ramets formed subset A, size classes 3, 4, and 5 formed subset B, and

subset C contained size classes 4, 5, and 6. The Tukey HSD posthoc test showed two subsets of species; subset A was composed of *Q. laevis*, *Q. inopina*, *Q. geminata*, and *Q. chapmanii* and subset B included *Q. geminata*, *Q. chapmanii*, and *Q. myrtifolia* (Table 1).

Two of the four shrubby oaks showed declines in acorn production for their largest size class. The largest ramet size class of *Q. geminata* exhibited declines in acorn production in all vegetative associations, as did the largest size class of ramets of *Q. myrtifolia* in southern ridge sandhill (Fig. 1). In addition, the percentage of bearing ramets remained constant or declined slightly from size class 5 to 6 for the tree growth form *Q. laevis* in both sand pine scrub and southern ridge sandhill, and the mean number of acorns per bearing ramet declined slightly from size class 5 to 6 for the highly clonal *Q. inopina*. Such declines may suggest that large ramets of these clonal species may become senescent.

The combined effects of ramet-size variation and differences among species produced more variation in some oaks than others. For example, the coefficients of variation showed that *Q. myrtifolia* was the most variable for numbers of acorns produced per bearing ramet in each of the three associations, while *Q. laevis* exhibited relatively low variability (Table 2). This may be a partial consequence of the relatively high numbers of acorns per bearing ramet for *Q. myrtifolia* vs. the relatively low numbers for *Q. laevis*.

Acorn production and ramet size in red vs. white oaks—

The smallest individuals (0.3–0.8 m) of the three red oaks (*Q. laevis*, *Q. myrtifolia*, and *Q. inopina*) exhibited very low incidence (<5%) of acorn production across all vegetation associations and on average never generated more than five acorns per bearing ramet (Fig. 1). In contrast, even though the smallest size classes of the two white oaks (*Q. geminata* and *Q. chapmanii*) had a low frequency of acorn production compared to larger size classes, the frequencies of small ramets bearing acorns were markedly higher than for red oaks. As many as 26% of the smallest size class of *Q. chapmanii* in scrubby flatwoods produced acorns, as did 15% of the smallest *Q. geminata* in southern ridge sandhill. The highest mean number of acorns per bearing ramet in the smallest size class was 12 for *Q. geminata* in southern ridge sandhill.

For the largest size classes, variation among red and white oak species overlapped (Fig. 1). For example, the highest incidence of bearing ramets was 91% for the >3.2 m size class of the white oak *Q. chapmanii* in scrubby flatwoods and 80% for the 2.7–3.2 m size class of the red oak *Q. myrtifolia* in southern ridge sandhill. The lowest frequencies for the largest size class were 50% for the white oak *Q. geminata* and 51% for the red oak *Q. laevis*, both in sand pine scrub. Among the largest size classes, *Q. myrtifolia* bore the highest numbers of acorns per bearing ramet (up to 78–98 per ramet in southern ridge sandhill and scrubby flatwoods) while another red oak, *Q. laevis*, produced the lowest numbers per ramet (≤ 14 per ramet). The white oaks exhibited intermediate means with up to 61 acorns per bearing ramet for *Q. chapmanii* and up to 38 per bearing ramet on *Q. geminata*. The largest size classes of the closely related *Q. myrtifolia* and *Q. inopina* (Johnson and Abrahamson, 1982; Abrahamson et al., 1998) exhibited vastly different mean numbers of acorns per bearing ramet. Overall, there were no significant differences for the percentages of ramets bearing acorns or the number of acorns per bearing

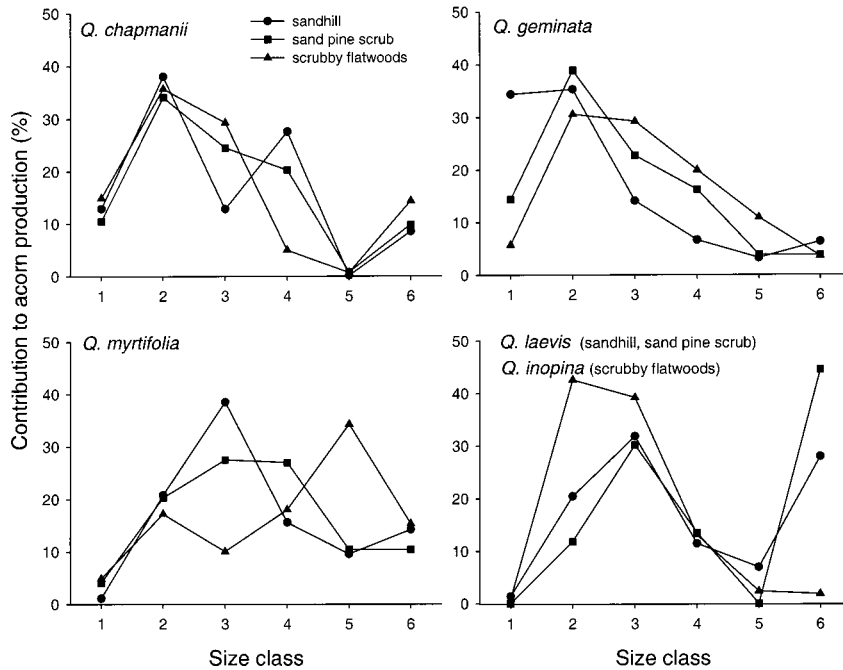


Fig. 2. Percentage contribution of different ramet-size classes to acorn production for four oak species in three xeric upland vegetative associations in south-central Florida. Mean number of acorns for different size classes based on 27 yr of counts, and mean density of ramets derived from vegetation censuses of the study grids in 1969, 1979, and 1989 (ramet density for *Q. inopina* is based on 1979 and 1989 surveys, as the identity of ramets of *Q. myrtifolia* and *Q. inopina* were not differentiated in 1969). Symbols for plots shown in graph for *Q. chapmanii* apply to all graphs. Ramet lengths included in each size class as follows: 1 = 0.3–0.8 m, 2 = 0.9–1.4 m, 3 = 1.5–2.0 m, 4 = 2.1–2.6 m, 5 = 2.7–3.2 m, 6 = >3.2 m.

ramet between comparable size ramets of the red oak section and white oak section.

Size-class contributions to community-level acorn production—The proportional contribution of ramet-size classes to acorn production in the five oak species in different associations weighted according to the density distribution of ramet-size classes in the three study grids showed a general trend of the intermediate-sized ramets contributing relatively more to overall acorn production (Fig. 2). In spite of the greater ramet density of smaller ramets, intermediate-sized ramets generally produced more acorns per unit area because of the low acorn counts of small-sized ramets. Similarly, although large-sized ramets had higher acorn counts than intermediate-sized ramets, their low density reduced their contribution. Exceptions to this general trend are *Q. myrtifolia* in scrubby flatwoods, in which ramets of the next to the largest size class contributed more to acorn production than those of more intermediate size classes, and *Q. laevis*, which in both sandhill and sand pine scrub

exhibited a strong bimodal curve with high production by one of the smaller and the largest size classes. In the case of *Q. myrtifolia*, the difference reflects a higher percentage of large individuals on the open-canopied scrubby flatwoods grid than in the other associations. The strong bimodal trend for *Q. laevis* results both from low frequency of ramets in size class 5 plus the higher frequency of larger ramets of this tree-growth form species compared to the shrubby oaks.

Multi-annual variation in acorn production across vegetation associations—Over the 27-yr span of acorn monitoring, annual production was relatively synchronized within a given oak species across vegetation associations (Table 3). The percentage of bearing ramets was positively correlated between associations, with the single exception of *Q. myrtifolia* in southern ridge sandhill and scrubby flatwoods. But even for this exception, the correlation coefficient approached significance ($r = 0.38$, $P = 0.07$). Annual variations in the numbers of acorns per bearing ramet within a species also were posi-

TABLE 3. Pearson correlation coefficients (r) and probabilities for annual acorn production measures within oak species occurring in two or more vegetation associations. Percentages of bearing ramets were arcsine transformed prior to correlation. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, and ^{NS}, not significant. *Quercus laevis* does not occur in scrubby flatwoods.

Species	Southern ridge sandhill vs. sand pine scrub		Southern ridge sandhill vs. scrubby flatwoods		Sand pine scrub vs. scrubby flatwoods	
	Ramets bearing acorns (%)	No. of acorns/bearing ramet	Ramets bearing acorns (%)	No. of acorns/bearing ramet	Ramets bearing acorns (%)	No. of acorns/bearing ramet
White oaks						
<i>Quercus chapmanii</i>	0.81***	0.72***	0.60***	0.20 ^{NS}	0.50**	0.49**
<i>Quercus geminata</i>	0.50**	0.17 ^{NS}	0.65***	0.58***	0.70***	0.28 ^{NS}
Red oaks						
<i>Quercus myrtifolia</i>	0.55**	0.61***	0.38 ^{NS}	0.41*	0.68***	0.76***
<i>Quercus laevis</i>	0.85***	0.83***	—	—	—	—

tively correlated between associations in seven of ten comparisons. One contrast for *Q. chapmanii* and two comparisons for *Q. geminata* were nonsignificant. *Quercus laevis*, which had low CVs for both acorn production measures, exhibited the strongest correlations of acorn production measures across associations (Tables 2 and 3).

In striking contrast, there were few significant correlations (four of 18 comparisons for the percentages of bearing ramets and three of 18 contrasts for mean number of acorns per bearing ramet) of acorn production measures between oak species within a vegetation association. Furthermore, the significant correlations that did occur were between species of the same section of *Quercus*. For example, the white oaks *Q. chapmanii* and *Q. geminata* growing in sand pine scrub were correlated significantly for the percentage of bearing ramets and number of acorns per bearing ramet ($r = 0.65$, $P < 0.001$ and $r = 0.45$, $P = 0.02$, respectively) and also had a significant correlation for percentage of bearing ramets in scrubby flatwoods ($r = 0.69$, $P < 0.001$). Similarly, for the red oaks *Q. myrtifolia* and *Q. laevis* there was a significant association for both the percentage of bearing ramets and number of acorns per bearing ramet ($r = 0.53$, $P = 0.005$ and $r = 0.45$, $P = 0.02$, respectively) in southern ridge sandhill. Contrasts between oak species of different sections produced only two significant correlations, one of which was negative. *Quercus myrtifolia* and *Q. chapmanii* growing in southern ridge sandhill were correlated negatively for the number of acorns per bearing ramet ($r = -0.41$, $P = 0.03$), while *Q. myrtifolia* and *Q. geminata* in scrubby flatwoods showed a positive correlation for the percentage of bearing ramets ($r = 0.44$, $P = 0.03$).

DISCUSSION

Influence of ramet size and vegetation association on acorn production—As we expected based on findings from other plants (Harper and White, 1974; Schmid, Bazzaz, and Weiner, 1995; Mendoza and Franco, 1998; Reekie, 1998), acorn production of individual ramets was correlated with ramet size. Acorn yields and the frequency of individuals bearing acorns have previously been shown to increase with size and maturity in oaks with tree-growth forms (e.g., Goodrum, Reid, and Boyd, 1971; Moody, 1985). However, our results are apparently the first to document this pattern for highly clonal, shrubby oaks.

Increases in both the frequency of reproduction and amount of reproduction contribute to this pattern. However, changes in the percentage of bearing ramets has a stronger effect on acorn yield than the changes seen in the numbers of acorns per bearing ramet (Fig. 1; Table 1). This pattern suggests that individual ramets must accumulate reserves in order to reach size thresholds that allow allocation of resources to reproduction. Furthermore, all oaks, regardless of their degree of clonal growth, expressed this general increase in acorn yield with size. *Quercus inopina*, the most clonal of these oaks, had <10% bearing ramets in the smallest size class, whereas the largest size class had >70% bearing ramets. This increase related to ramet size was greater than that for *Q. laevis*, the least clonal and most treelike of these xeric oaks.

These results suggest that there may be little sharing of reserves among ramets and that there is limited integration of ramets within the same genotype in the absence of fire, as individual oak clones typically contain a mix of small and large ramets (Johnson, Abrahamson, and McCrea, 1986; A. F.

Johnson and W. G. Abrahamson, unpublished data). Long-term data for oak size-class distribution within these vegetation associations and for individual ramets of *Q. inopina* show that ramets of a single genotype do not senesce at the same size or age and that there is appreciable turnover of ramets even in the absence of fire (Givens et al., 1984; Menges et al., 1993; A. F. Johnson and W. G. Abrahamson, unpublished data). It appears, however, that the growth of ramets within a genet may be more integrated immediately following fire, as the catastrophic loss of all ramets of a genotype results in the synchronous sprouting of new ramets (Abrahamson, 1984a, b; Abrahamson and Abrahamson, 1996). Our observations of post-fire development of ramets of a given oak species indicate that the sizes of ramets become progressively more variable with time since fire, resulting in an increasingly irregular shrub profile.

Acorn production declined markedly in the largest ramet size classes of *Q. geminata* in all vegetative associations and in the southern ridge sandhill population of *Q. myrtifolia*. This pattern suggests that over time, larger ramets of these clonal oaks may senesce. This conclusion is supported by results from long-term monitoring of permanent vegetation quadrats within the grids sampled for the present study. Each of the long-unburned associations exhibits a marked turnover of ramets in which ramets continuously die and are replaced by new sprouts (Givens et al., 1984; Menges et al., 1993). This “thinning” process results in higher acorn yields under conditions of long-term absence of fire, as the replacement of larger ramets by multiple intermediate-size ramets enhances acorn yields (Fig. 2). While few studies of oaks have mentioned such yield declines with increased tree size, Downs and McQuilkin (1944) found that intermediate-sized red and white oaks in southern Appalachia expressed higher production levels than the largest individuals. Because of their multi-stemmed, clonal growth habits, it is probable that the individual ramets of the shrubby oaks in our study are more prone to early senescence than are typical “tree” oaks.

Crop size for a given oak species was strongly related to vegetation association. Acorn production levels for oaks growing in sand pine scrub were consistently lower than levels in southern ridge sandhill or scrubby flatwoods. This reduction is most likely the consequence of reduced light in sand pine scrub. Light levels are lowest and canopy coverage is most nearly complete in sand pine scrub as a consequence of the dense overstory of *Pinus clausa*, whereas old-growth southern ridge sandhill is intermediate in both light levels and canopy coverage. Scrubby flatwoods is the most open canopied of the three associations studied (Abrahamson and Rubinstein, 1976; Abrahamson et al., 1984; Abrahamson and Hartnett, 1990; Myers, 1990; Abrahamson, 1995, 1999).

Size-class contributions to community-level acorn production—Annual crops of acorns are obviously important for oaks to recruit new individuals and to colonize new sites. These crops are also crucial to many species of other trophic levels. Acorns are an important food resource for a large number of animals, including insects (e.g., acorn weevils), birds (e.g., scrub jays, blue jays, acorn woodpeckers, red-headed woodpeckers, and turkeys), and mammals (e.g., white-footed mice, eastern chipmunks, white-tailed deer, and feral hogs) (van Dersal, 1940; Matschke, 1964; Goodrum, Reid, and Boyd, 1971; MacRoberts and MacRoberts, 1976; Landers et al., 1979; Smith and Layne, 1986; Smith and Scarlett, 1987; DeGrange

et al., 1989). The densities of rodents, for example, can be highly correlated with the previous year's acorn production (Wolff, 1996a, b). Furthermore, acorn production levels have been implicated in food web links of rodent populations with gypsy moth populations, which in turn can affect the well-being of their oak hosts. Similarly, the food web links of acorns to deer movements may influence tick populations and hence potentially alter the risk of Lyme disease (Ostfeld, Jones, and Wolff, 1996; Jones et al., 1998).

Our findings demonstrate a clear relationship between oak size-class density and acorn production in the three xeric upland vegetation associations, with intermediate-sized individuals tending to contribute most to total number of acorns per unit area. This trade-off between size-class density and overall acorn production has an important implication for prescribed fire management in these habitats. For example, stands treated with consistently short fire-return intervals will be largely composed of smaller size-class oaks, which, although typically numerous, have low acorn production and which will cause consequent reduction in the carrying capacity for acorn consumers. Given an hypothetical scenario in which these xeric habitats eventually proceed from an oak shrub to small-tree dominated status in the long absence of burning, acorn yields available to insects and vertebrates might also be less than with a heterogeneous shrub layer because the effect of generally higher acorn production of large individuals might be negated by a lower maximum density of large individuals. Thus, management of stands with a frequency and intensity of prescribed fire that maintains a mosaic of unburned to lightly burned to intensively burned patches with a predominance of intermediate-sized oaks should maximize acorn yields for the benefit of acorn consumers. It is of interest that even in the long-unburned stands in this study, there was no evidence of reduction of acorn production over the 27-yr period of monitoring, which reflects the maintenance of the small to intermediate-sized shrub layer by the mechanism of thinning (Givens et al., 1984; Menges et al., 1993; A. F. Johnson and W. G. Abrahamson, unpublished data).

Allocation of resources between acorn numbers and acorn size—The marked variability in the percentages of bearing ramets and the numbers of acorns among ramets within a species, among species, and across vegetation associations likely reflects differing plant carbon and nutrient stores among individuals of different sizes and species, differences in species' life-history strategies from the highly clonal *Q. inopina* to the small tree *Q. laevis*, and variation in habitat-related external resources, including amount of light, soil moisture, and nutrient levels. An additional factor that can strongly influence the number of acorns per ramet is the trade-off between allocation of resources to seed numbers, seed size, and seed quality (Harper, 1977).

For example, the highest numbers of acorns per bearing ramet were recorded for ramets of the small-fruited *Q. myrtifolia*, while the lowest numbers were determined for the large-fruited *Q. laevis*. *Quercus myrtifolia* has the smallest acorns of those studied with mean (± 1 SE) fresh masses of 0.61 ± 0.03 g, 0.86 ± 0.03 g, and 0.98 ± 0.05 g for southern ridge sandhill, scrubby flatwoods, and sand pine scrub, respectively (Abrahamson and Abrahamson, 1989). In contrast, *Q. laevis* acorns are two to four times heavier within the same vegetation association (2.38 ± 0.14 g and 2.04 ± 0.21 g for southern ridge sandhill and sand pine scrub, respectively). The fresh

masses of acorns in our study ranked from smallest to largest in the order: *Q. myrtifolia* < *Q. inopina* < *Q. geminata* < *Q. chapmanii* < *Q. laevis*. Larger seeds can offer seedlings more resources during a critical phase of early establishment; however, larger seed size often comes with the cost of reduced seed numbers and reduced dispersal (Harper, 1977; Bonfil, 1998; Hewitt, 1998).

Acorn quality also may influence the balance of the acorn numbers and sizes. For example, the acorns produced by the three species of red oaks contain more tannin, fat, and energy per unit mass than acorns of the two white oaks (Abrahamson and Abrahamson, 1989; Fleck and Layne, 1990). Furthermore, among the red oaks, the small-fruited *Q. myrtifolia* and *Q. inopina* have significantly higher levels of energy, fat, protein, and carbohydrates than the large-fruited *Q. laevis*. In fact, the concentrations of crude fat in acorns of shrubby oaks *Q. myrtifolia* and *Q. inopina* (26.8 and 24.8%, respectively) are among the highest reported for any oak (Abrahamson and Abrahamson, 1989). Crude fat concentrations of 19–20% are typical for red oaks (Bonner and Vozzo, 1987). Thus, the two species of small-fruited red oaks living on the nutrient-poor sands of Florida's xeric uplands are producing extremely high-quality acorns.

Correlation of acorn production within and among oak species—Over the 27-yr span of the study, acorn production was relatively synchronized within a given oak species across vegetation associations, as well as among oak species within the same oak section, in spite of the variations in environmental conditions across associations. While such synchrony could be generated by similar responses to weather factors or to an external cue such as fire (Keeley and Bond, 1999), it may represent an evolved response to optimize reproductive success. Synchronous flowering of a species across a region may enhance fertilization and seed set during years with strong flowering responses (Norton and Kelly, 1988; Houle, 1999) as a higher concentration of pollen increases the probability of pollination for wind-pollinated species. In addition, synchronous flowering may reduce the proportion of seeds attacked by seed predators due to predator satiation (Janzen, 1971, 1976; Koenig et al., 1999).

These relationships probably reflect the difference in the reproductive chronology of the species of the white oak and red oak sections. In white oak species, staminate floral buds are initiated in the spring and pistillate floral buds in late summer of one year and flowers are produced and, if fertilized, develop into mature acorns in the second year. In contrast, oaks of the red oak section initiate staminate and pistillate floral buds in the spring and fall, respectively, of one year, flowers are produced the following year, and ovules are fertilized and the acorns mature in the third year (Sork, Bramble, and Sexton [1993] and references therein).

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