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Post-fire recovery of acorn production by four oak species in southern ridge sandhill association in south-central Florida[1]

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We examined post-fire recovery of two components of acorn production (percentage of bearing ramets [stems] and number of acorns per bearing ramet) for four species of oaks in southern ridge sandhill vegetation in south-central peninsular Florida. Annual counts of acorns on two white oaks (*Quercus chapmanii* and *Q. geminata*) and two red oaks (*Q. laevis* and *Q. myrtifolia*) were conducted annually (except in 1991) on two 2.7-ha grids from 1969 to 1998. A prescribed burn was conducted on one of the grids in May 1993. Newly sprouted ramets of both white oaks produced acorns during the first year following the fire, whereas red oaks required 3 yr (*Q. myrtifolia*) or 4 yr (*Q. laevis*) to produce acorns. The difference in the timing of post-fire acorn production between the white and red oak species reflected the difference in the number of years from flower bud initiation to mature acorns in the two groups, with the additional year-long lag in *Q. laevis* probably attributable to the fact that it is typically a tree rather than a shrub species. The data suggested that percentage of bearing ramets in the smallest size class of the two white oak species was markedly lower in the burned than unburned grid in the first year of post-fire acorn production and higher in the fifth year, but these trends were not evident for the red oaks. Among all four species, differences between mean number of acorns in burned and unburned grids were significant in only two cases (the largest size class of both white oak species in the fifth year). There was no evidence of recruitment from acorns on the burned grid, possibly due to the rapid redevelopment of the shrub layer because of low mortality of the extensive clonal root systems. Rapid post-fire recovery of acorn production in xeric fire-prone habitats is presumably the result of selection to increase the probability of recovery and persistence following sufficiently intense fires that result in high oak mortality. The timing and magnitude of post-fire acorn production in sandhill and other xeric Florida associations has a potential impact on a wide variety of insects, birds, and mammals that feed on acorns, as well as on the species with which they interact.

Key words: acorn; fire ecology; Florida; fruiting patterns; *Quercus*; southern ridge sandhill.

The length of time required to achieve the size necessary for reproduction varies greatly among woody plants (Harper and White, 1974). For example, shrubs tend to have shorter juvenile periods than trees, and plants developed from seeds require longer juvenile phases than clonally produced ramets (Harper, 1977; Abrahamson, 1980). For species in fire-prone environments, the length of time from fire to seed production is an important life-history variable given its potential impact on recruitment and persistence. Therefore, where fire has historically been a recurrent and often frequent environmental perturbation, we might expect adaptations that enable rapid sprouting and minimal delay until reproduction following burning. The rate and magnitude of post-fire recovery of reproduction by plants producing seeds or fruits used by animal species also has important implications at the community level.

During the course of their evolution, the shrubby oaks characteristic of xeric upland associations of peninsular Florida have been subjected to periodic fires (Abrahamson and Hartnett, 1990; Myers, 1990; Abrahamson and Abrahamson, 1996a, b). Consequently, we predicted that these oaks should exhibit rapid sprouting and recovery of acorn production following burning. This study examined trends in acorn production for four species of oaks over a 5-yr period following a prescribed fire in a southern ridge sandhill association. The oak species were *Q. chapmanii* (Chapman's oak) and *Q. geminata* (sand live oak) of the white oak group (*Quercus* section *Quercus*) and *Q. myrtifolia* (myrtle oak) and *Q. laevis* (turkey oak) of the red/black oak group (*Quercus* section *Lobatae*) (Jensen, 1997; Nixon and Muller, 1997).

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MATERIALS AND METHODS

Description of study area—The study was conducted on the Archbold Biological Station (ABS), 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, USA. Prominent landscape features of the region are residual sandhills, relic beach ridges, and paleo-sand dunes, which reflect higher sea levels during the Pliocene (Brooks, 1981). Elevations in the general area range from 38 to 65 m above mean sea level (United States Geological Survey, Childs, Florida, 7.5′ quadrangle).

The climate of the study site is characterized by hot, wet summers and mild, dry winters. The highest monthly mean daily temperature (27.5°C) occurs in August and the lowest (16.0°C) in January. The rainy season normally extends from June through September, with ~60% of the annual precipitation (67-yr mean = 1351 mm) falling during this 4-mo period (ABS weather records).

Southern ridge sandhill vegetation, occurring on excessively well-drained sands, is a characteristically three-layered community, with an open overstory of *Pinus elliottii* var. *densa* (south Florida slash pine) and occasional *Pinus clausa* (sand pine); a lower deciduous canopy of *Q. laevis* and *Carya floridana* (scrub hickory); a generally dense shrub layer largely composed of *Q. myr-*

tifolia, *Q. geminata*, *Q. chapmanii*, *Serenoa repens* (saw palmetto), and *Sabal etonia* (scrub palmetto); and a ground layer of *Aristida stricta* (wiregrass), various forbs, and sprouts of the shrub-layer species (Abrahamson et al., 1984; Myers, 1990).

Based on photographs (fig. 621A in Myers, 1990) and early accounts, the study site had experienced recurrent and frequent fires and was maintained as an open stand of south Florida slash pines, a low, sparse shrub layer, principally of turkey oaks, and a well-developed ground layer of wiregrass and forbs until 1927, the time of the last fire that was reportedly widespread and uniformly intense. During the 66-yr fire-free period that followed, the southern ridge sandhill site was extensively invaded by sand pines and shrubby oaks from surrounding sand pine scrub association, resulting in much denser shrub and ground cover than in sandhill sites burned at the more typical frequency of 1–10 yr (fig. 6.21B in Myers, 1990). In May 1993, a prescribed burn conducted on a portion of the study area killed almost all aboveground parts of the ground and shrub layer vegetation, as well as a majority of the mature sand pines and slash pines of the overstory.

Monitoring of acorn production—Annual counts of acorns of each species were conducted from 1969 to 1998 (except for 1991) on two 2.7-ha grids consisting of a 12 × 12 array of permanently marked point stations at 15-m intervals. The grids were separated by a 15-m wide bare sand fire lane and 15-m boundary strips of natural vegetation on each side. One of the grids was included in the prescribed burn in May 1993 and the other served as an unburned control.

Acorns were censused in the autumn at a time when the nuts were sufficiently developed to allow normal and aborted individuals to be distinguished but before they were ripe enough to be harvested in significant numbers by birds and rodents. All normally developed acorns and fresh caps present on each sampled ramet (stem) were counted. Counting acorns on taller individuals (>4 m), which was more difficult and undoubtedly less accurate than for individuals <3 m, was facilitated by use of a long bamboo pole to move the upper branches around to get a more complete view. The height of sampled ramets was recorded to the nearest 0.3 m, and for purposes of this study ramets were grouped into the following three size classes: 1 = 0.3–1.4 m; 2 = 1.5–2.6 m; and 3 = >2.6 m.

From 1969 to 1996, 60 ramets of each species were sampled on each grid. Acorns were counted on a ramet in each of the four quadrants centered on a station marker at 15 stations evenly distributed over the grid. The acorn-sampling stations were the same as those used in vegetation surveys in 1969, 1979, and 1989 (Givens et al., 1984; Menges et al., 1993). The nearest ramet to the station marker was selected for counting unless it was damaged, abnormal, or likely from the same clone as a ramet sampled in another quadrant. In such cases, the next nearest ramet to the station marker and not obviously of the same clone was selected. No more than five ramets ≤0.6 m of a given species were sampled, as only rarely did oaks that small produce acorns; otherwise, the size distribution of sampled ramets reflected that of the population. In 1997 and 1998, sample sizes for size classes with low counts in the regular censuses were augmented by additional counts of ramets selected randomly at sites other than the regular sampling stations. This increased total sample sizes for different species on both burned and unburned grids from 60 to 70–86 ramets in 1997 and to 76–93 ramets in 1998.

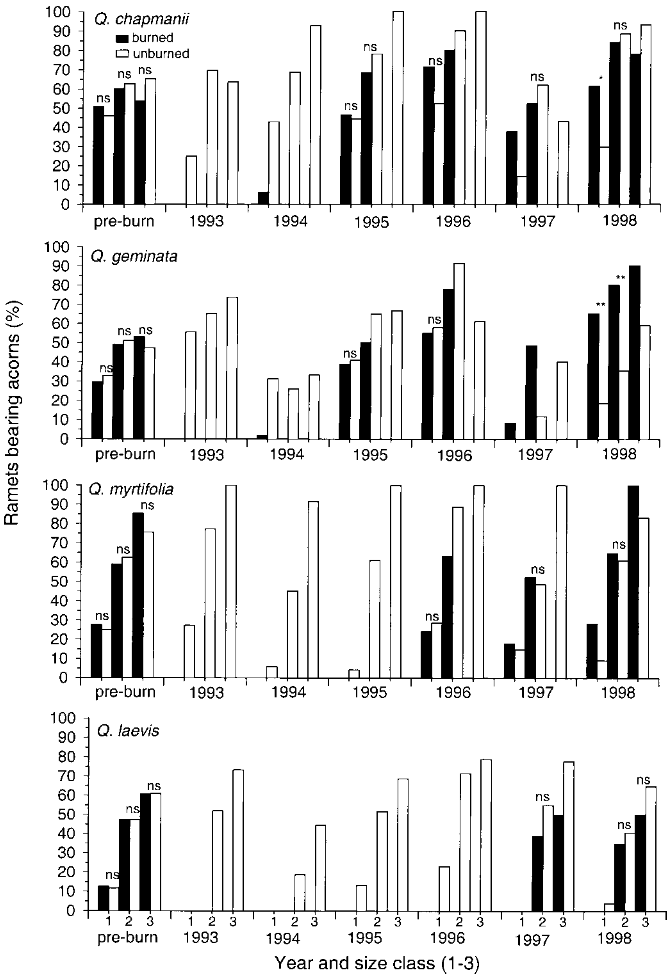

Fig. 1. Percentage of ramets bearing acorns for three size classes of four oak species in two 2.7-ha grids in southern ridge sandhill association in south-central Florida prior to (1969–1992, except 1991) and for 5 yr (1993–1998) following a prescribed burn on one grid in May 1993. Solid bars = burned grid and open bars = unburned grid. Minor ticks on the *x*-axis represent the following size classes: 1 = 0.3–1.4 m; 2 = 1.5–2.6 m; 3 = >2.6 m. Results of chi-square tests of differences between frequencies of bearing and non-bearing ramets for given size classes with minimum sample >5 per cell on burned and unburned grids are indicated as: ns, $P > 0.05$; *$P < 0.05$; **$P < 0.01$.

RESULTS

Pre-burn data from 1969 to 1992 showed that for all species both percentage of bearing ramets (Fig. 1) and number of acorns on bearing ramets (Fig. 2) were correlated with ramet size, the former relationship being stronger in the two red oak than white oak species. The four species also differed in overall levels of acorn production. In terms of the percentage of bearing ramets, the rank is as follows: *Q. chapmanii* (59.1%) > *Q. myrtifolia* (45.9%) > *Q. geminata* (40.3%) > *Q. laevis* (34.1%). In mean number of acorns per bearing ramet, the rank is as follows: *Q. myrtifolia* (28.5) > *Q. chapmanii* (18.9) > *Q. geminata* (12.6) > *Q. laevis* (7.3). All species exhibited marked yearly variation in acorn production, with coefficients of variation for mean acorns per bearing ramet as follows: *Q. myrtifolia*, 204.3%, *Q. geminata*, 202.0%, *Q. laevis*, 171.0%, and *Q. chapmanii*, 169.6%. There were no discernable long-term trends in overall or size-class-specific levels of acorn production for any species during the 30-yr period of monitoring of unburned grids.

Acorn production parameters for comparable size classes of a given species were in close agreement between grids, with no significant differences (χ^2 tests, $P > 0.05$) between grids in frequencies of bearing ramets and only a single significant value (Mann-Whitney *U* tests, $P > 0.05$) for mean number of acorns in the case of the largest size class of *Q. geminata*.

All species rapidly recovered pre-burn acorn production levels for given size classes following the prescribed burn, with the red oaks lagging behind the white oaks (Figs. 1 and 2). Predictably, no acorns were produced by any species in au-

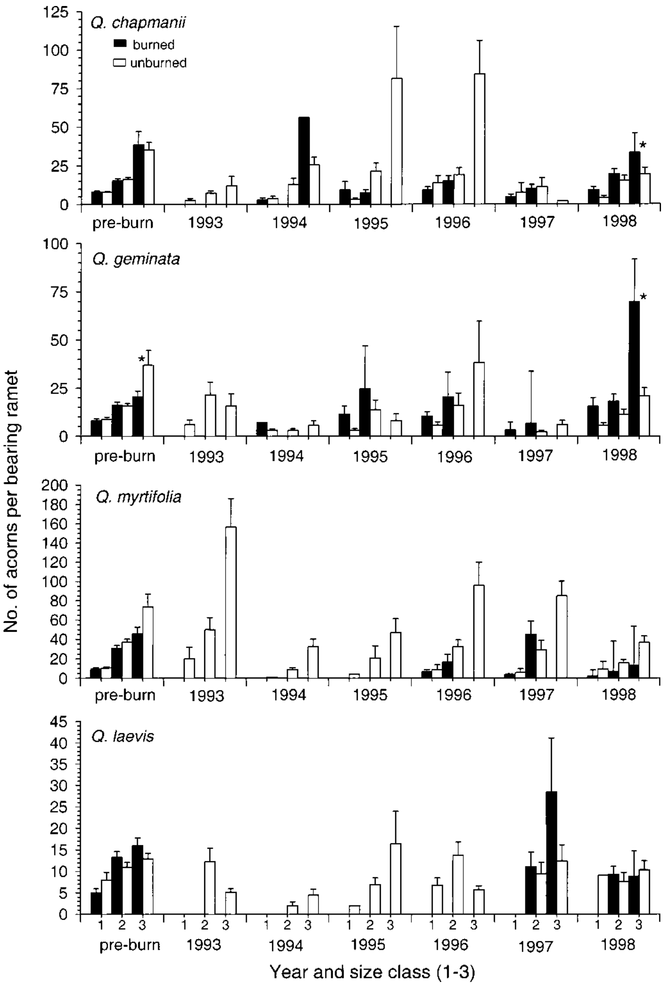

Fig. 2. Mean (±1 SE) number of acorns per bearing ramet in three size classes of four oak species on two grids in southern ridge sandhill association in south-central Florida prior to (1969–1992, except 1991) and for 6 yr (1993–1998) following a prescribed burn on one grid in May 1993. Solid bars = burned grid and open bars = unburned grid. Minor ticks on the x-axis represent the following size classes: 1 = 0.3–1.4 m; 2 = 1.5–2.6 m; 3 = >2.6 m. Significant differences (Mann-Whitney U tests) in ranks of numbers of acorns on ramets of a given size class in burned and unburned grids indicated as *$P > 0.05$; in all other cases with counts for both burned and unburned grids, differences were not significant.

tumn of the year (1993) of the fire. However, some new ramets in the smallest size classes of both white oak species bore acorns the following year. Although the data suggest that for both species the percentage of bearing ramets in a given size class was much lower on the burned than unburned grid, this could not be statistically tested because of sample sizes <5 for the burned grid. However, the data suggest that numbers of acorns on bearing ramets did not differ between burned and control grids in either species. In subsequent years, there were no significant differences between grids in acorn production parameters for either white oak species until 5 yr post-fire, when both had a significantly higher proportion of bearing ramets in some size classes (Fig. 1) and a higher mean number of acorns in the largest size class (Fig. 2) on the burned grid.

For species in the red oak group, the first post-fire bearing ramets of *Q. myrtifolia* and *Q. laevis* appeared at 3 and 4 yr, respectively, and in all cases where sample sizes permitted statistical testing, there were no significant differences between burned and control grids in percentage of bearing ramets or mean number of acorns for any size class of either species (Figs. 1 and 2).

DISCUSSION

Scrub oaks quickly produce new ramets following fire (Abrahamson, 1984a, b; Abrahamson and Abrahamson, 1996a, b), and the present study documents that these ramets promptly initiate flower development. Production of acorns by new ramets of both *Q. chapmanii* and *Q. geminata* on the burned grid in the year following fire indicates that they initiated floral buds within a short time after the fire, assuming that, as characteristic of the white oak group, (Sork, Bramble, and Sexton [1993] and references therein) staminate floral buds were initiated in the spring and pistillate floral buds in late summer of the year of the fire with flowering and production of acorns occurring the following year. Of the red oaks on the burned plot, *Q. myrtifolia* produced its first acorns 3 yr after the burn, which indicates a recovery of acorn production following fire equally as prompt as the white oaks, given the 3-yr period required for full fruit development in the red oak group (staminate and pistillate floral buds initiated in the spring and autumn, respectively, in the first year; flowering during the spring of the second year; and fertilization of the ovules and development and maturation of acorns in the third year) (Sork, Bramble, and Sexton [1993] and references therein). The lag of an additional year before acorns were produced by the other red oak, *Q. laevis*, correlates with the fact that it is normally a tree-sized rather than shrub-type oak and thus may inherently begin acorn production at a larger size. Supporting this interpretation of the data is the fact that the earliest acorn production in this species occurred in a larger size class than for the three scrub oaks. An additional factor in the longer delay in post-fire acorn production of *Q. laevis* may be a higher threshold of resource accumulation needed for acorn production than for the three shrubby oaks due to the relatively larger mass (30–74%) of its acorns (Abrahamson and Abrahamson, 1989).

Although the present study suggests that rapid post-fire recovery of fruit production may be characteristic of oaks adapted to xeric fire-prone environments, comparative data are sparse, as most studies of post-fire recovery of oaks have dealt with ramet growth and not acorn production. However, Ostertag and Menges (1994) reported acorn counts for the scrub oak *Q. inopina* at eight post-fire intervals from 1 to 64 yr in different scrubby flatwoods sites on ABS. Their results showed first post-fire acorn production in a 5-yr post-fire stand, but as no stands at 3- or 4-yr post-fire were sampled, reproduction may have begun at 3 yr as it did in the red oak *Q. myrtifolia* in the present study. In fact, this was confirmed by observations by R. Curry cited by Ostertag and Menges (1994). The generally low mean acorn counts (<1–4), small sample sizes from sites of different post-fire ages, possible site differences in soil types, lack of data on the size classes of different samples, and absence of control for intensity of fire in the different study sites complicate the interpretation of long-term trends in post-fire acorn production for the species. However, their data appear to agree with the present study that acorn production of scrub oaks in xeric Florida habitats recovers rapidly following fire and is maintained over a long fire-free interval. In a study of acorn production recovery of two oak species following clear-cutting, which presumably mimics the effects of a fire, Wolgast (1972) found that ramets of the white oak *Q. prinoides* bore acorns during the second growing season and that the red oak *Q. ilicifolia* produced acorns during the third growing season.

Woody plants of xeric environments typically have considerable persistence and prolonged longevity; however, the opportunities for colonization and establishment of seedlings appear to be limited (Johnson and Abrahamson, 1990; Menges and Hawkes, 1998). Colonization and establishment of new oak genets are probably most frequent after fire, although it should be noted that in the present study no seedlings of any species were observed on the burned grid during the 5 yr of post-fire monitoring. Demographic studies of two long-lived palmetto species as well as other species that co-occur with these oaks found that recruitment episodes were rare and suggested that recruitment is connected to canopy gaps created by fire (Abrahamson, 1999). Theoretically, gaps created by sufficiently intense fires should offer more opportunities for recruitment than the conditions in unburned areas (Johnson and Abrahamson, 1990; Hawkes and Menges, 1995, 1996; Abrahamson and Abrahamson, 1996a, b; Menges and Hawkes, 1998; Quintana-Ascencio and Menges, 1998; Abrahamson, 1999). Although woody plants of xeric Florida uplands can persist under closed canopies for long periods of time (Abrahamson and Abrahamson, 1996a, b), the flowering and fruiting of many of these species appear to be stimulated by the higher light levels created by gaps (Abrahamson, 1999). Thus, fire may not only serve as a stimulus to initiate flowering, it may also influence whether new genotypes colonize and establish in xeric uplands. The effect of canopy development on acorn production is illustrated by a comparison of acorn production of the same four species in a mature sand pine scrub association and the southern ridge sandhill association, with pine canopy coverage of 75 and 27%, respectively (Abrahamson et al., 1984). The mean number of acorns produced by the oaks in sand pine scrub was only 29.0% (range for individual species = 10.8–51.0%) of that in southern ridge sandhill (J. N. Layne, unpublished data).

The lack of evidence of any significant post-burn recruitment from acorns in spite of the rapid recovery of acorn production documented in the present study may be a consequence of the intensity of the prescribed burn being insufficient to cause appreciable mortality of the root systems of the extensive genets, so that rapid redevelopment of ramets and return to preburn oak density reduced opportunity for acorn germination or seedling survival. Increased predation on acorns by granivorous birds and rodents that exhibited population increases on the burned grid (J. N. Layne, unpublished data) may also have reduced acorn survival.

At the community level, oaks and their acorns play an important role in the population biology and interspecific interactions, including host–parasite–disease, predator–prey, and intra- and interspecific competitive relationships in many animal species in different geographic regions (e.g., Van Dersal, 1940; Goodrum, Reid, and Boyd, 1971; Smith and Layne, 1986; Smith and Scarlett, 1987; DeGrange et al., 1989; McShea and Schwede, 1993; Elkinton et al., 1996; Ostfeld, Jones, and Wolff, 1996; Wolff, 1996; Healy et al., 1997; Jones et al., 1998; Siscart, Diego, and Lloret, 1999; McShea, 2000). Acorns are an important food resource for over a dozen species of insects, birds, and mammals in the southern ridge sandhill and associated xeric upland associations in our study area (Fleck and Layne, 1990), and it can probably be assumed that the timing and magnitude of acorn production following fire in these habitats have an appreciable effect on their population dynamics and interspecific relationships.

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