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ARTICLE

Fire effects on acorn production are consistent with the stored resource hypothesis for masting behavior

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Abstract: Highly variable patterns of seed production ("masting") have been hypothesized to be driven by internal dynamics of resource storage and depletion. This hypothesis predicts that if seed production is artificially reduced, then the availability of unused stored resources should result in subsequent enhancement of the seed crop. We tested this prediction in two oak species with contrasting patterns of annual seed production (highly variable and relatively constant) by means of controlled burns at various frequencies over a 17-year period. We found that controlled burns reduced acorn production by both species in the year of the burn. In the species with relatively constant productivity, acorn production returned to baseline levels in the year following a burn; however, in the species with highly variable productivity, acorn production significantly increased the year following a burn. These results support a key prediction of the stored resource hypothesis by means of a long-term experimental test in wild tree populations.

Key words: masting, acorn production, resource allocation, fire, *Quercus*.

Résumé : On croit que la dynamique interne de l'emmagasinage et de l'épuisement des ressources serait responsable de la très forte variation dans la production de graines (année semencière). Cette hypothèse prédit que si la production de graines est artificiellement réduite, la disponibilité des ressources inutilisées devrait se traduire par une augmentation subséquente de la production de graines. Nous avons vérifié cette prédiction chez deux espèces de chêne avec différents profils de production annuelle de graines, soit très variable dans un cas et relativement constant dans l'autre cas, en effectuant des brûlages dirigés à différentes fréquences sur une période de 17 ans. Nous avons trouvé que les brûlages dirigés ont réduit la production de glands chez les deux espèces l'année du brûlage. Chez l'espèce dont la productivité était relativement constante, la production de glands est revenue au niveau de base l'année qui a suivi un brûlage. Par contre, chez l'espèce dont la productivité était très variable, la production de glands a significativement augmenté l'année qui a suivi un brûlage. Ces résultats supportent une prédiction clé de l'hypothèse de l'emmagasinage des ressources grâce à un test expérimental à long terme dans des populations naturelles d'arbres. [Traduit par la Rédaction]

Mots-clés : année semencière, production de glands, allocation des ressources, feu, *Quercus*.

Introduction

Many long-lived species of plants show highly variable patterns of seed production from year to year (Kelly and Sork 2002; Silvertown 1980). When intermittent episodes of intense reproduction are synchronized across a population ("masting" behavior), evidence suggests that a fitness advantage is conferred via increased fertilization rates and (or) decreased seed predation (Koenig et al. 1994b; Kon et al. 2005; Silvertown 1980). However, the proximate mechanisms that produce masting patterns in wild plant populations are only beginning to be understood.

The cost of producing a large crop of fruits or cones, in terms of carbohydrates and mineral nutrients, can be considerable (Kozlowski and Keller 1966). Because of these substantial costs, it has been hypothesized that within a given year, masting plants are faced with a resource allocation trade-off between growth and reproduction (Norton and Kelly 1988; Sork et al. 1993). Although negative correlations between growth and reproduction are documented in some masting species (Harper 1977; Koenig and Knops 1998), it has also been found that such relationships can be confounded by covariation with a third variable (Roff 2002; Knops et al. 2007). This third variable can be the environment affecting growth and reproduction in opposite ways, or it can be storage of

resources, which potentially drive trade-offs between life-history characters across and (or) within years.

Here we define "resource storage" as resources that accumulate in the plant and can be mobilized to support future biosynthesis (Chapin et al. 1990). Examples of storage compounds include carbohydrates, lipids, and mineral nutrients. Resource storage is hypothesized to play a role in the mechanism for masting as follows: producing a large crop of seeds demands nutrients that depletes a plant's reserves, which then require more than one growing season to re-accumulate. We refer to this as the "stored resource hypothesis".

Although the stored resource hypothesis has received considerable theoretical support (Crone et al. 2005; Isagi et al. 1997; Satake and Iwasa 2002; Satake and Bjørnstad 2008), empirical evidence has been mixed. A key prediction of the hypothesis is that resources should accumulate between mast years and be depleted following a masting event. This prediction has been supported in some studies (Miyazaki et al. 2002; Crone et al. 2009) but not in other studies (Ichie et al. 2005, 2013; Hoch et al. 2013) when carbohydrates were the currency of storage investigated (Miyazaki 2013). There has been more consistent support when mineral nutrients have been examined as the stored resource, but experimental work in this area is still rare (Crone and Rapp 2014).

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Fig. 1. Annual population mean natural log transformed acorn counts for bur oaks (gray bars) and pin oaks (black bars). Error bars represent ±1 standard error. There is no column for bur oaks in 1995 because of a total acorn crop failure throughout the study population.
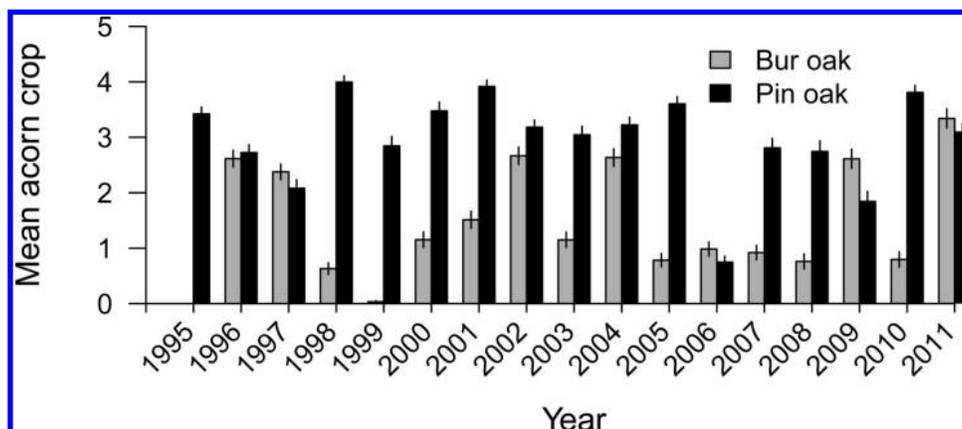
Uncertainty surrounding the stored resource hypothesis lies partly in the limited temporal scale of inquiry, as most studies examine only one or two large reproductive efforts, whereas long-term experiments are uncommon, with some notable exceptions (Smaill et al. 2011; Rapp and Crone 2015).

Here, we take advantage of a long-term program of prescribed burns to test a key prediction of the stored resource hypothesis: reducing or eliminating reproduction in one year results in a surplus of stored resources driving enhanced reproduction in a subsequent year. Prescribed burns conducted during spring have been found to reduce acorn production in that season, at least partly due to damage to flowers and floral primordia (Peter et al. 2011). Thus, burns are expected to reduce investment in current reproduction. Concurrently, burns add a transient pulse of mineral nutrients to the soil (White et al. 1973; Schoch and Binkley 1986; Boerner et al. 1988; Gray and Dighton 2006). Both of these effects are expected to increase resource availability to the trees and, therefore, increase reproduction in the subsequent year via the stored resource hypothesis.

We used prescribed burning to test the role of stored resources in two species of oaks (family Fagaceae, genus *Quercus*) that differed in their masting patterns. One species (bur oak, *Quercus macrocarpa* Michx.) exhibits highly variable annual seed production (masting), whereas the other species (pin oak, *Quercus ellipsoidalis* E.J. Hill) does not. Comparing the effects of fire (and reduced seed production) between two species with contrasting patterns of seed production provides a rigorous test of the stored resource hypothesis. Although costs of reproduction are very common in plants (Obeso 2002), the stored resource hypothesis predicts that they manifest differently in masting and nonmasting species. In masting species, factors increasing the costs of reproduction in one year are likely to affect reproduction in future years, whereas in nonmasting species, such costs are likely to affect other functions such as growth or defense in the same year (Crone and Rapp 2014). Therefore, we predicted that prescribed burns, by curtailing investment in reproduction during the year of the treatment, would enhance reproduction the following year in the masting species where reproductive investment involves significant resource storage and depletion but would have little or no effect in the nonmasting species. In other words, if internal resource dynamics are controlling patterns of masting, then burns should reduce acorn production in both species the year of the burn but should significantly enhance acorn production in the following year only in bur oaks (the masting species).

Materials and methods

We measured annual acorn production of 90 individual bur oaks and 89 individual pin oaks at Cedar Creek Ecosystem Science Reserve in Bethel, Minnesota, USA. Bur oak is a member of the white oak section of the genus (section Quercus), has acorns that mature in one growing season (a "1-year" species), and produces a highly variable acorn crop (population coefficient of variation (CV_p) = 0.70, Fig. 1) that is within the typical range for masting species (Koenig et al. 2003). Diameter at breast height (DBH, 1.3 m), as measured in 1995, for the bur oaks study population ranged from 11.0 cm to 68.8 cm, with a mean ± standard deviation (SD) of 34.7 ± 11.5 cm. Pin oak is a member of the red oak section of the genus (section Lobatae), requires two growing seasons to mature acorns (a "2-year" species), and produces a relatively constant acorn crop (CV_p = 0.28, Fig. 1). DBH in 1995 for the pin oak population ranged from 17.0 cm to 89.0 cm, with a mean ± SD of 44.3 ± 14.9 cm. During the study, pin oak experienced high fire-induced mortality, with 26 (29%) individuals dying. Mortality of bur oak was substantially less, with only six individuals (7%) dying. Dead individuals were not replaced during the study.

Prescribed burning was initiated at Cedar Creek in 1964 to restore and maintain oak savannah vegetation and to investigate the effects of fire frequency on vegetation (Peterson and Reich 2001). The various treatments were spread across 19 burn units varying in size from 2.4 to 30 ha. We counted acorns on trees distributed evenly among six sites that experienced fire frequencies ranging from 0 to 12 fires during the 17-year study (Table 1). These particular sites were selected to represent two of the lowest fire frequencies, two intermediate fire frequencies, and two of the highest fire frequencies. Except in two cases, prescribed burns occurred in April or May after snowmelt but before leaves appeared on the oaks. In 2001, at two sites, there were prescribed burns in October. We treated these cases as "not burned" sites; however, considering these cases as "burned" sites did not alter the results of the analyses. Fire behavior varied with weather conditions and fuel load but was generally of low intensity with mean flame lengths < 1 m (Peterson and Reich 2001).

Acorn production by each tree was measured every August or late July from 1995 to 2011 using visual surveys in which two observers scanned different parts of the canopy and counted as many acorns as they could in 15 s (Koenig et al. 1994a). Counts were then added, yielding the number of acorns per 30 s (N30). For all analyses, values were ln transformed (ln (N30+1) = LN30) to reduce the correlation between the mean and the variance.

Data analysis

To determine the effects of fire on acorn production, we constructed a series of linear mixed-effects models for each species. "Year" was included as a categorical fixed effect in all models to account for interannual variation. Random effects were generally "tree ID" nested within "site", except for the analysis of differ-

Table 1. Summary of fire frequencies and sample sizes, with the number of trees remaining in 2011 in parentheses, at each study site.

Site ID	Fire frequencies	Sample sizes	
		Bur oak	Pin oak
104	12	15 (13)	15 (8)
105	9	15 (11)	15 (6)
107	6	15 (14)	15 (11)
110	0	15 (15)	15 (13)
113	2	15 (15)	15 (11)
116	6	15 (14)	14 (14)

Note: Fire frequencies are out of 17 years.

ences among sites, in which "site" was included as a categorical fixed effect and "tree ID" was included as a random effect. We used mixed models with "tree ID" as a random effect because of the repeated measures experimental design.

To examine the potential effects of site and fire frequency on acorn production, we first modeled the effects of site and year on acorn production. Second, we examined the effect of prescribed burns on acorn production in the year of the burn. We categorized each "tree × year" combination as either "burned" or "not burned" and tested the effect of this factor on acorn production along with the main effect of year.

Third, we examined the 1-year time-lagged effects of prescribed burns on acorn production. To do this, we assigned each tree × year combination a categorical variable reflecting whether it was burned in the focal year t (yes or no) and whether it was burned in the previous year $t - 1$ (yes or no). This yielded four categories: not burned in year t or year $t - 1$, burned in year t but not year $t - 1$, not burned in year t but burned in year $t - 1$, and burned in both year t and year $t - 1$ (sample sizes are listed in Figs. 2a and 2b). We then tested the effects of this variable on acorn production in year t, again including year in the analysis.

Because pin oaks require two growing seasons to mature acorns, we also investigated 2-year time-lagged effects of burns on acorn production in this species. Similarly to the 1-year time-lag analysis, we assigned each tree × year combination a categorical variable reflecting whether or not a tree was burned in years t, $t - 1$, and $t - 2$, where t is the focal year. Thus, there were eight possible permutations of the variable. We again used a linear mixed model with the main effects of the 2-year time-lagged variable and year with acorn production in year t as the response variable. Although we report results of this model only for pin oaks, we also ran the model for bur oaks and confirmed that the results were consistent with the 1-year time-lag analysis.

Except where noted, the values reported are mean effect sizes ± standard error in the natural log scale of the response variable. All analyses were performed in R 2.14.0 (R Development Core Team 2011).

Results

Comparisons among sites failed to reveal systematic effects of fire frequency on acorn production for either species. For bur oak, no site had a significantly different pattern of acorn production ($P > 0.05$ for all sites). For pin oak, significantly lower acorn production was found in site 113 (one fire in 17 years; effect size = −0.61 ± 0.24, $P = 0.015$); otherwise, there were no significant differences among the sites.

In both species, prescribed burns reduced acorn production (bur oak: effect size = −0.20 ± 0.08, $P = 0.015$, Fig. 3a; pin oak: effect size = −0.18 ± 0.09, $P = 0.045$, Fig. 3b). Bur oak exhibited significantly increased acorn production the year following a prescribed burn (effect size = 0.35 ± 0.09, $P = 0.0001$, Fig. 2a), even if the tree

was burned again in the focal year (effect size = 0.38 ± 0.13, $P = 0.004$, Fig. 2a). A prescribed burn the year following a "not burned" year, however, significantly reduced acorn production (effect size = −0.21 ± 0.10, $P = 0.04$).

In contrast to the pattern found in bur oak, there were no 1-year time-lagged effects on acorn production in pin oak (Fig. 2b), even though the difference between the first two treatments was similar in size to that of the model treating burns as a binary variable (Fig. 3b). Furthermore, the 2-year time-lagged analysis indicated that only one of the eight possible iterations of the variable had a significant effect on acorn production by pin oaks, namely reduced acorn production when trees were not burned in year $t - 2$ but were burned in both years $t - 1$ and the focal year t (effect size = −0.45 ± 0.19, $P = 0.016$).

Discussion

Previous studies support the assumption that prescribed burns, by reducing investment in current fruit production, enhance both nutrients and carbohydrates subsequently available to the trees (Goldschmidt and Golomb 1982; Weinbaum et al. 1994; Choi and Kang 2007; Crone et al. 2009). Furthermore, low-level burns are known to increase soil nutrients and enhance foliar nutrient concentrations (White et al. 1973; Schoch and Binkley 1986; Boerner et al. 1988; Gray and Dighton 2006). Thus, although we did not directly measure nutrients or carbohydrates, the pattern of controlled burns implemented during the study is likely to have had a strong influence on the resource dynamics of the trees.

Assuming that this was the case, our results are consistent with the hypothesis that stored resources play a key role in the masting patterns of these tree species. Particularly persuasive evidence comes from the contrasting results found for bur and pin oaks. As predicted, only bur oak, a species with highly variable acorn production typical of masting, exhibited increased acorn production the year after the acorn crop was significantly depressed by burning. Acorn production in pin oak, which reproduces nearly every year, was not enhanced either one or two years following burns.

These results are consistent with the hypothesis that costs of reproduction in masting plants are paid in terms of future reproduction. It could be fruitful in future research to compare resource allocation dynamics of masting and nonmasting plants to further test the stored resource hypothesis. Masting plants may have a unique pattern of resource storage and depletion leading to highly variable seed production, or these storage dynamics may be common patterns that act in concert with a synchronizing cue to produce what we observe as masting.

The influence of weather could potentially confound our results or provide alternative explanations. For example, there were late spring frosts in 1995 and 1999, which coincided with near total crop failures in the bur oaks. However, prior work has found that acorn production during the course of this study was primarily correlated with summer weather, rather than spring weather (Koenig and Knops 2014). Furthermore, the trees in our study were distributed among sites that experienced prescribed burns in different years and at various frequencies. Therefore, although all of the trees were within a few kilometres of each other and experienced essentially the same weather in every year, they differed in the pattern of burning to which they were subjected. Thus, although weather factors may have increased the statistical noise in our analyses, they are unlikely to have introduced any systematic biases.

Our study corroborates some previous research on alternate bearing (analogous to masting) in orchard trees, which has demonstrated that resources accumulate during "off years" where there is little or no fruit production and are depleted by mass fruit production in "on years" (Goldschmidt and Golomb 1982; Weinbaum et al. 1994; Rosecrance et al. 1998). Although several studies have provided some support for the importance of stored resources to

Fig. 2. Natural log transformed acorn counts in year t for each 1-year time-lag variable, where "yes" or "no" indicates whether trees were burned or not burned in year t (focal year) and year $t-1$ (previous year). Tukey's notches on the boxplots indicate the median, $\pm 1.58(IQR/\sqrt{N})$, where IQR is the interquartile range and N is the sample size. (*a*) Bur oak data (N for each treatment from left to right is 698, 297, 314, and 169, respectively), and (*b*) pin oak data (N for each treatment from left to right is 660, 258, 281, and 135, respectively). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
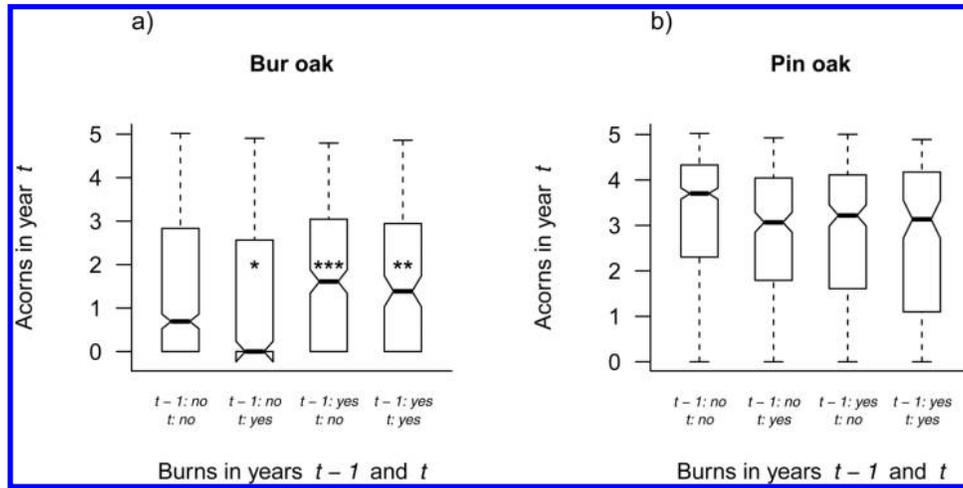

Fig. 3. Natural log transformed acorn counts for trees that did not experience a controlled burn ("not burned") vs. those that did experience a controlled burn ("burned"). All tree × year combinations are included. Tukey's notches on the boxplots indicate the median, $\pm 1.58(IQR/\sqrt{N})$, where IQR is the interquartile range and N is the sample size. (*a*) Bur oak data (N for each treatment from left to right is 1012 and 466, respectively), and (*b*) pin oak data (N for each treatment from left to right is 941 and 393, respectively). *, $P < 0.05$.
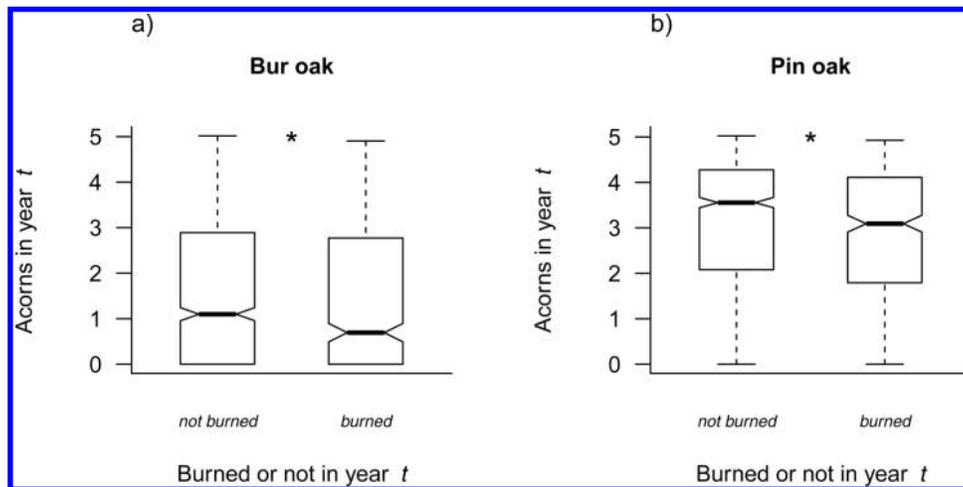
masting behavior, few prior studies have included a comparison with what amounts to a nonmasting control (Ichie et al. 2013; Crone and Rapp 2014).

There are two major issues that limit our understanding of the importance of stored resources to masting behavior. First, both stored carbohydrates and stored mineral nutrients have been investigated simultaneously in very few taxa. However, mounting evidence suggests that the relevant limiting resource currency is specific to species and possibly to habitat (Goldschmidt and Golomb 1982; Crone et al. 2009; Ichie and Nakagawa 2013; Sala et al. 2012). Second, empirical research on the stored resource hypothesis has typically been short term. This is particularly relevant to wild tree populations that experience considerable environmental heterogeneity. Although our study did not directly measure stored resources, it is one of the few long-term studies to address this issue.

Another aspect of our results that remains incompletely explained is the mechanism by which low-level prescribed burns reduce current year acorn production. Peter et al. (2011) found that burned *Quercus garryana* Douglas ex Hook. stands suffered dam-

aged buds and flowers, but this was only partly attributable to the heating effects of the fire. In our study, both focal species exhibited reduced acorn production in years that plots were burned. However, controlled burns took place prior to budburst, and thus the flowers of the two species would have been in very different stages when burning occurred. For bur oak, a 1-year species that matures acorns in a single growing season, the flowers for the autumn's acorn crop would have been in the bud stage. For pin oak, a 2-year species that requires two growing seasons to mature acorns, the flowers for the current year's acorn crop would have been present since the previous year, and the flowers for the next year's acorn crop would have been in the bud stage. The fact that acorn production by pin oak the year following a burn was not affected suggests one of two possibilities: either the burns did not affect the buds of the two species in the same way, or the burns did not mechanically affect the buds at all and some other process reduced acorn production the year of burns. Our finding that bur oak exhibited enhanced acorn production in years following a

burn, even if it was burned a second time, supports the latter hypothesis. Additional work on this issue is clearly warranted.

In conclusion, our work provides empirical evidence consistent with the hypothesis that stored resources play an important role in masting behavior, a result that counters the null hypothesis that masting is driven solely by differences in annual availability of resources (the "resource tracking" hypothesis; Kelly and Sork 2002). In particular, our evidence suggests that masting intensity varied in tandem with resource storage across two sympatric species, one of which is a masting species that exhibits high annual variability in acorn production whereas the other does not. Seed production of masting species can have cascading effects on wildlife populations (Jones et al. 1998; Ostfeld and Keesing 2000; Koenig and Knops 2005; Clotfelter et al. 2007), and thus environmental factors such as fire frequency that influence resource availability can play potentially important roles in ecosystem dynamics.

Acknowledgements

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