

Caught in a fire trap: Recurring fire creates stable size equilibria in woody resprouters

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Abstract. Globally, fire maintains many mesic habitats in an open canopy state by killing woody plants while reducing the size of those able to resprout. Where fire is frequent, tree saplings are often suppressed by a “fire trap” of repeated topkill (death of aerial biomass) and resprouting, preventing them from reaching adult size. The ability to tolerate repeated topkill is an essential life-history trait that allows a sapling to persist until it experiences a long fire-free interval, during which it can escape the fire trap. We hypothesized that persistence in the fire trap results from a curvilinear relationship between pre-burn size and resprout size, which causes a plant to approach an equilibrium size in which post-fire biomass recovery is equal to fire-induced biomass loss. We also predicted that the equilibrium stem size is positively related to resource availability. To test these hypotheses, we collected data on pre-burn and resprout size of five woody plant species at wetland ecotones in longleaf pine savanna subjected to frequent burning. As expected, all species exhibited similar curvilinear relationships between pre-burn size and resprout size. The calculated equilibrium sizes were strong predictors of mean plant size across species and growing conditions, supporting the persistence equilibrium model. An alternative approach using matrix models yielded similar results. Resprouting was less vigorous in dry sites than at wet sites, resulting in smaller equilibrium stem sizes in drier sites; extrapolating these results provides an explanation for the absence of these species in xeric uplands. This new framework offers a straightforward approach to guide data collection for experimental, comparative, and modeling studies of plant persistence and community dynamics in frequently burned habitats.

Key words: *fire; fire trap; Fort Bragg, North Carolina, USA; longleaf pine savanna, southeastern USA; persistence equilibrium model; persistence niche; resprouting; shrub; topkill; tree; wetland-savanna ecotone; woody-plant dynamics.*

INTRODUCTION

Fire plays a fundamental role in governing tree cover in mesic savannas worldwide, maintaining vegetation in a more open state than otherwise would occur (Bond et al. 2005, Staver et al. 2011). Burning has this effect even where it has relatively little impact on tree survival or on the number of stems largely because of the influence of fire on tree size, rather than on the density of individuals (Higgins et al. 2007). In species capable of resprouting, fire reduces plant size by causing death of aerial biomass (topkill), which may require years to replace. If fire occurs frequently, resprouting individuals may be maintained in a suppressed state for decades (Waldrop et al. 1992, Higgins et al. 2007), caught in a “fire trap” of repeated topkill and resprouting (Bond and Midgley 2001).

Although these suppressed stems may be too small to have substantial influence on vegetation structure while in the fire trap, they form a sapling bank that can support rapid increases in tree cover during a long

interval without fire. To persist under frequent burning, a sapling must be capable of tolerating the repeated loss of all of its aerial biomass. This regular destruction of biomass represents a substantial loss of resources and results in a prolonged reduction in photosynthetic capacity (Schutz et al. 2009). If the sapling consistently and repeatedly recovers less biomass than was lost in the preceding fire, it is evident that it will become progressively smaller and presumably must eventually die. If it consistently regenerates more biomass during a fire-free interval than was lost in the preceding fire, then the plant would become progressively larger, and eventually could escape the fire trap by reaching a fire-resistant size. It appears, however, that neither of these cases is typical for savanna trees exposed to frequent fire. Instead, experiments have revealed long-term persistence of saplings in the fire trap (Waldrop et al. 1992, Higgins et al. 2007), suggesting a stasis in which the aerial biomass recovered during a fire-free interval is roughly equal, on average, to the amount lost during the preceding fire. Understanding how this balance is maintained should provide valuable insight into woody-plant dynamics in frequently burned ecosystems.

We hypothesize that the balance between biomass loss and biomass recovery arises from a curvilinear scaling

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relationship between pre-burn size and post-recovery size (henceforth referred to as a “resprout curve”). Evidence from a Neotropical savanna indicates that, after some fire-free interval, resprout size scales in a positive curvilinear manner with pre-burn size (Hoffmann and Solbrig 2003), ultimately approaching an asymptote as shown in Fig. 1. The shape of this resprout curve determines whether a plant fully recovers its pre-burn size by the end of the interval. Of particular importance is the point at which the resprout curve intersects the 1:1 line, as this represents an equilibrational size in which the resprout size at the end of the fire interval is identical to the pre-burn size. A plant that was larger than the equilibrational size prior to burning will not fully recover its original size during the interval, and its final size will be closer to the equilibrium (Fig. 1A). Similarly, a plant that was smaller than the equilibrational size will surpass its original size during the subsequent fire-free interval, and therefore its final size will similarly be closer to the equilibrium.

If this process is repeated, sapling response to recurring fire can be understood as an updating function, where $S_{n+1} = F(S_n)$. Here S_n is the size just prior to burning, S_{n+1} is the size at the end of the subsequent fire-free interval, and F defines the curvilinear function. Thus, as this updating function is applied over successive fire cycles, plant size should gradually approach the equilibrium.

Equilibrational plant size should be influenced by any factor that affects the amount of recovery after fire, including the length of fire interval, season of burn, growing conditions, and characteristics of the species. For example, under high resource availability, growth of resprouts should be faster, and equilibrational plant size will be greater (Fig. 1B). Under very low resource availability, a resprout curve might cross the 1:1 line only at the origin, in which case the plant is not expected to persist under repeated burning (Fig. 1B). In this case, the plant would undergo a “death spiral” of successive decline until it becomes too small to survive.

In our present study we explore the validity of this “persistence equilibrium” model for explaining the dynamics of plants subjected to repeated burning. Our study site was located in species-rich, pyrophytic wetlands embedded in longleaf pine savanna in the southeastern United States. We selected five resprouting species typical of these habitats that survive in a shared fire regime, ranging in size from shrubs to canopy trees. We test whether models of equilibrational plant size predict differences in sapling size among species and among sites differing in resource availability, and consider their generality in explaining plant persistence and species composition in disturbed habitats.

METHODS

Study site and species

Growth characteristics of resprouting shrubs and trees were measured in the Sandhills region of southeastern

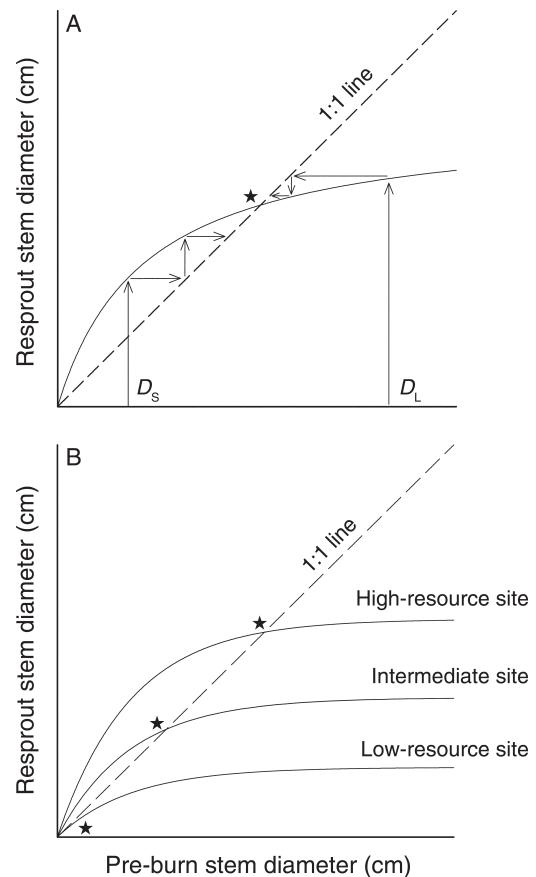


FIG. 1. (A) An illustration of the hypothesized equilibrium (star) that arises from the balance between biomass loss and its recovery under repeated topkill (loss of aerial biomass by burning). The solid curve represents the idealized relationship between pre-burn stem diameter and stem diameter of resprouts at some interval after fire. Repeated burning will tend to cause plants to approach an equilibrational stem diameter that corresponds to the point of intersection between the curve and a 1:1 line. The arrows show trajectories of plant size over repeated fire cycles for a plant with a small initial stem diameter (D_s) and for a plant with a large initial stem diameter (D_L). From either starting point, the plant approaches the equilibrational size. (B) Hypothesized effect of resource availability on the resprout curve, which results in different equilibrium points.

United States Atlantic coastal plain at Fort Bragg, North Carolina (35°07' N, 79°10' W). Fort Bragg is a military reservation occupying a 73 469-ha remnant of a once-vast expanse of longleaf pine savanna. Mean annual rainfall is ~1200 mm; rainfall occurs evenly throughout the year. Average summer temperature is 26°C; average winter temperature falls to 7°C (Sorrie et al. 2006). Prior to 1991, fire history at the study site is not well documented. Since then, however, the area has received prescribed burns at 3-yr intervals, maintaining a savanna dominated by longleaf pine (*Pinus palustris*). Fort Bragg is characterized by rolling hills and sandy soil, underlain by impermeable clay. High rainfall and rapidly draining soils create a mosaic of xeric uplands,

mesic lowland flats, and hydric seeps or streamheads. Vegetation in these wetlands is variable, due to differences in fire history and hydrology. The wetter portions are generally occupied by forest or evergreen shrubland known as “pocosin.” With frequent burning, the pocosin vegetation may be replaced by wet savannas with abundant grasses, ferns, and forbs (Sorrie et al. 2006). These wet savannas are occupied by a diverse plant community, including many rare and endangered forbs (Sorrie et al. 2006).

Five common and representative resprouting species were chosen for study. *Ilex glabra* (Aquifoliaceae) is an abundant evergreen shrub capable of forming thickets under fire suppression. Two common subcanopy species were selected, the evergreen *Persea palustris* (Lauraceae) and the deciduous *Magnolia virginiana* (Magnoliaceae). Finally, two canopy-dominant species were examined as well: the shade-intolerant resprouting pine *Pinus serotina* (Pinaceae) and the shade-tolerant deciduous maple tree *Acer rubrum* (Sapindaceae). *P. serotina* is the dominant tree in many pocosins and wet savannas, whereas *A. rubrum* is more common as an adult in successional forest. At the study site, all species occur predominantly in wet soils adjacent to streams and seeps and are absent or scarce in the uplands under frequent burning.

Data collection

We studied 16 wetland–savanna ecotones that had been subjected to burning at 3-yr intervals and were last burned three years previously so that all resprouts are of a common age. At each site we set up two parallel 50-m transects, each aligned to accompany the contour of the slope so that soil conditions along the transect were relatively uniform. The lower transect of each pair was placed to represent relatively wet conditions with a shallow water table while the upper transect occurred on better-drained soil nearer the upper limit of distribution of the study species along the gradient. Two wells of PVC tubing were installed at each transect, and the depth of the water table was monitored monthly for eight months. The a priori classification of sites as wet or dry was successful for characterizing differences in soil moisture: in dry sites, mean depth to water table was 71.6 cm compared to 23.9 cm for wet sites ($F_{1,30} = 68.4$, $P < 0.0001$). Surface soil (0–10 cm) was collected at each transect and submitted for nutrient analysis to the Soil Testing Laboratory of the North Carolina Department of Agriculture and Consumer Services (Raleigh, North Carolina, USA), and the wet sites had significantly higher organic matter, cation exchange capacity, K, Mg, Na and Fe, but significantly lower Mn ($P < 0.05$; Appendix A: Table A1).

We measured stem height and diameter for the five study species along transects. Stem diameter was measured at a height of 10 cm. For individuals with multiple stems, we measured only the largest stem. For the clonal shrub *Ilex glabra*, an individual was defined as a stem (or group of stems) separated from other stems

by at least 20 cm. All sites had been exposed to low-intensity burns, so the previous woody stems were typically killed but not consumed by fire. This allowed us to determine the diameter and, in most cases, height of each stem prior to fire. We counted growth rings of a subset of these dead stems to verify that they were three years old at the time of burning. To quantify shrinkage resulting from water loss in these dead stems, we collected fresh stems of each species and measured diameter before and after air-drying. A correction factor based on the regression of the fresh and dry stems was used to adjust the measurements of pre-burn diameter, where y is fresh diameter (mm) and x is dry diameter (mm): *A. rubrum*, $y = 1.048x - 0.050$; *I. glabra*, $y = 1.085x - 0.160$; *M. virginiana*, $y = 1.032x + 0.181$; *Persea palustris*, $y = 1.023x + 0.257$; *Pinus serotina*, $y = 1.064x + 0.335$ ($P < 0.001$ and $R^2 > 0.99$ for all species).

Analysis

To characterize the curvilinear relationship between pre-burn size (S_n) and resprout size (S_{n+1}), we used least-squares nonlinear regression to fit the Michaelis-Menten (Monod) equation to our data. To facilitate analysis, we parameterized the equation as

$$S_{n+1} = (k_1 S_n) / (k_1 - k_2 + S_n)$$

where k_1 and k_2 are parameters that define the shape of the relationship. In this form, k_2 is directly interpretable as the equilibrium size, where resprout size equals pre-burn size. We used the nonlinear regression function of SPSS 18 (SPSS 2009) to fit these parameters and to test whether k_2 differed significantly from 0. To test whether the resprout curves differed significantly between wet and dry sites, we compared the fit of two alternative models. In the first, the parameters were assumed to be the same in wet and dry sites, while in the second, the parameters were allowed to differ between wet and dry sites. The difference in sums of squares between models was tested against the error sums of squares of the second model using an F test.

The dynamics shown in Fig. 1 are based on an idealized, deterministic relationship between pre-burn and resprout size, but in reality there is considerable noise in the relationship. It is not clear what effect this may have on the tendency of plants to reach an equilibrium size after repeated burning, so we also analyzed the data using matrix models. To generate these models, the individuals of each species were classified by stem diameter. Classes were formed by \log_{10} -transforming diameter and creating intervals of 0.1 units (e.g., $10^{0.3}$, $10^{0.4}$, etc). We determined the stable size distribution of these matrices using Poptools 3.2 (Hood 2010) and estimated the mean size of this distribution by taking a weighted average of the midpoint diameters of each class. Weights were assigned based on the relative abundance of each size class in the stable size distribution.

RESULTS

Size of resprouts consistently demonstrated curvilinear scaling relationships with pre-burn size (Fig. 2A–E). Consequently, there was a sharp decline in the ratio of resprout:pre-burn size as pre-burn diameter increased (Fig. 2F–J). Specifically, plants that were smaller than the equilibrium size prior to burning tended to undergo a net increase in size, while plants that were larger than the equilibrium tended to undergo a net decrease in size (Fig. 2F–J), implying eventual convergence at an equilibrium. A parallel analysis using stem height, rather than diameter, revealed qualitatively similar patterns (not shown).

Importantly, calculated equilibrium size strongly predicted mean stem diameter in all species examined (Fig. 3A; $r^2 = 0.92$). For all the resprout curves, the parameter that defines the equilibrium stem diameter (k_2) was significantly greater than 0 ($t > 4.26$, $P < 0.001$), indicating a positive equilibrium size and an expectation of long-term persistence. Over all species and growing conditions, the observed mean diameter was 7% greater than the predicted equilibrium diameter. The mean diameters calculated from the matrix models performed similarly well for predicting mean size (Fig. 3B; $r^2 = 0.97$), with the observed means being 8% greater than the predicted values overall. The matrices used in this analysis are given in Appendix B.

Resource availability had a large effect on observed resprout size and predicted equilibrium size. On wet sites, the resprout curve was shifted upward, relative to dry sites, for four of the five species (Fig. 2A–D). As a result, the predicted equilibrium size was 40%–57% higher in the wet sites for these species. Similarly, observed mean size of resprouts was significantly higher in wet sites, compared to dry sites, for these four species (range, 29%–64%; Fig. 4). For these species there were significant negative relationships between depth to water table and mean resprout diameter (Fig. 4). Only *Pinus serotina* deviated from this trend, exhibiting no linear relationship with depth of water table (Fig. 4), while equilibrium diameter and mean resprout diameter were greater in dry sites than in wet sites (Figs. 2E and 3).

DISCUSSION

The capacity to tolerate repeated loss of aerial biomass (topkill) is an important dimension of plant life histories in frequently burned ecosystems (Bond and Midgley 2001). What determines whether a plant can persist under these conditions? As we argue here, one necessary condition is the ability to consistently recover enough biomass in the intervals between fires to avoid an unsustainable decline in plant size. Our results show that this is achieved in our study species because plant size approaches a stable equilibrium in which biomass loss during fire is balanced by biomass recovery between fires. The equilibrium arises from a curvilinear scaling relationship between pre-burn and resprout size. Despite considerable variation in adult size, the five examined

species were remarkably similar in the shape of their scaling relationship (Fig. 2A–E), matching patterns observed in Neotropical savannas (Hoffmann and Solbrig 2003) and suggesting a widespread pattern. The parameters of the resprout curves accurately predicted mean diameter across species and sites (Fig. 3A), suggesting that this scaling relationship governs the size distribution of resprouters in disturbed habitats.

This evidence provides a conceptual and predictive basis for determining the capacity and size at which resprouters will persist under frequent burning. The equilibrium stem size at which individuals persist under recurring fire can be quantified with our model as the value of the scaling parameter k_2 of the resprout curve. Any factor that causes a shift in the resprout curve should have predictable effects on equilibrium size. For plants growing in sites with higher nutrient and water availability, the resprout curve was shifted upward relative to low-resource sites (Fig. 2). Consequently, for four of the five species, equilibrium size was 29%–68% larger in sites with higher soil moisture and nutrient levels (Fig. 3), relative to low-resource sites. Similarly, equilibrium size varied nearly three-fold across species. Increased fire frequency should have an effect that is qualitatively similar to that of low resource availability. The reduced recovery time between fires would likely result in a downward shift in the resprout curve, resulting in a smaller equilibrium size or even a failure to persist. These effects have considerable implications for population and community dynamics.

The persistence equilibrium provides a direct means of quantifying important aspects of the fire trap. For example, the fire trap of repeated topkill and resprouting should preclude sexual reproduction in any species for which the equilibrium size is below the minimum reproductive size. The study species had equilibrium stem diameters of <1.6 cm (Fig. 2) and equilibrium heights of <1.5 m (not shown). Although we lack information on reproductive size, the equilibrium sizes appear to be well below the minimum reproductive sizes of the four tree species. Only the shrub, *Ilex glabra*, commonly flowers at these small sizes, and resprouts of this species commonly produce fruits within the 3-yr intervals between fires at the study site.

The size of a sapling while caught in a fire trap should substantially influence the likelihood that its stem reaches a fire-resistant size during an eventual longer interval without fire. If the equilibrium size of a stem is close to the size at which it is no longer susceptible to topkill, then little additional growth is needed to allow it to escape the fire trap. High-resource sites, for example, should promote more rapid escape from the fire trap by enhancing sapling size in addition to promoting more rapid growth during an extended fire-free interval (Hoffmann et al. 2012). Differences among species should have similar effects and could contribute to shifts in species dominance under changing fire regimes. In some cases, the equilibrium size may be sufficiently

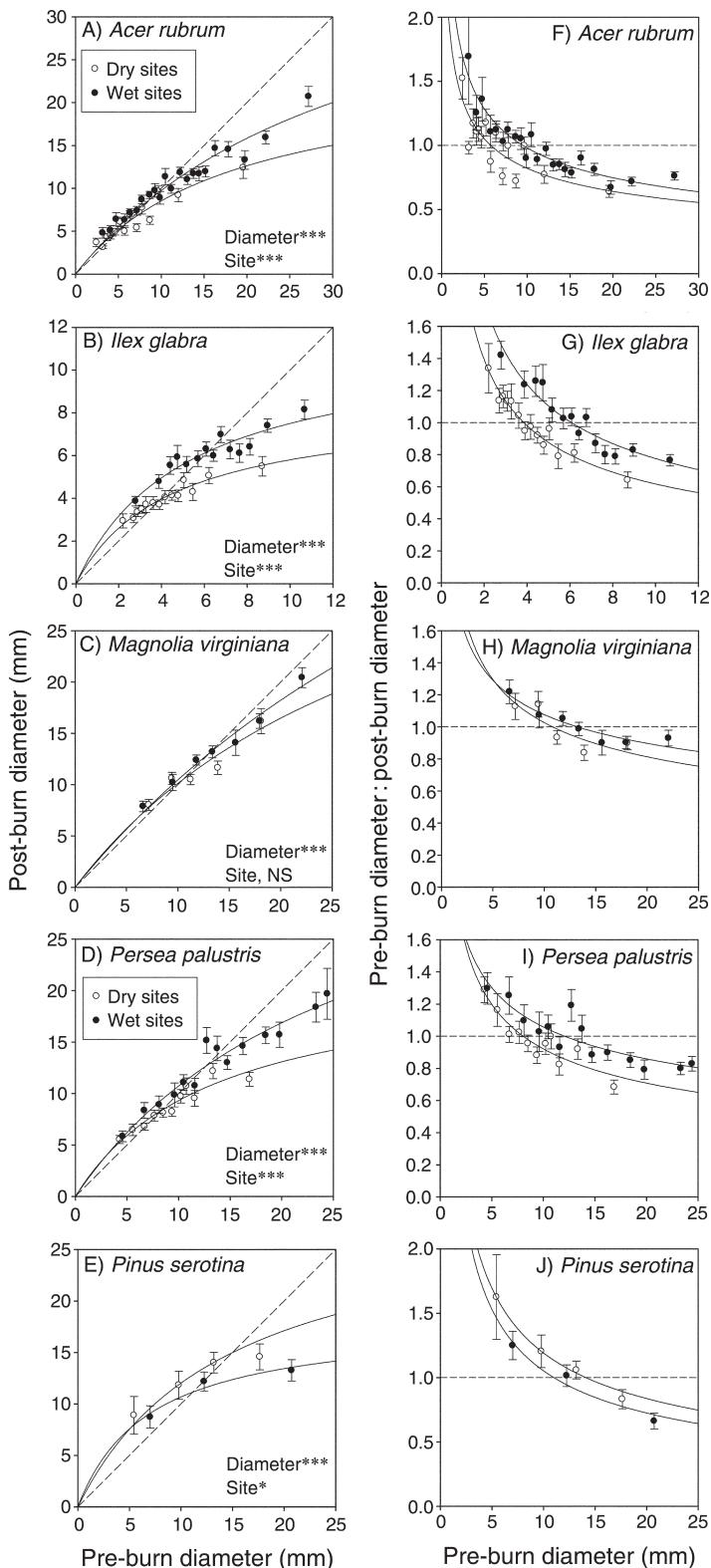


FIG. 2. Curvilinear relationships that underlie the persistence equilibrium. Data are means \pm SE. (A–E) Resprout curves for the relationship between pre-burn diameter and diameter three years after burning for saplings of five resprouting trees shrubs. The predicted equilibril size, which is the point where the curve crosses the 1:1 line, was significantly greater than 0 for all curves. (F–J) Net change in plant size as a function of pre-burn size. Each point represents mean values \pm SE for 15 individuals. Asterisks indicate statistically significant effects of pre-burn diameter and site moisture level; NS indicates not significant.
 * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

close to a fire-resistant size so that some individuals may escape the fire trap despite being subjected to frequent fire. This could explain the unusual ability of *Eucalyptus* spp. to escape the fire trap under annual burning (e.g., Bond et al. 2012). Such results could also arise from high variability in growth rates of resprouts (Wakeling et al. 2011). To account for this variability, matrix models offer a more appropriate approach for predicting stable size distributions. For our five study species, however, predictions based on matrices were remarkably similar to those generated from resprout curves (Fig. 3).

There is no consensus in the literature regarding whether stem height, stem diameter, or bark thickness is the best indicator of whether a stem has escaped the fire trap (Midgley et al. 2010). This uncertainty has little consequence for the approach we introduced here, because it can be implemented using any measure of plant size. Although here we only presented results for stem diameter, a parallel analysis using stem height (not shown) had qualitatively similar results.

Differences in the shape of the resprout curve among species may explain why some species fail to persist under frequent burning despite being able to resprout after a single fire (Fensham et al. 2003, Enright et al. 2011). At the study site, for example, some resprouting species, such as *Nyssa biflora* and *Liriodendron tulipifera*, are abundant in unburned pocosin, but are strikingly uncommon in sites that have been repeatedly burned. Similarly this approach may reveal why a species may tolerate frequent burning in some environments, but not in others. For example, in a study to understand limits to tree success in high-altitude grasslands, Wakeling et al. (2012) found that savanna trees are able to establish and survive in grassland, but they had lower growth rates than in savanna. If the growth rate is sufficiently reduced so that the resprout curve lies entirely below the 1:1 line, this would preclude persistence under frequent burning. More generally, persistence can be limited by any factor that depresses the resprout curve substantially such that $k_2 \leq 0$, including low resource availability, suboptimal temperatures, competition, or high fire frequency.

Based on the equilibrium size, all of our study species are predicted to persist under regular burning in both high- and low-resource sites, but this is not surprising considering that we chose species that remain common at these sites after two decades of repeated burning. Upslope from the study sites, however, all five species decline sharply in abundance and are absent in the uplands. This absence might be explained by the trend towards smaller equilibrium size in drier conditions. Since mean resprout size under frequent burning can be used as a proxy for equilibrium size (Fig. 3), the decline in mean resprout size with increasing depth to water table (Fig. 4) suggests this as an explanation for a failure to persist in the uplands. Extrapolating the trends in Fig. 4, these study species are predicted not to persist under current fire regimes wherever water tables are deeper

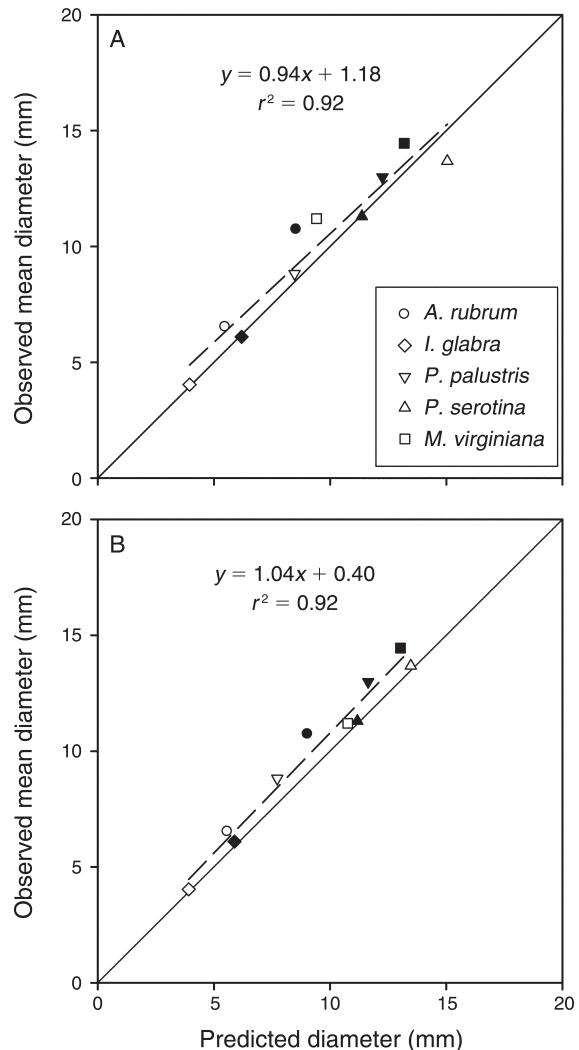


FIG. 3. Regression of observed mean diameter vs. (A) predicted equilibrium size and (B) mean size predicted from matrix models. Open symbols indicate mean values in dry habitats, and solid symbols indicate mean values from wet habitats. See Fig. 2 key for genus names.

than 2–3 m. While this trend may be a direct response to resource availability, the role of competition should not be discounted. Biomass loss caused by frequent fire can reverse competitive hierarchies along resource gradients (Brewer 2011), so competition with upland species may contribute to the decline in resprout size along the gradient.

The curvilinear relationships between pre-burn and post-burn size reflect a general tendency for small individuals to recover their pre-burn size more quickly than large individuals. Data published elsewhere suggest that this may be a general pattern for woody plants (Khan and Tripathi 1989, Hoffmann and Solbrig 2003, Neke et al. 2006, Hoffmann et al. 2009). This could result from a trend of declining allocation to root biomass (Enquist and Niklas 2002, Poorter et al. 2011)

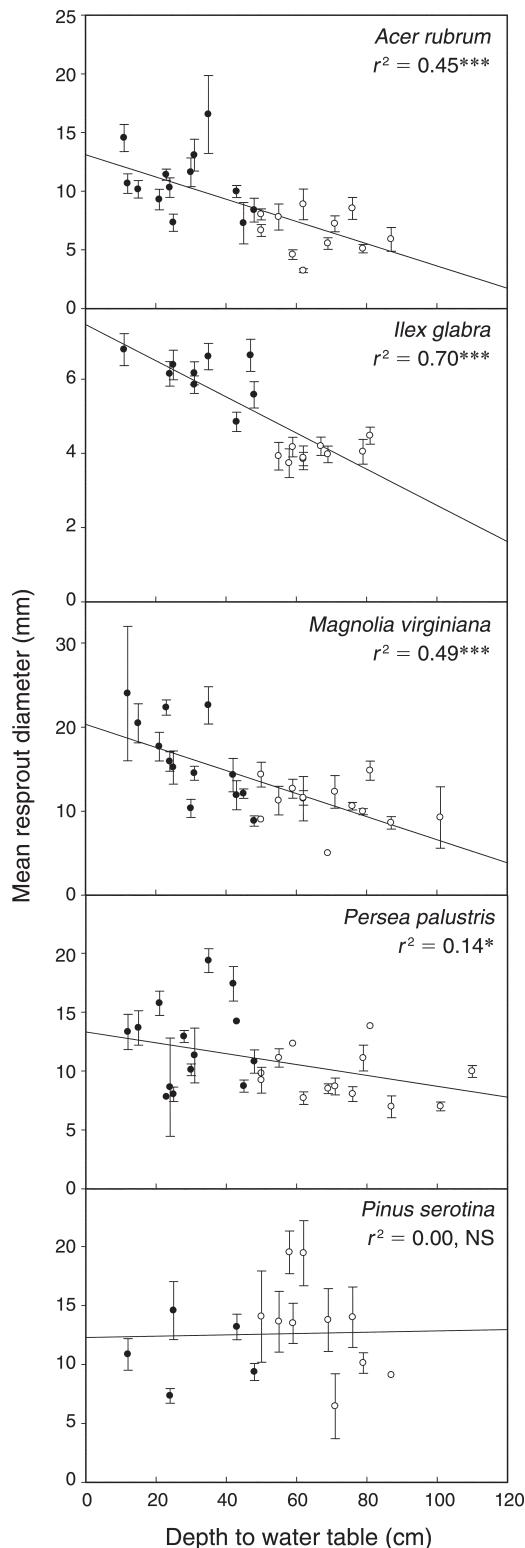


FIG. 4. Relationship across study sites between depth to water table and mean size of resprouts. Each symbol represents the mean diameter of all individuals sampled at a single transect. Open and solid symbols indicate transects categorized a priori as dry and wet sites, respectively. Statistical significance of correlations is indicated by asterisks.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS, not significant.

or declining concentration of root nonstructural carbohydrates (Machado and Reich 2006, Wigley et al. 2009) as plants grow. Also, large stems may inherently require more time to construct, delaying the complete conversion of reserves into shoot biomass, and slowing the return to a condition of net carbon gain. Distinguishing among these alternative explanations for the curvilinearity of resprout curves should provide insight into the constraints on evolution of fire response, while informing more mechanistic models of fire impacts on population and vegetation dynamics.

Models of population or vegetation dynamics commonly assume that resprout growth is dependent on size prior to fire but is otherwise unaffected by fire history (Hoffmann 1999, Higgins et al. 2000, Hanan et al. 2008, Holdo et al. 2009, Staver et al. 2009). If this assumption is valid, the approach we introduced here will be a valuable tool for predicting equilibrium size for a range of fire frequencies using easily obtained data. Specifically, with repeated size measurements on a cohort of resprouts, it is straightforward to fit resprout curves for various times after fire, thereby permitting estimates of equilibrium size under a wide range of fire intervals. This could be used, for example, to predict fire or clipping frequencies that could reverse woody-plant encroachment into savanna and grassland environments, a common management goal in longleaf pine ecosystems (Jacqmain et al. 1999, Drewa et al. 2002).

Unfortunately, it is not clear whether the parameters of the resprout curve would be substantially affected by previous fire history. Under repeated burning the plant may undergo successive depletion of nutrient or carbohydrate reserves, resulting in a downward shift in the resprout curve relative to plants that had been burned for the first time or had been subject to less frequent burning. Alternatively, the resprout curve may shift upward, as a result of altered patterns of resource partitioning. We avoided this issue in our study by restricting our data collection and interpretation to plants subjected to repeated burning at 3-yr fire intervals, so that any such shift would already have occurred. However, it would be worthwhile to test for such shifts to explore whether the persistence equilibrium can be predicted adequately under variable fire histories.

Striking a balance between biomass loss and recovery is a necessary, but not a sufficient, condition for persistence under repeated burning. To survive, a plant must also be able to generate new buds or maintain a bank of dormant buds (Zammit 1988, Bell and Pate 1996) and must contain the spread of fungi that can enter the wounded stem and cause root decay (Keim et al. 2006, Wolken et al. 2009). More generally, most or all species exhibit some amount of immediate, fire-induced mortality among saplings (Rutherford 1981, Williams et al. 1999, Hoffmann and Solbrig 2003, Werner and Franklin 2010), which would cause gradual attrition of the population if not offset by new recruitment. Hence,

plants may fail to persist for multiple reasons, and more study is needed to distinguish among these mechanisms.

The persistence equilibrium model has implications for conservation and management of land with a legacy of fire. Woody resprouters commonly invade grasslands and savannas during fire suppression, reducing diversity of herbaceous plants (Waldrop et al. 1992, Lett and Knapp 2005, Brudvig 2010) and competing with rare species (Brewer 2005, Patterson and Clarke 2007). Once established, many resprouters are notoriously difficult to eliminate by reintroducing fire (Waldrop et al. 1992, Pendergrass et al. 1998, Drewa et al. 2002, Lett and Knapp 2005), but this should be attainable if fire is sufficiently frequent to depress the resprout curve below the 1:1 line. Alternatively, historically grassy habitats may be restored if woody plants persist but are maintained at sizes too small to suppress herbaceous plants (Waldrop et al. 1992). Their size and potential for shading herbaceous species will be closely linked to the equilibrium stem size and to the parameters of the resprout curve. Ultimately, consideration of the resprout scaling parameters can assist managers in achieving diversity and habitat objectives.

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SUPPLEMENTAL MATERIAL

Appendix A

A table summarizing the soil properties of wet and dry sites (*Ecological Archives* E093-196-A1).

Appendix B

Tables of matrices used to model stable size distribution of resprouts, by species and site type (*Ecological Archives* E093-196-A2).