Forest Ecology and Management 429 (2018) 158–174

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Leaf and bark functional traits predict resprouting strategies of understory woody species after prescribed fires

P. Casals[a,*], T. Valor[a], A.I. Rios[a], B. Shipley[b]

[a] *Forest Sciences Centre of Catalonia, CTFC, Ctra de St. Llorenç de Morunys, km 2, 25280 Solsona, Spain*
[b] *Département de biologie, Université de Sherbrooke, 2500 Boul. de la université, Sherbrooke, Québec J1K 2R1, Canada*

ARTICLE INFO

Keywords:
Bark investment
Burning season
Deciduous
Evergreen
Leaf area
Light availability
Plant functional traits
Specific leaf area

ABSTRACT

In temperate forests, both deciduous and evergreen species with small or large leaves coexist in the understory and resprout after prescribed burnings. This diversity of traits suggests that there are different strategies operating after the initial resprout growth to re-acquire space, capture resources and resist additional stresses. This study aims to understand resprout vigor 3 years after burning of woody understory species with different leaf traits and bark investment (i.e., the ratio between bark thickness and basal stem diameter).

In two temperate forests, we burned one stand in late spring and another in fall. After 3 years, we studied resprout number and resprout basal diameter and length of ten individuals of six species per stand. Three species were common in both forests and three were different. Therefore, species of both forests were grouped in three groups based on leaf traits and in three different groups according to their bark investment. Besides the expected positive effect of pre-fire plant size, resprout number and vigor were higher after burning in spring than in fall. The higher resprout volume in evergreens, with small specific leaf area (SLA), than in deciduous species, with large SLA, may be related to evergreens having a longer possible growing season than deciduous species. In addition, species in different leaf groups differed in the ratio of resprout length to diameter growth, suggesting that it is important for deciduous small-leaved species to grow tall rapidly before they are shaded by large leaved species. In contrast, no direct effect of light availability on resprout vigor was detected. Bark investment did not explain resprout vigor but did affect resprout number in the low bark investment group. In this group, resprout number decreased with increasing maximum fire temperature. Based on our results, burning in the fall is advisable when the management objective is to minimize the recovery of the understory. In addition, to reduce the dominance of understory woody species with low bark investment, our study suggests that understory fires must be performed with moderate to high intensity.

1. Introduction

The capacity to resprout is an important trait found in a wide range of plant species that allows the persistence of individuals after the destruction of most of their aboveground biomass (Noble and Slatyer, 1980; Bond and Midgley, 2001). The initial recovery after such destruction is produced from a bank of protected meristems, which are supplied by stored reserves (Bell and Pate, 1996; Canadell and López-Soria, 1998). Once these meristems begin to develop, resprouting vigor (i.e., the growth rate of resprouting shoots) depends on both the allocation of stored resources and the capacity to acquire new ones (Cruz et al., 2003a; Kobe, 1997). The coexistence of resprouting species with different combinations of functional trait values suggests the existence of alternative adaptive strategies operating after a perturbation. Although the success of these strategies depends on the specific characteristics of the disturbance (Kauffman and Martin, 1990), it may also be related to different trait values that better capture resources and resist additional stresses.

After the destruction of aboveground biomass, woody resprouters in the Mediterranean basin often regenerate from basal buds positioned at the root collar or in specialized lignotuberous structures at or just below ground level (Bond and Midgley, 2001; Clarke et al., 2013; Paula and Pausas, 2013). The allocation of resources to increase bark thickness to protect these meristematic tissues from overheating during surface fires may come at a cost to growth (Hoffmann et al., 2012; Lawes et al., 2013). Therefore, bark investment may be an adaptive trait in temperate forests that generally experience low-intensity understory fires (Jackson et al., 1999; Keeley et al., 2011; Pausas, 2015; Pellegrini et al.,

---

[*] Corresponding author at: Forest Sciences Centre of Catalonia, CEMFOR-CTFC, Ctra de St. Llorenç de Morunys, km 2, 25280 Solsona, Spain.
E-mail address: pere.casals@ctfc.cat (P. Casals).

https://doi.org/10.1016/j.foreco.2018.07.002
Received 17 March 2018; Received in revised form 30 June 2018; Accepted 1 July 2018

2017). Since the heat insulation by bark increases with the square of its thickness (Hare, 1965), we hypothesized that the investment in bark thickness relative to stem growth may explain higher number of resprouting meristems following low-to-moderate intensity fires.

Prescribed burns are generally performed in the Mediterranean basin either at the beginning of fall, just after the first rains but before the rainy period, or at the end of winter and early spring, before the onset of spring rains. Fall burns performed under dry fuel conditions may be more intense than in moister conditions (Knapp et al., 2005; Kauffman and Martin, 1990), which could lead to high shrub mortality and a reduction in the number of viable resprouting meristems. However, if spring burns are conducted during active aboveground growth, burning may reduce subsequent resprouting vigor because the stored reserves have already been used to support shoot and leaf growth after dormancy (e.g., de Groot and Wein, 2004; Harrington, 1989; Hoch et al., 2003). Hence, differences in plant phenology and physiological status may interact with the burning season and affect resprouting vigor. We hypothesized that burning after the initiation of spring growth, when the carbohydrate reserves are at their lowest levels (de Groot and Wein, 2004), would reduce resprouting vigor in comparison with burning during or just before the dormant season, at least for deciduous species.

In addition to the physiological status and burning season, it is possible to hypothesize certain links between leaf functional traits and resprouting behavior. For instance, although resprouting ability and vigor is generally related to the size of individuals before burning (e.g., Hodgkinson, 1998; Kauffman and Martin, 1990; Lloret and López-Soria, 1993), the weakness of these relationships under shade conditions have been explained by differences in light availability (Cruz et al., 2003b; Quevedo et al., 2007). Hence, higher light availability seems to drive the height growth of resprouts, especially in more fertile habitats (Knox and Clarke, 2011). If so, this suggests that specific leaf area (i.e., leaf surface area per unit leaf mass; SLA) plays some role, since the meta-analysis by Shipley (2002) found that SLA is positively correlated with relative growth rate in low light conditions but the strength of the relationship decreases with increasing daily light input. In addition, Iwasa and Kubo (1997) stated that resprouting species that have a slow leaf turnover and a lower SLA (e.g., evergreens) will also invest more in reserves and structures to resist further disturbance, and hence have slow resprouting growth. Therefore, we hypothesize a tradeoff between the number of resprouting buds and the subsequent growth of resprouts under shade conditions. This tradeoff mediated by variation in SLA could be related to the differential allocation of resources to bark thickness, which confers bud protection in species with low SLA or to resprout growth in species with high SLA. Independently of SLA, leaf area (LA) is important for leaf energy and water balance (Niinemets et al., 2007 and references therein). The reduction in LA in environments limited by photosynthetic carbon acquisition has been explained based on the excessive cost for the construction of large leaves and support biomass (Niinemets et al., 2007). Light-demanding species have, in general, larger leaves compared to shade-tolerant species. However, two interspecific responses have been described in order to compete for light after a perturbation: the production of small leaves that can be shed once overshaded and new ones grow above them; and the production of large leaves to overtop and outshade their neighbors (Poorter and Rozendaal, 2008 and references therein). Therefore, we expected that deciduous resprouters with high SLA but small LA would invest in growing upwards to acquire light, and avoid shading by large broadleaved deciduous species (large LA).

In temperate forests, both deciduous and evergreen species with small and large leaves coexist in the understory and resprout after perturbations. This study takes advantage of this richness of plant functional traits to investigate the strategies of resprouting groups after understory burning and, specifically, how resprout number and vigor relate to easily-measured leaf or bark investment traits that might reflect different allocation trade-offs. Understory prescribed burns are

Table 1
Characteristics of the four stands and prescribed burnings.

Site	Stand and burn season	Site characteristics										Prescribed burning characteristics[d]			
		Long., °E	Lat., °N	Altitude, m a.s.l.	Slope, %	Aspect	Rainfall[a], mm	mean T[a], °C	Canopy openness[b], %	Tree density[c], n ha^{-1}	Tree basal area[c], m^2 ha^{-1}	Burnt surface, ha	Max fire temperature[d], °C	Combustion time[d], min,T > 120 °C	Mineral soil WC, %
Lloreda	Spring (5/Jun)	1.5706	42.0569	715	30	N	732	11.7	19.2–23.1	2611	31.5	1.1	418 (107–834)	8 (0–19)	34.3 (10.3)
	Fall (8/Nov)	1.5771	42.0620	826	25	N	766	11.1	19.3–23.7	2277	44.9	1.6	492 (222–729)	95 (5–408)	9.6 (0.4)
Miravé	Spring (12/Jun)	1.4494	41.9515	723	25	NE	677	11.5	23.2–28.7	2722	32.3	0.9	409 (60–718)	5 (0–18)	30.4 (8.2)
	Fall (17/Oct)	1.4496	41.9508	723	25	NE	677	11.5	20.6–24.5	2744	32.6	1.2	310 (60–747)	9 (0–36)	12.8 (0.4)

[a] Climate variables were estimated using a georeferenced model (Ninyerola et al., 2000). Http://territori.gencat.cat/atles_climatic/02/.

[b] Canopy openness was estimated using the GLA software (Frazer et al., 1999) on hemispherical canopy photographs, taken skyward from 0.50 m above the forest floor with a 180° hemispherical lens in the center of the four quadrants of a 900 m-plot.

[c] Tree density and basal area calculated for trees with a diameter larger than 2.5 cm at a height of 1.30 m (Valor et al., 2017).

[d] Maximum fire temperature (°C) and time in minutes with temperatures above 120 °C at the litter surface, estimated by 18 k-thermocouples per stand (Mean and range between parenthesis).