Forest Ecology and Management 310 (2013) 321–326

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Sprouting extends the regeneration niche in temperate rain forests: The case of the long-lived tree *Eucryphia cordifolia*

Antonio B. Escandón [a,1], Susana Paula [b,1], Roke Rojas [c], Luis J. Corcuera [a], Rafael E. Coopman [c,*]

[a] *Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile*
[b] *Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile*
[c] *Laboratorio de Ecofisiología para la Conservación de Bosques, Instituto de Conservación, Biodiversidad y Territorio, Universidad Austral de Chile, Casilla 567, Valdivia, Chile*

ARTICLE INFO

Article history:
Received 29 June 2013
Received in revised form 20 August 2013
Accepted 21 August 2013
Available online 17 September 2013

Keywords:
Niche breadth
Root suckers
Gap colonization
Sapling survival
Interactive abiotic stress

ABSTRACT

Sprouting is a widespread trait of geographical, ecological and taxonomical scales that allows resource exploitation, space colonization, vegetative reproduction and post-disturbance persistence. It is considered that persistence is the most frequent functional role of sprouting in woody plants. Here we propose that niche differentiation between sprouts and saplings extends the regeneration niche to suboptimal conditions for sexual recruitment. To test this hypothesis, we sampled root suckers (sprouts) and saplings of the long-lived tree species *Eucryphia cordifolia* Cav. in an even-aged coastal temperate rain forest. Canopy openness was measured over each recruit as a proxy of regeneration niche. Sapling survival was checked after two years. The entire forest canopy openness range was used as an estimation of niche availability. Light and microclimatic conditions were recorded for different canopy openness. Sprouts and saplings occupied a narrow range of the canopy openness near to the closest extreme of the gradient (4.8–14.1%). The distribution of saplings was explained by the lower survival of small saplings under more open canopies, as a consequence of the interactive effect of higher evaporative demand and radiation load in more opened canopies. Although the niches of sexual and vegetative recruits slightly overlapped (31% of the interquartile range on average), sprouts inhabit the more opened sites. Therefore, sprouts extend the regeneration niche to suboptimal conditions for sapling establishment. Our results contribute toward explaining the high colonization ability of *E. cordifolia* in this kind of forest, whose composition is strongly driven by gap dynamics.

1. Introduction

Sprouting is a widespread, ancestral trait, appearing in a wide range of ecosystems and lineages (Wells, 1969; del Tredici, 2001; Bond and Midgley, 2003; Vesk and Westoby, 2004). The very high frequency of sprouting at both ecological and taxonomical scales reflects its functional diversity (van Groenendael et al., 1996; del Tredici, 2001); it allows populations: (1) to exploit resources when they are scarce or heterogeneously distributed in space (exploitation function); (2) to increase the competitive ability by fast colonization of gaps in high productive ecosystems (colonization function); (3) to increase reproduction in stressful environments or in species with low sexual reproductive success (reproduction function); and (4) to regenerate vegetatively after disturbances of different severities (i.e. resprouting *sensu* Clarke et al., 2013; persistence function). It is considered that clonal growth in herbaceous species mostly allows gathering resources, space colonization and reproduction, whereas the primary benefit of sprouting for woody species is recovering after disturbances (Peterson and Jones, 1997). In fact, resprouting is a cornerstone trait determining resilience to disturbances in woody plant communities (Keeley, 1986; Bond and Midgley, 2001).

In ecosystems under a low-severity disturbance regime, sprouting of woody plants occurs in the absence of major disturbances, suggesting other functional meanings of sprouting (Jeník, 1994; Peterson and Jones, 1997). For instance, clonal growth by spreading non-splitting sprouts is frequent in stressful environments such as marsh wetlands or tree-lines (Pennings and Callaway, 2000; Peltzer, 2002). The subsidy of water, sugars and nutrients from parent plants increases the chance of survival of non-splitting sprouts under abiotic stressful conditions (Wiehle et al., 2009). In the high productive rain forests, competition induces biotic stress and strongly determines species assemblage (Kraft et al., 2008). In these ecosystems, woody plants show almost all forms of sprouting and most of them increase colonization rates and thus competitive ability (Grubb, 1987; Jeník, 1994).

Opportunities of colonization in rain forests mainly occur after canopy openness, such as tree-fall gap formations (Denslow, 1987).

---

* Corresponding author. Tel.: +56 63 293037; fax: +56 63 221230.
E-mail address: rafael.coopman@uach.cl (R.E. Coopman).

[1] These two authors contributed equally to this work.

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.08.046

Commonly, sexual regeneration is in competitive disadvantage against sprouts due to their lower growth rates during early developmental stages (Farahat and Lechowicz, 2013). This is exacerbated in gaps where microsite conditions are likely to become unsuitable for seedling establishment. The interaction between the sudden increment of high irradiance and subsequent evaporative demand in gaps might lead to some level of drought (Tognetti et al., 1994; Flexas et al., 1999). This is especially true for shade saplings, which present several traits toward the maximization of light capture, which are antagonistic to those described for water stress resistance, resulting in an exacerbated water stress sensibility (Valladares and Pearcy, 2002). In these cases, sprouts would extend the regeneration niche to suboptimal conditions where the chance of sexual recruitment is low.

The regenerative dynamics of the coastal temperate rain forest of south-central Chile is strongly driven by the occurrence of individual tree-fall gaps, which increases environmental heterogeneity, thus allowing the coexistence of different plant functional types (e.g. Armesto and Fuentes, 1988; Gutiérrez et al., 2008). Specifically, gaps are suitable for the seedling establishment of shade-intolerant species, whose survival is negligible in deep shaded microsites because the low carbon gain induces carbon starvation (Givnish, 1988). For intermediate shade-intolerant species, such as the long-lived tree species *Eucryphia cordifolia* Cav., small gaps seem to be adequate for sexual recruitment (Lusk et al., 2006; Gutiérrez et al., 2008). This species produces high amounts of viable seeds from an early age onward, which can be dispersed over long distances (Escobar et al., 2006). Although germination is usually greater in understory conditions, it is not negligible in gaps (Figueroa and Lusk, 2001). Therefore, the spatial pattern of sexual recruitment of *E. cordifolia* (i.e. at intermediate canopy openness) is not explained by seed availability and germination but by seedling establishment and survival. In fact, although seedlings of this species have been recorded immediately after gap formation, most of them fail to survive after two years (González et al., 2002). In addition to sexual recruitment, this species profusely sprouts from roots, even in the absence of disturbances; contrary to sexual recruits, root suckers show very low mortality (Donoso et al., 1985; Veblen, 1985; González et al., 2002). The coexistence of the two regeneration mechanisms in *E. cordifolia* and gap dynamics of the coastal temperate rain forest provides an excellent model to evaluate the role of sprouting in extending the niche regeneration to limiting conditions for sexual recruitment. To test this hypothesis, we addressed the following questions: (1) does niche selection exist in sprouts and saplings of *E. cordifolia*?; (2) which environmental condition constrains the survival of *E. cordifolia* saplings?; (3) does niche differentiation between sprouts and saplings extend the niche regeneration? In order to fulfill these aims, we considered the canopy openness as a proxy of ecological niche, since it involves the availability of key resources like light and water (Brown, 1993; Maherali et al., 1997).

2. Material and methods

2.1. Study site

This study was conducted during the growing seasons of 2011–2013 in a 30 ha secondary coastal temperate rain forest located in south-central Chile (Katalapi Park: 41°31′8″S, 72°45′2″W, elevation ca. 90 m a.s.l.). The forest structure corresponds to ca. 35 year old even-age forest where the taller individuals reach up to 10 m, but with some old-growth remnant trees. The study site presents several open areas previously used for cattle activities. For the last 27 years, the forest has been protected from anthropogenic alterations (logging, cattle), allowing for regeneration of both sun and shade species. The most frequent tree species are *Nothofagus nitida* (Phill.) Krasser, *Nothofagus dombeyi* (Mirb.) Oerst, *Laureliopsis philippiana* (Looser) Schodde, *Aextoxicum punctatum* R. et P., *E. cordifolia* Cav., *Drimys wintery* J.R. et G. Forster, and several Mirtaceae (Saldaña et al., 2005; Lusk and Corcuera, 2011; Coopman et al., 2011).

This area presents a maritime temperate climate, with annual rainfall of ca. 1900 mm concentrated between April to November (ca. 77% annual rainfall; data from 1861 to 2001; Tepual Airport weather station: 41°25′S, 73°05′85″W; Meteorological Office of Chile, http://www.meteochile.gob.cl/) and a mild dry season during December to March. In this period, the mean air temperature reaches 15 °C, the lowest air relative humidity range between 45% and 55% and a 15-day-long dry period frequently occurs within each summer. Climatic details for the study area are shown in Coopman et al. (2010).

2.2. Forest canopy openness

The forest canopy openness gradient was determined on 8 transects 100 m long on average randomly distributed along the forest. To ensure that we included the entire light gradient, transects were started in open sites located at the edge of the forest and continued through the closed forest. Hemispherical photography was used to measure canopy openness (Chazdon and Field, 1987) by using a Coolpix 4500 digital camera equipped with a FC-E8 fisheye lens (Nikon, Tokyo, JP). A photograph was captured at 5 m intervals along each transect at 40–60 cm height, resulting in a total of 161 photographs. The camera was hand leveled and oriented so that the top of the image faced north. Photographs were taken on homogeneous overcast days. The resulting photographs were analyzed for the percentage of canopy openness (hereafter CO) with the Gap Light Analyzer 2.0 software (GLA; Frazer et al., 1999).

2.3. Canopy openness and microsite environment

To relate CO with microsite conditions we recorded photosynthetic photon flux density (PPFD), air temperature (Ta) and relative humidity (RH) at different CO ranges from 2% to 100% (see Fig. 1). In the open site (100% CO), we used a Li-1400 data logger connected to LI250, Li 1400-104 and Li 1400-106 sensors (Li-Cor Inc., NE., USA). For measurements inside the forest, we installed H21-002 HOBO meteorological stations connected to S-LIA-M003 and S-THA-M0xx sensors (Onset, MA, USA). Data were recorded at 30 min intervals from 2007 until 2013 (except 2010 due to technical troubles). The air vapor pressure deficit (VPD) was determined according to Murray (1967):

$$\mathrm{VPD} = \mathrm{Pv} - ((\mathrm{RH}/100) * \mathrm{Pv}),$$

where Pv is calculated as follows: $\mathrm{Pv} = 0.611 \exp [17.27\ \mathrm{Ta}/(\mathrm{Ta} + 237.3)]$.

2.4. Regeneration niche

More than 90% of the surface area of the forest was inspected looking for saplings. Regarding sprouts, previous observations indicated that they only appear close to mature trees. Therefore, sprouts were recorded in 15 plots of 200 m^2 established around mature trees, in such a way that each plot covered a wide range of canopy openness (i.e. from big gaps to closed forest). *E. cordifolia* sprouts from the root collar and from roots (root suckers; e.g., Veblen, 1985). However, for the aim of this study, we only sampled root suckers, because basal sprouts are generally associated to severe damage (persistence function; Jeník, 1994). Sampled recruits were taller than 2 cm in height but shorter than 175 cm. We excluded older recruits (i.e. taller), because environmental conditions