SHORT COMMUNICATION

The onset of precipitation mediates plant–avian disperser interaction in recalcitrant seeds: the case of *Cryptocarya alba* (MOL) Looser, in Mediterranean ecosystems, Central Chile

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Background: Arid and semi-arid environments impose limitations on plant regeneration. This is especially important during biotic dispersal in plants with recalcitrant seeds, in relation to when and where birds disperse these seeds.

Aims: We examined the effect of the onset of seasonal precipitation on the regeneration of *Cryptocarya alba* (Lauraceae), comparing seedling recruitment during early and late onset of precipitations.

Methods: We conducted field experiments using bird-dispersed and gravity-dispersed seeds; half of the seeds were placed during the initiation of precipitations; the other half was kept, then was placed in the forest ground 2 months later. We compared seedling recruitment probability among treatments.

Results: Seedling recruitment was positively affected by avian dispersal. Seedling recruitment was significantly increased only for the fraction of bird-dispersed seeds that matched with the beginning of precipitations.

Conclusions: The ecological context as well as seed recalcitrance are critical in determining the fate of bird-dispersed seeds. Although this trait may be not adaptive in seasonal ecosystems, it is correlated with other traits that are adaptive (seed size, directed dispersal, spread of the dispersal season), thus explaining the persistence of species with recalcitrant seeds in such environments.

Keywords: bird frugivory; Central Chile; *Cryptocarya alba*; La Campana National Park; seed recalcitrance

Introduction

Similarly to other semi-arid areas of the world, Mediterranean central Chile exhibits strong inter-annual variation in precipitation (Di Castri and Hajek 1976; Quintana 2004). This climatic variability has profound implications for ecosystem dynamics, affecting the physiology of plants, primary production, and plant–animal interactions (Valladares et al. 2004; Resco de Dios et al. 2007; Valladares and Gianolli 2007; Gutiérrez et al. 2010). One kind of climatic variability rarely considered in ecological studies is the onset of the rainy season (McLaren and McDonald 2003; Stella et al. 2006). In central Chile, for instance, rains may begin as early as January or as late as June, with the mode falling in April (Figure 1). Such variability may be important for plants whose seeds have a short life span (<1 year) and which do not have the physiological or morphological attributes to resist desiccation (seed recalcitrance, sensu Farnsworth 2000). Although seed recalcitrance places constraints on plant regeneration under conditions of water limitation, an important fraction of species with this attribute (ca. 10%) occur in highly seasonal, stressful environments (Pammenter and Berjak 2000; Pritchard et al. 2004). This is the case in Mediterranean central Chile, where 11% of tree species,

including all Lauraceae (*Beilschmiedia berteroana* (Gay) Kosterm, *Cryptocarya alba* (Mol.) Looser and *Persea lingue* (Ruiz et Pav.) Nees ex Kopp) have recalcitrant seeds (Figueroa and Jaksic 2004).

Cryptocarya alba (Mol.) Looser is a dominant late-successional shade-tolerant tree that inhabits cool south-facing slopes and moist ravines in central Chile (Armesto and Martínez 1978; Armesto and Pickett 1985; Hoffmann 1997). Fruits are reddish-pink, one-seeded drupes with a thin pericarp; seeds are recalcitrant, i.e. they do not maintain a seed bank from year to year and they remain viable and alive in the ground for up to 5 months (Chacón and Bustamante 2001). After exposure to dry conditions for that length of time, all non-germinated seeds will have desiccated and died (Bustamante et al. 1996). Seed dispersal occurs from March to October, seed germination from June to July, and seedling establishment from September to October. Birds, such as *Mimus thenca* Mol., *Pyrope pyrope* Kittlitz and *Turdus falklandii* King, consume the pericarp of fruits and regurgitate the seeds under perch trees; they are effective dispersers as they increase seed germination and deposit them in safe sites (closed habitats, under parent plants) for regeneration (Bustamante et al. 1996). Native foxes consume seeds and increase

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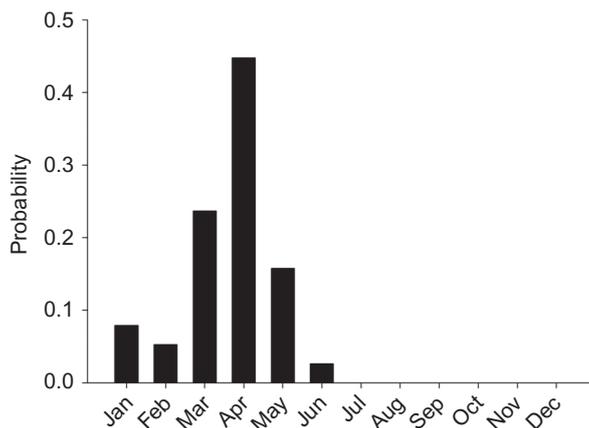*Corresponding author. Email: ramironte@gmail.com

Figure 1.   Monthly distribution of the onset of seasonal precipitation in a Mediterranean ecosystem, central Chile. Data were obtained from a 38-year time series (1961–1998), Dirección Metorológica de Chile.

germination significantly as well; however, they are ineffective dispersers as they deposit seeds mostly in unsafe sites (open habitats) unsuitable for germination and recruitment (Bustamante and Simonetti 1992). Post-dispersal seed predators, such as native rodents (e.g. *Abrothrix longipilis* Waterhouse, *A. olivaceus* Waterhouse, *Oligoryzomys longicaudatus* Bennett, *Phyllotis darwini* Waterhouse), can significantly reduce seedling recruitment (Bustamante and Simonetti 2000; Celis-Diez et al. 2004).

The objective of this study was to examine the extent to which the onset of the rainy season modulates the effects of biotic dispersal and seed predation on demographic processes that occur during the first two stages of the life cycle (seeds, seedlings) of *Cryptocarya alba*. We predicted the fate of seeds under two contrasting scenarios: if seeds were dispersed soon after the start of the rainy season, they would be deposited in moist soils with appropriate conditions for rapid germination; therefore high survival and seedling recruitment would be expected. Alternatively, if seeds were dispersed early before the rainy season began, seeds would remain on the ground for a long time and seedling recruitment would decrease significantly due to increased seed death by desiccation (Tsegaye et al. 2011).

Materials and methods

Experiments were conducted at La Campana National Park (32° 57 S; 71° 08′ W), a protected area declared a Biosphere Reserve by UNESCO (Meynard 2002). Sclerophyllous forest is the most representative vegetation of this protected area, characterised mainly by the tree species *Cryptocarya alba*, *Peumus boldus* Mol. (Monimiaceae), *Quillaja saponaria* Mol. (Rosaceae) and *Lithraea caustica* (Mol.) H. et A. (Anacardiaceae) (Villaseñor and Serey 1981; Luebert et al. 2002).

During March 1992, we selected bird-dispersed seeds, collected under perch trees (bird-dispersed seeds are easily recognised because they are regurgitated with the pericarp completely removed; see Bustamante et al. 1993) and gravity-dispersed seeds (mature fruits with the pericarp intact, normally dispersed by gravity, found under or near parent plants; Célis-Diez and Bustamante 2005).

To 'manipulate' the onset of precipitation, we took advantage of the fact that during the 1992 rainy season, average annual precipitation was almost double the norm and was continuously distributed throughout the year (ca. 600 mm; annual average 330 mm) and it began around 15 March, concomitantly with the beginning of *C. alba* seed dispersal. As soon as the first precipitation occurred, we placed seeds on the forest ground, in points located each 10–15 m along transects, ($n = 10$, each 100 m long). We prevented edge effects by rejecting points that fell within a band 10 m wide from the forest edge. Treatments consisted of bird-dispersed vs. gravity-dispersed seeds, which were placed along the line transects at random.

In the meantime, we maintained seeds (bird dispersed and gravity dispersed) in the field for 2 months; the seeds were hung in bags inside a shed (30 cm above the ground), exposed to the air but protected from contact with rainwater. We decided not keep them on the ground during this time because soils were extremely wet. At the end of May, we placed these seeds on the forest floor, across the same transects we established in March. In this way, we could simulate two contrasting abiotic scenarios: (i) early onset of precipitation (March) and (ii) late onset of precipitation (May). We are aware that the latter treatment (i.e. late onset of precipitation) did not mimic the real conditions exactly, because we could not avoid exposing the seeds to the considerable increase in atmospheric humidity that normally occurs during the rainy season. This experimental limitation is discussed in more detail.

Thus, the experimental design consisted of a 2×2 factorial design (bird-dispersed vs. gravity-dispersed seeds; early vs. late onset of precipitation). For each experimental treatment we placed 10 replicates; each replicate comprised 20 seeds placed in circular plastic cages (50 cm diameter) covered completely with wire mesh to prevent access by seed/fruit consumers. Thus, the total number of replicates in the four treatments was 40, using a total of 800 seeds. We focused exclusively on avian dispersers; in spite of

foxes being conspicuous seed dispersers (Bustamante and Simonetti 1992), the quantitative and qualitative impact of birds is significantly more important (Bustamante et al. 1996; Bustamante 2009).

In January 1993, we evaluated seedling recruitment probability, P(R), defined as the number of recruited seedlings divided by the initial number of seeds available on the ground. We decided to use P(R) as it integrates demographic processes that seeds and seedlings undergo during the first stages of the life cycle, thus represents a net effect. We did not continue the experiment past March 1993, because 100% of seedlings had by then desiccated and died. This result is consistent with other studies which document extremely low seedling survival and episodic recruitment for most tree species in Central Chile (Fuentes et al. 1984). A factorial ANOVA was performed to assess the effect of the treatments on P(R). Data were arcsine transformed in order to satisfy ANOVA assumptions.

Results

Seedling recruitment probability was significantly increased by avian dispersal (ANOVA, $F_{1,34} = 5.1$; $P = 0.03$; bird dispersed seeds: 0.34 ± 0.08; gravity-dispersed seeds: 0.20 ± 0.10; average $\pm$ 2 se); we did not detect significant differences in the onset of precipitation treatment (ANOVA, $F_{1,34} = 1.17$; $P = 0.29$; early onset 0.30 ± 0.11; late onset 0.23 ± 0.1; average $\pm$ 2 se). Interestingly, a significant statistical interaction was detected between the onset of precipitation and avian dispersal (ANOVA, $F_{1,34} = 6.55$; $P = 0.02$; Figure 2) i.e. under the early onset of precipitation treatment, birds significantly increased seedling recruitment (Tukey, $P = 0.01$), while under the late onset of precipitation treatment, this parameter converged between precipitation treatments (Tukey, $P = 0.99$) (Figure 2).

Discussion

In this study, we found that the onset of precipitation acts to modulate interactions between avian dispersers and *C. alba*

in a subtle way: it significantly increased seedling recruitment only for the fraction of seeds dispersed under conditions of an early onset rainy season (March). In this case, *C. alba* seed desiccation (Chacón and Bustamante 2001) presumably did not occur, because rapid germination and seedling recruitment occurred. For seeds dispersed under conditions of a late onset of the rainy season (May), birds were neutral for seedling recruitment, because the dehydration suffered by bird-dispersed seeds (without pericarp) was compensated by the gravity-dispersed seeds (with pericarp) which were kept protected from water loss (Chacón and Bustamante 2001), causing a zero net effect. We cannot rule out the possibility that the absence of an effect in the late onset of precipitation treatment was caused by ameliorated air humidly conditions (80–90%) from March to May, in contrast to the natural conditions at the end of the dry season (mean air humidly ca. 45%) (Peñaloza et al 2001). Temperature might be an important driver for changes in seedling recruitment. However, this factor may be unimportant in our case as the soil temperature remains fairly constant in the interior of forests from March to May (Del Pozo et al. 1989).

Our results highlight the importance of considering seed recalcitrance in disentangling the complexity of the seedling recruitment process of *C. alba* in central Chile. Seed recalcitrance presumably evolved independently across diverse plant lineages in non-seasonal, tropical ecosystems or flooded wet environments (Pammenter and Berjak 2000; Tweddle et al. 2003). In the case of *C. alba*, seed recalcitrance could be a conserved trait (a legacy) that evolved from ancestors living in a tertiary tropical forest distributed in central Chile, before the Andean uplift (Villagrán and Hinojosa 1996). In such ancient environments, seed recalcitrance could be an adaptation for rapid germination and seedling recruitment to maximise seedling development under constant favourable environmental conditions (Alpert and Oliver 2002; Kermode and Finch-Savage 2002).

To examine why plants with recalcitrant seeds could persist in variable environments such as Mediterranean ecosystems implies examining ecological aspects besides
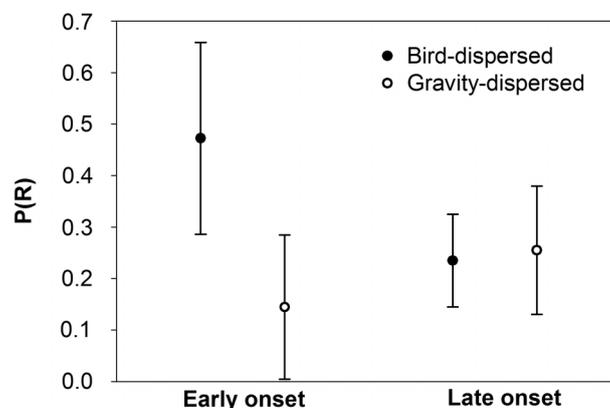

Figure 2.   Recruitment probability of *Cryptocarya alba* seedlings during early vs. late onset of seasonal precipitation, bird-dispersed vs. gravity-dispersed seeds, Parque Nacional La Campana, Region V, Chile. Values represent the average $\pm$ 1.96 se.

the presumed historical inertia of this trait (Herrera 1992). Specifically, there are other fruit/seed traits, strongly correlated with seed recalcitrance, which are considered adaptive in seasonal environments. Firstly, species with seed recalcitrance have fleshy fruits (Daws et al. 2005). Fleshy fruits attract birds and mammals, and favour plant regeneration via a directed dispersal mechanism to safe sites (sensu Harper 1977) with suitable abiotic conditions for regeneration. In Mediterranean ecosystems, safe sites may be located under nurse plants; these plants also act as perches for birds which regurgitate seeds, concentrating them beneath the nurse plants, thus additionally providing shelter to seeds and seedlings during the dry season (Armesto and Pickett 1985; Debusshe and Isenmann 1994; Aerts et al. 2006; Valiente-Banuet et al. 2006).

Secondly, dispersed recalcitrant seeds may overcome the abiotic stress simply by remaining protected against desiccation inside disperser scats even at unsafe sites (the case of foxes which disperse seeds in open habitats), thus buffering seeds against dehydration (Bustamante 2009). Thirdly, seed recalcitrance is positively correlated with seed size (Pritchard et al. 2004). Large size can reduce the rate of seed drying by conferring rapid germination and vigorous seedling growth during a favourable season (Berjak et al. 1984; Daws et al. 2005), thus enabling the seedlings to survive and persist in a seedling bank for a longer time (Farnsworth 2000). In addition, we cannot reject the possibility that recalcitrant seeds may persist in variable environments just by allometry: large seeds (as most recalcitrants) desiccate slowly, because as a seed increases in size its surface area (over which moisture is lost) increases as a squared function, while its volume (which holds the moisture) increases as a cubed function (Chacón and Bustamante 2001).

In seasonal environments, seed dispersal coincides with periods of precipitation in plants that produce recalcitrant seeds (e.g. Pritchard et al. 2004; Daws et al. 2005). However, this is not a general rule (Hill and Edward 2010). One way to understand to what extent this phenological uncoupling determines plant regeneration is to examine the time span of seed dispersal. Given that seasonal precipitation may vary in terms of onset, abundance or both, one reproductive strategy for these plants could be to spread seed dispersal throughout the year, in order to assure that a fraction of seed production coincides with the amount of precipitation required for regeneration. In the case of *C. alba,* seed dispersal lasts for ca. 8 months (from March to October). This is an uncommon phenological pattern among the native trees of central Chile, shared only by the other coexisting Lauraceae species, *Persea lingue* and *Beilschmiedia miersii* (Henriquez and Simonetti 2001; Vergara et al. 2010).

The effects of inter-annual climatic variability on the sign and magnitude of biotic interactions has been extensively examined in diverse studies (e.g. Valladares et al. 2004; Resco de Dios et al. 2007; Valladares and Gianolli 2007; Gutiérrez et al. 2010). However, subtle variations

such as the onset of seasonal precipitation have rarely been explored, even though it has been considered an important source of environmental variation for plants (McLaren and McDonald 2003). Understanding the mechanisms underlying these interactions will be a fruitful avenue for future research in seasonal environments.

Notes on contributors

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