

Bird frugivory and the fate of seeds of *Cryptocarya alba* (Lauraceae) in the Chilean matorral

Frugivoría por aves y el destino de las semillas de
Cryptocarya alba (Lauraceae) en el matorral chileno

RAMIRO O. BUSTAMANTE¹, ALAN WALKOWIAK², CAROLINA A. HENRIQUEZ¹
and ITALO SEREY¹

¹Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile,
Casilla 653, Santiago, Chile. E-mail: rbustamat@abello.dic.uchile.cl
²Empresa Eléctrica Pangué S.A., Avda. Suecia 488, Providencia, Santiago

ABSTRACT

We evaluated the effect of frugivorous birds on the germination and establishment of *Cryptocarya alba*, a common tree of the Chilean matorral. Although the removal of the pericarp of fruits increased germination rate, bird-dispersed seeds loose germination capacity at a higher rate than those dispersed by gravity alone. Seeds dispersed toward dense habitats survived, germinated and established at a higher proportion than those dispersed in sparse habitats. However, the survival of established seedlings was null at the end of summer, in both types of habitat. We conclude that seedling germination and establishment is more likely when dispersal is coupled with the rain season and it occurs in dense habitats. We discuss the implications of these effects of frugivores in the context of the regeneration processes of this species in the Chilean matorral.

Key words: dispersal, germination, regeneration, seedling establishment, seed predation.

RESUMEN

Nosotros evaluamos el efecto de las aves frugívoras en la germinación y establecimiento de *Cryptocarya alba*, un árbol común del matorral chileno. Aunque la remoción del pericarpio de los frutos incrementó las tasas de germinación, las semillas dispersadas por aves perdieron la capacidad de germinación a una tasa mayor que las dispersadas por gravedad solamente. Las semillas dispersadas a hábitats densos sobrevivieron, germinaron y se establecieron en una mayor proporción que las dispersadas a hábitats raros. Sin embargo, la sobrevivencia de plántulas establecidas fue nula al finalizar el verano en ambos tipos de hábitats. Nosotros concluimos que la germinación de semillas y establecimiento de plántulas es más posible cuando la dispersión se encuentra asociada a la época de lluvias y ocurre en parches densos de vegetación del matorral chileno. Finalmente, discutimos las implicancias de los efectos de las aves frugívoras en el contexto de la regeneración de esta especie en el matorral chileno.

Palabras clave: depredación de semillas, dispersión, establecimiento de plántulas, germinación, regeneración.

INTRODUCTION

Seed dispersal is a crucial process throughout the life cycle of plants (Solbrig 1980). It allows an increase of germination and establishment away parent plants (Howe & Smallwood 1982), and subsequently the colonization of plants to unoccupied habitats (Harper 1977, Jordano 1992). Among the diverse set of dispersal agents, the effects of frugivores (birds, mammals) on plant population structure and demography have received a particular attention (Herrera & Jordano 1981, Pratt & Stiles 1983, Johnson et al.

1985, Loiselle 1990, Jordano 1992, Stiles 1992, Herrera et al. 1994). Recent evidences show that the study of the ecological factors which mediate plant-frugivorous bird interaction poses a more complex picture about the nature of this biotic interaction. For example, clumps of seeds deposited in faeces and regurgitates may attract predators which reduces seed survival (Janzen 1982). The passage of seeds through the animal guts may kill insect predators, compensating seed survival (Janzen et al 1985, Hauser 1994, Miller 1994). Additionally, seeds may be deposited in microsites where germination

and establishment are unlikely, reducing recruitment (Bustamante et al. 1992). Clearly, frugivory is a complex interaction whose effects on seed and seedling demography will be dependent of the ecological context where it takes place (Thompson 1982, Greenwood 1985). Here, we show an example where the outcome of frugivores on plant recruitment is conditioned by the biotic and abiotic context where it takes place. The study system is the tree *Cryptocarya alba* (Mol.) Looser (Lauraceae) and the frugivorous birds which disperse its seeds in the Chilean matorral. Specifically, we evaluated how fruit consumption by birds affect seed germination. Moreover, we monitored the fate of bird-dispersed seeds in open versus closed habitats. Finally, we discussed to what extent the effect of birds on germination is reflected in seed and seedling demography.

METHODS

Cryptocarya alba is a sclerophyllous tree distributed through the south-facing slopes and humid ravines of the Chilean matorral (Armesto & Martínez 1978). Its fruits are red, one-seeded drupes (1-2 cm long) with a thin pericarp that disperse from March to July. Dispersal agents are foxes (*Pseudalopex* sp.; Jaksic et al. 1980, Armesto et al. 1987) and birds (*Columba araucana* Lesson, *Mimus thenca* (Molina), *Pyrope pyrope* (Kittlitz), *Turdus falklandii* Quoy et Gaynard; Bustamante 1992). Many fruits fall passively beneath parent plants as well (Bustamante 1992). Bird-dispersed seeds are easily identified in the field because they are regurgitated in clumps, intact and without pericarp under perch trees (Bustamante et al. 1993). *Cryptocarya alba* is considered a late-successional species (Armesto & Pickett 1985), that germinates and establishes under the canopy of the sclerophyllous forests. The seeds are considered recalcitrant because they lose viability and die up during the fifth or sixth months after dispersal (Bustamante et al. 1992).

Study area

Experiments were performed between April 1992 to March 1993 at La Campana Natio-

nal Park (32° 57' S, 71° 08' W), located in the mediterranean ecosystem of central Chile. The vegetation in this zone is sclerophyllous forest (Villaseñor & Serey 1980/81) where it is possible to recognize two contrasting habitats: sparse habitats (42% cover; Maldonado 1990), dominated by *Baccharis linearis* (R. et P.) and *Muehlenbeckia hastulata* (J.E.Sm.) Johnst. and dense habitats (95% of cover; Maldonado 1990) with *Cryptocarya alba* and *Peumus boldus* as dominant trees.

Germination tests

During April 1992, we collected propagules previously dispersed by birds (without pericarp) and by gravity (ripe fruits and with the intact pericarp). We took special care that all the selected propagules were not damaged by physical and/or biotic causes.

Propagules were stored in mesh bags and maintained in the laboratory under controlled temperature (20° C) and relative air humidity (40-50%). We performed six experiments, once a month, between April and September, by taking random samples of seeds from the mesh bags. We compared germination between bird-dispersed versus gravity-fallen propagules by disposing them in Petri dishes with filter paper, in dark conditions, 15° C and water *ad libitum*. We used 10 Petri dishes per treatment and 10 seeds per Petri dish. We recorded the number of germination each 2 days, from the first day after initiated the experiment. Observations were performed for 65 days. After this time, no evidence of further germination was detected.

Fate of seeds and seedlings

In order to evaluate the fate of seeds and seedlings, we focused only on bird-dispersed seeds because they are distributed in both closed and sparse habitats; fallen-gravity propagules were never found in sparse habitats. During June 1992, we distributed 600 seeds dispersed by birds in 30 groups, 20 seeds per groups, randomly disposed on the ground. This density is appropriate for experiments as birds generate dense patches of seeds under perch trees (R.O. Bustamante, obs. pers.). This procedure was repeated both

in sparse and dense habitats. The total area we used for the experiments was about 0.5 ha. per habitat-type. In January 1993, we counted the number of seeds removed or destroyed by fungus, the number of germinated seeds, the number of seeds that germinated and died, and the number of seeds that were established as seedlings. We assumed that the responsible agents of seed removal were birds and rodents (see also Vásquez et al. 1995 for a detailed study of seed predation by birds and rodents). By the end of the summer (March 1993), we counted the number of surviving seedlings. This information was analyzed by using fate diagrams (sensu Price & Jenkins 1986). This method enabled the estimation of: (i) $P(S_0)$: the probability of a seed to survive predation; (ii) $P(G)$: the probability of a seed to germinate; (iii) $P(S_1)$: the probability of a seed that failed to germinate survives; (iv) $P(R)$: the probability that a seed recruit to seedling stage; and (v) $P(S_2)$: the probability of survival of a seedling at the end of the Summer.

RESULTS

Germination tests

Bird-dispersed seeds germinated at a higher proportion than gravity-dispersed seeds (Wilcoxon, $Z = 3.8$, $P \ll 0.001$; $Z = 3.4$, $P \ll 0.001$; $Z = 2.2$, $P < 0.05$ for April, May and June, respectively). In July 1992, no differences between treatments were detected (Wilcoxon, $Z = 0.9$, $P = 0.16$; Table 1). During August and September 1992, germination was zero in both treatments (Table 1). Overall, bird-dispersed seeds tended to loose germination capacity at a higher rate than gravity-dispersed seeds (slope comparison test, $t = -5.34$, d.f. = 76, $P < 0.005$, Table 1).

Fate of seeds and seedlings

Seed predation was significantly lower in the dense habitat compared to sparse habitats (proportion tests, $Z = -8.6$, $P < 0.0004$; Figure 1). Fungi were the most conspicuous seed consumers in dense habitats (82% of consumption); birds and rodents were most

important in sparse habitats (69% of consumption; Figure 1). Seeds germinated in higher proportion in dense habitats than in sparse habitats (proportion test, $Z = 3.6$, $P = 0.0006$; Figure 1). The proportion of seeds which established as seedling, $P(R)$, was higher in sparse habitats (proportion test $Z = 1.78$, $P = 0.03$; Fig. 1). The proportion of seeds that germinated and established as seedling, $P(G \text{ and } R)$, was similar in both habitat-types (proportion test, $Z = -0.85$, $P = 0.27$; Fig. 1). A global comparison, that is $P(\text{So and } G \text{ and } R)$ detected a significant difference in the dense habitats in relation to sparse habitat (proportion test, $Z = -6.80$, $P < 0.0001$, Figure 1). Finally, the 100% of seedlings died by dessication and herbivory at the end of the summer in both habitat-types (Figure 1).

DISCUSSION

Birds and seed germination

Birds affected the germination of *Cryptocarya alba* seeds in a subtle way. The removal of pericarp increases germination sig-

TABLE 1

Germination percentage (mean \pm 1 se) for gravity-dispersed and bird-dispersed seeds in *Cryptocarya alba*. Experiments were performed from April to September 1992 under lab conditions. Ten seeds per replicate, number of replicates $n = 10$. The asterisc (*) indicates the slope of the regression curve estimated along the time for each treatment

Porcentaje de germinación (promedio \pm 1 ee) para semillas dispersadas por aves y por gravedad en *Cryptocarya alba*. Los experimentos fueron realizados desde abril a septiembre 1992 bajo condiciones de laboratorio. Diez semillas por réplica, número de réplicas $n = 10$. El asterisco indica la pendiente de la curva de regresión a lo largo del tiempo para cada tratamiento

Months	Gravity-dispersed seeds	Bird-dispersed seeds
April	56.0 \pm 4.7	100.0 \pm 0.0
May	55.5 \pm 5.2	81.0 \pm 2.3
June	8.0 \pm 2.0	20.0 \pm 2.6
July	7.0 \pm 2.6	3.0 \pm 1.5
August	0.0	0.0
September	0.0	0.0
* Slope	-1.9 \pm 0.2	-3.5 \pm 0.1

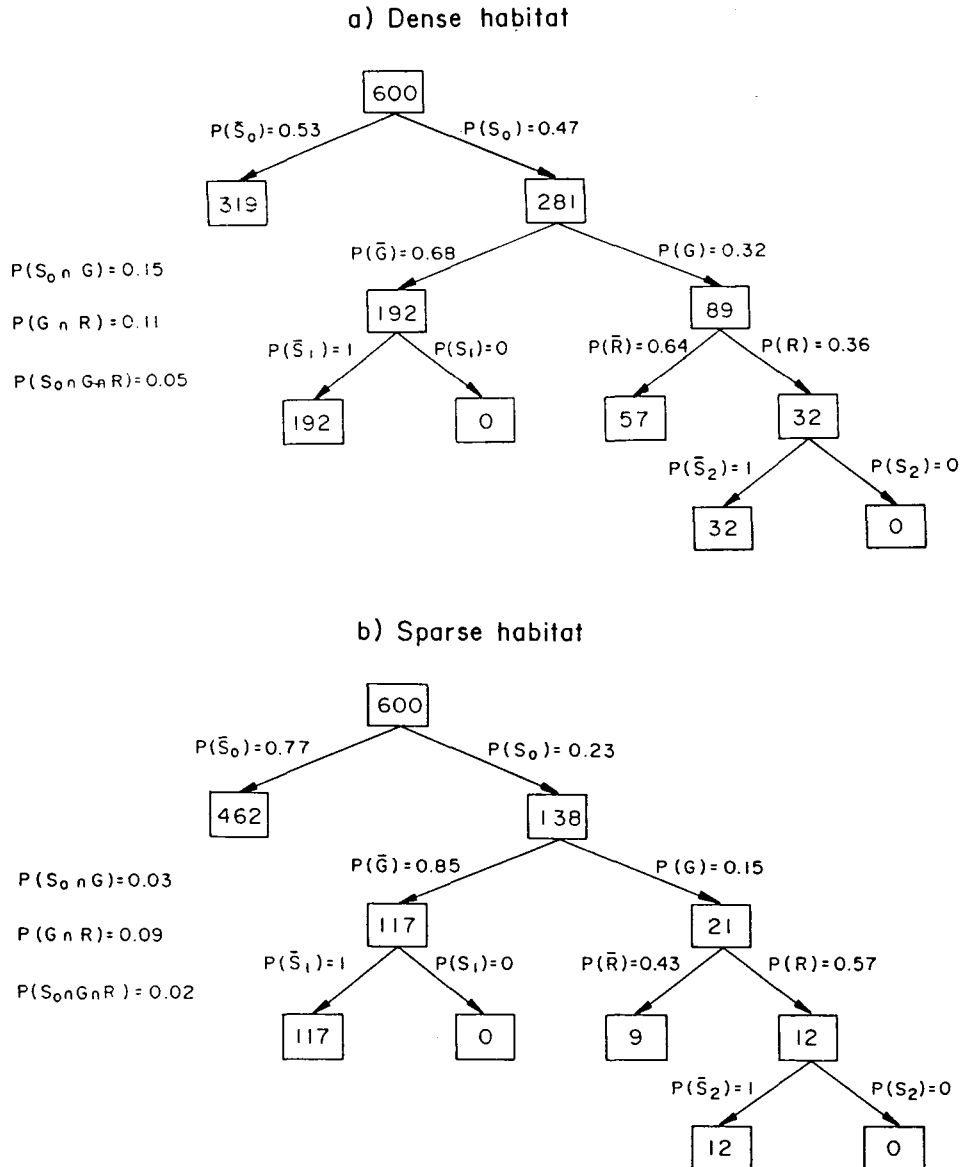


Fig. 1: Fate diagrams from bird-dispersed seeds of *Cryptocarya alba* in a) dense habitats and b) sparse habitats, Chilean matorral. The initial number of seeds disposed in the field for both treatments was 600. $P(S_0)$ = the probability of a seed to survive predation, $P(G)$ = the probability of a seed to germinate, $P(R)$ = the probability that a seed recruit to seedling stage, $P(S_1)$ = probability that a seed that failed to germinate survives, $P(S_2)$ = the probability a seedling to survive at the end of the Summer.

Diagramas de destino para semillas de *Cryptocarya alba* en a) hábitat denso y b) hábitat ralo, matorral chileno. El número inicial de semillas dispuestas en el campo para ambos tratamientos fue de 600. $P(S_0)$ = probabilidad de una semillas de sobrevivir a la depredación, $P(G)$ = probabilidad de una semilla de germinar, $P(R)$ = probabilidad de una semilla de reclutar al estado de plántula, $P(S_1)$ = probabilidad que una semilla que no germinó, sobreviva, $P(S_2)$ = probabilidad de una plántula de sobrevivir hasta fines del verano.

nificantly during the first months but later, this effect decreases to become zero (Figure 1). This results may be explained presumably by the protection of the pericarp against

desiccation. It is possible that exposed seeds lose water in such a way that they in turn lose germination capacity faster than those seeds with the intact pericarp. That is, if

bird-dispersed seeds are transported when water conditions for germination are critical, the potential positive effect on germination, may become irrelevant later. In the Chilean matorral, the duration of the rainy season is highly variable among years (Di Castri & Hajek 1976, Espinoza et al. 1988). Moreover, the duration of the dispersal phase of *Cryptocarya alba* is variable among years as well (R.O. Bustamante pers. obs.). This may result, in a temporal disacoupling between dispersal of seeds and rains: the fraction of seeds dispersed by birds before precipitations will die by desiccation, irrespective of an initial potential beneficial effect of birds on seed germination. They will affect seed germination positively only to the fraction of seeds that are dispersed after the occurrence of precipitations. This hypothesis is amenable to be tested by field experiments.

Fate of seeds and seedlings

Birds disperse seeds both in the dense and in the sparse habitats. Once seeds arrive to sparse habitats, they have a lower survival and germination probability (Figure 1) due to factors such as seeds predators and water stress. Interestingly, P(R), the probability that a seed recruit to seedling stage, was higher in sparse habitats (Fig. 1). It is possible that the conditions of higher luminosity, typical of sparse habitats in the Chilean matorral (Del Pozo et al. 1989) increased seedling recruitment initially, in a similar way as documented for some shade-tolerant tree species growing in large gaps in forests (Becker & Wong 1985, Murray 1988). P(G and R) were similar in both dense and sparse habitat (Figure 1), reflecting a compensatory effect in demographic processes that is, higher P(G) but lower P(R) in dense habitats in contrast to a lower P(G) but a higher P(R) in sparse habitat. Overall, the lower P(S and G and R) observed in the sparse habitat (Fig. 1), suggest that seed predation in sparse habitat is so intense that is able to reduce seedling recruitment even in presence of the compensatory effect detected in this study.

Seedling survival in sparse habitats is constrained by severe mortality attributable to desiccation and herbivory, thus precluding

potential for recolonization to such habitats (Fuentes et al. 1983, Fuentes et al. 1984, Fuentes et al. 1986). The death of the 100% of *Cryptocarya alba* seedlings in sparse habitats (Figure 1b), corroborates this assertion. However, the death of the 100% of seedlings in dense habitats (Figure 1a), shows that the regeneration process inside the remnants forests is severely precluded as well. Regeneration studies in the matorral suggest that this process is an episodic event that occurs during extremely rainy years (Fuentes et al. 1986). As during 1992 precipitations were abundant, the lack of regeneration both in dense and sparse habitat suggests additional constraints for regeneration of *Cryptocarya alba* and other shade-tolerant species in the Chilean matorral. The anthropogenic activities have changed the matorral from a continuous cover of native vegetation to a discontinuous and isolated fragments of native vegetation, surrounded by a seminatural matrix (Fuentes & Hajek 1979, Fuentes 1994). We suggest a strong edge effect (*sensu* Murcia 1995), which is expressed in (i) modifications of the abiotic conditions inside the remnant fragments and (ii) the intrusion of herbivores (rabbits, cows and horses). This changes induced by the fragmentation of the matorral should reduce the potential for regeneration of *Cryptocarya alba* and other similar species even during rainy years. Further research is needed to evaluate the magnitude of the edge effect during wet and dry years in the matorral and to elucidate its importance for the regeneration of this species.

An alternative mode of regeneration seems to be the vegetative reproduction from lignotubers (Montenegro et al. 1983). In fact, vegetative reproduction has been considered an important source of plant regeneration once human disturbances remove the cover of the matorral (Araya & Avila 1981, Montenegro et al. 1983). This reproductive mode may be efficient for rapid regrowth (Montenegro et al. 1983). However, it may be deleterious for the plant populations in the long term, because genetic variability may be severely eroded.

In summary, the effect of frugivores birds on *Cryptocarya alba* seeds will depend on when and where they disperse the seeds.

Germination and establishment will be more feasible when dispersal is coupled with the beginning of rains and birds disperse seeds in dense habitats. Moreover, the effect of frugivorous birds on the seedling dynamics of this species becomes unimportant as other biotic (predators) and abiotic factors (water stress) preclude seed and seedling survival. Additional research is needed in order to elucidate at what extent the fragmentation of the matorral precludes the potential for regeneration of shade tolerant species such as *Cryptocarya alba*.

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