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The effect of seed size on germination and seedling growth of *Cryptocarya alba* (Lauraceae) in Chile

El efecto del tamaño de la semilla sobre la germinación y crecimiento de plántulas de *Cryptocarya alba* (Lauraceae) en Chile

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ABSTRACT

Seed size is a life history trait that may affect the fitness of parent plants and the population regeneration process. It has been observed that large seeds increase germination, seedling growth, and survival. As a consequence, large seeds can produce more vigorous and competitively superior seedlings. In this study, we evaluated the effect of seed size on germination and seedling growth in *Cryptocarya alba* (Mol.) Looser (Lauraceae), a common tree of the central Chilean matorral. We collected seeds at "Quebrada de la Plata" (Metropolitan Region), and we sowed them under laboratory conditions. We defined three seed size classes based on seed length: small, medium and large seeds. Large seeds germinated in greater numbers than small seeds. Seedlings coming from large seeds had larger shoots and a greater probability of producing leaves. Further, seedling size (measured as dry biomass in roots, shoots and leaves) was strongly affected by seed size, although root allocation was proportionally higher in seedlings coming from small seeds, while leaf allocation was higher in seedlings coming from large seeds.

Key words: seed size, seed germination, seedling growth, seedling size, *Cryptocarya alba*.

RESUMEN

El tamaño de la semilla es una característica de historia de vida que puede afectar la adecuación biológica de las plantas madres y los procesos de regeneración poblacional. Se ha observado que las semillas grandes aumentan la germinación, el crecimiento y la sobrevivencia de las plántulas. Como consecuencia, las semillas grandes pueden producir plántulas más vigorosas y competitivamente superiores. En este estudio se evaluó el efecto del tamaño de la semilla en la germinación y crecimiento de plántulas de *Cryptocarya alba* (Mol.) Looser (Lauraceae). Se recolectaron semillas en la "Quebrada de la Plata" (Región Metropolitana) y posteriormente fueron sembradas bajo condiciones de laboratorio. Se definieron tres clases de tamaño de semillas basadas en la longitud de estas: semillas chicas, medianas y grandes. Las semillas grandes germinaron en mayor proporción que las semillas chicas. Las plántulas derivadas de semillas grandes tuvieron tallos más largos y una mayor probabilidad de producir hojas. Además, el tamaño de las plántulas (medido como biomasa seca de raíces, tallos y hojas) fue fuertemente afectado por el tamaño de la semilla, aunque la asignación de biomasa a la raíz fue proporcionalmente mayor en plántulas derivadas de semillas pequeñas, mientras que la asignación de biomasa a las hojas fue mayor en plántulas derivadas de semillas grandes.

Palabras clave: tamaño de semilla, germinación de semillas, crecimiento de plántulas, tamaño de plántulas, *Cryptocarya alba*.

INTRODUCTION

Seed size is a life history trait that may affect the fitness of parent plants and the population regeneration process (Harper 1977, Fenner 1985, Silvertown 1989). Large seeds have positive effects on germination (Schaal 1980, Weis 1980, Zimmermann & Weis 1982, Dolan 1984, Stanton 1984, Morse & Schmitt 1985, Winn 1988, Tripathi & Khan 1990, Vera 1997), shoot growth rates (Weis 1980,

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Zimmermann & Weis 1982, Bonfil 1998), seedling biomass (Weis 1980, Howe & Richter 1982, Dolan 1984, Stanton 1984, Morse & Schmitt 1895, Hendrix et al. 1991, Bonfil 1998), and seedling survival (Schaal 1980, Morse & Schmitt 1985, Wulff 1986, Tripathi & Khan 1990, Vera 1997). Thus, seedlings originated from large seeds have greater competitive abilities in late-successional habitats (Salisbury 1942), in areas where water stress is an important source of seedling mortality (Baker 1972, Venable & Brown 1988) or in places where the duration of the growth season is short (McWilliams et al. 1968). One possible explanation for such success is that seedlings originated from large seeds develop deeper and larger roots which allow greater survival and growth when resources are scarce (Harper 1977, Stanton 1984). In some cases, seed size is positively correlated with the size of adults and their reproductive output (Stanton 1984, Dolan 1984).

The aim of this study was to evaluate the effect of seed size on germination and seedling growth in *Cryptocarya alba* (Lauraceae), a common shade-tolerant tree of Central Chile. First, we documented the size distribution of seeds deposited in the field. Second, we studied the percentage of germination, seedling growth and seedling biomass as a function of seed size under laboratory conditions. Third, we determined the probability that seedlings will produce three or more leaves as a function of seed size.

METHODS

Cryptocarya alba is a sclerophyllous tree distributed in south-facing slopes of the Chilean matorral. Fruits are red, one-seeded drupes with a thin pericarp, birds being the major dispersal agent. Dispersal occurs from March to July and seedling emergence occurs from September to October (Bustamante 1992). Bird-dispersed seeds are easily identified in the field because they are regurgitated intact and without pericarp under perch trees (Bustamante et al. 1996). The seeds are recalcitrant because they lose viability and die during the fifth or sixth month after dispersal (Bustamante et al. 1996).

We collected bird-dispersed seeds at "Quebrada de la Plata", Metropolitan Region (33° 28' S and 70° 51' W), during May 1996 from the ground and under perch trees. The study area is located in the Mediterranean region of central Chile, characterised by a climate with hot dry summers and cold rainy winters (Armesto & Martínez 1978). For lab experiments, we defined three size classes based on seed length: small (< 12 mm in length), medium (12 - 15.9 mm) and large (> 16 mm). These classes were defined arbitrarily from the seed size distribution observed for bird-dispersed seeds (Fig. 1). Seed length was considered an adequate estimate of seed size because there is a significant and positive correlation between seed length and fresh seed biomass (Spearman Correlation, $R = 0.87$, $p < 0.0001$). Bird-dispersed seeds show a similar size range

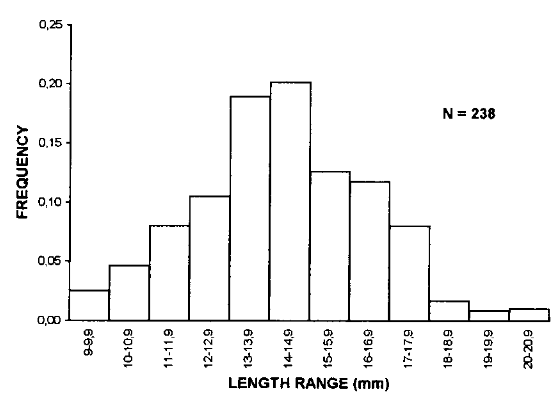

Fig. 1: Seed size distribution of bird-dispersed seeds in *Cryptocarya alba* collected at "Quebrada de la Plata" (Metropolitan Region). N = 238, (the total number of observed seeds).

Distribución de tamaño de semillas dispersadas por aves en *Cryptocarya alba* recolectadas en "Quebrada de la Plata" (Región Metropolitana). N = 238, (número total de semillas observadas).

to that of gravity-fallen seeds (undispersed seeds): bird-dispersed seeds ranged from 8.4-19 mm (14.1 ± 0.29, 2 SE) and undispersed seeds ranged from 9.0 to 20.2 mm (13.8 ± 0.27, 2 SE). We used bird-dispersed seeds because birds are the major dispersal agents and because they remove the pericarp of fruits, and therefore increase germination and establishment significantly (Bustamante et al. 1996).

Thirty seeds of each size class were randomly selected and sown in individual plastic pots filled with topsoil and placed at 20 ± 1° C and water *ad libitum*. The number of germinated seeds was recorded for a period of 2 months every 3 days. We considered that a seed had germinated if the radicle emerged at least 1 mm beyond the seed coat (Tripathi & Khan 1990). During the following two months, shoot length and the number of leaves were recorded every 10 days. Shoot growth rate (SGR) was calculated using the algorithm SGR = shoot length (t_2) - shoot length (t_1) / 10 days, with t_1 and t_2 being two consecutive measuring periods. At the end of the experiment, seedlings were placed in a drying oven at 75°C for 72 hours and weighed to the nearest 0.01 mg. Shoots, leaves and roots of each seedling were weighed separately. With this information, we calculated the proportion of biomass allocated to roots, shoots and leaves for each seed size class in relation to total biomass and we compared them by using an ANOVA with data arcsine transformed, to meet the assumptions of the test.

We determined the following probabilities for each seed size class: (1) P(G): probability that a seed germinates, (2) P(S): probability that a germinated seed develops a shoot, and (3) P(L): probability that a seedling produces three or more leaves at least of 1cm of length. We obtained a final result for each seed size class by calculating $P(L \mid G \cap S)$: the probability that a seedling will produce leaves given that the seed germinated and developed a shoot.

RESULTS

The cumulative germination curves differed significantly among the three seed size classes ($\chi^2 = 17.6$, d.f. = 2, $p < 0.05$, a posteriori Peto-Peto Wilcoxon test, $p < 0.05$ for all pair-wise comparisons) (Fig. 2). The final percentage of germination was different for the three seed size classes (Chi-square test for proportions, $\chi^2 = 19.42$, d.f. = 2, $p < 0.05$) (Zokal & Rohlf 1995); medium and large seeds did not differ (78.6% and 86.7% respectively, a posteriori Tukey test, $p > 0.05$), but these two size classes differed significantly from small seeds (43.3%, a posteriori Tukey test, $p < 0.05$). Germination time was significantly higher for medium sized seeds (Kruskall-Wallis test, H = 16.86, $p < 0.0001$; 32.54 ± 3.95 (X ± 2 SE), 39.77 ± 2.86 and 30.92 ± 2.29 days for small, medium and large seeds respectively), while no differences were detected between large and small seeds (a posteriori test, $p > 0.05$) (Siegel & Castellan 1988).

The effect of seed size on shoot length was significant (Repeated Measures ANOVA, F = 4.2, d.f. = 2, 164; p = 0.02; Fig. 3a), but no differences were detected between medium and large seeds (a posteriori Newman-Keuls test, $p > 0.05$). Shoot growth rate was affected by seed size (Repeated Measures ANOVA, F = 10.5, d.f. = 2, 141; p = 0.0002; Fig. 3b). Seedlings coming from small-sized seeds grew at the slowest rate (a posteriori Newman-Keuls test, $p < 0.05$) .

Root biomass was significantly different for the three seed size classes (Kruskall-Wallis test, H = 32.17, d.f. = 2, $p < 0.0001$) being greater in seedlings coming from large seeds, followed by seedlings coming from medium and small seeds (Fig. 4a). Shoot and leaves biomass differed significantly as well (Kruskall-Wallis test, H = 15.064, d.f. = 2, p = 0.001 and H = 16.197, d.f. = 2, $p < 0.0001$ respectively; Fig. 4a). However, we only observed

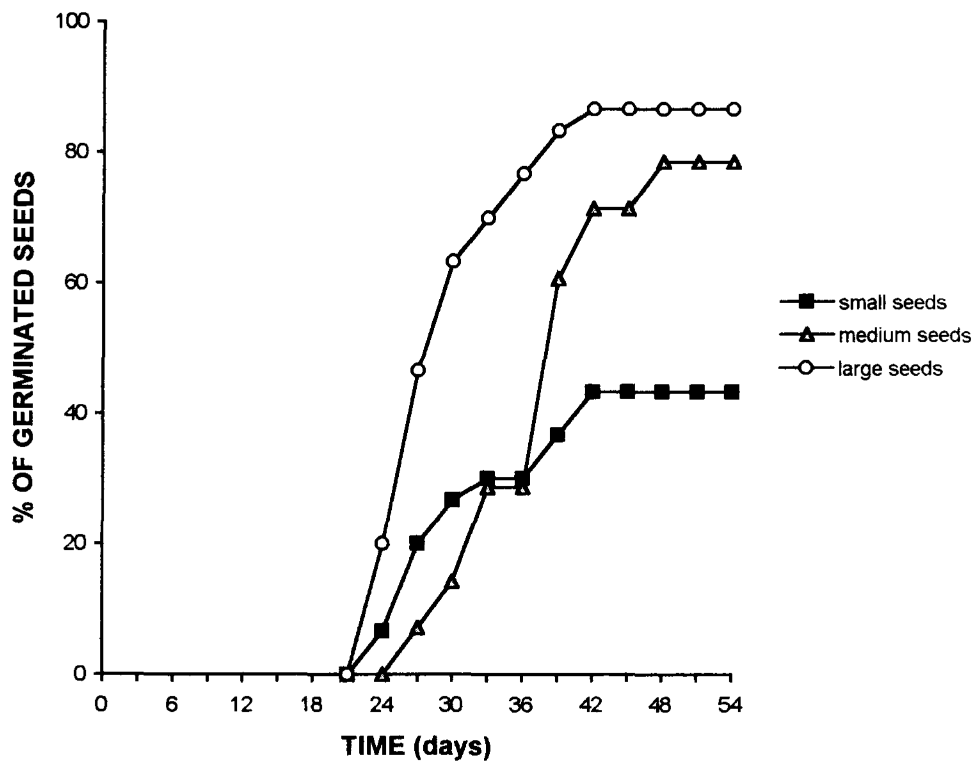

Fig. 2: Cumulative percentage germination curves of three seed size classes of *Cryptocarya alba* . The initial number of seeds placed for each seed size class was 30.

Curvas del porcentaje de germinación acumulado de las tres clases de tamaño de semillas de *Cryptocarya alba*. El número inicial de semillas dispuestas por cada clase de tamaño fue de 30.

significant differences between seedlings coming from small and large seeds in the case of shoots (a posteriori test, $p < 0.05$) and between seedlings coming from small and medium seeds, and seedlings from small and large seeds in the case of leaves (a posteriori test, $p < 0.05$) (Fig. 4a).

The proportion of biomass allocated to roots was significantly greater in seedlings coming from small seeds relative to that produced from medium and large ones (ANOVA, F = 3.69, d.f. = 2,45; p = 0.033; Fig. 4b). No differences were observed in the allocation of biomass to shoots by the three seed size classes (F = 0.55, d.f. = 2,45; p = 0.58; Fig. 4b). Finally, seedlings coming from large and medium sized seeds allocated significantly more biomass to leaves, than seedlings coming from small seeds (F = 6.893, d.f. = 2,45; p = 0.002; Fig. 4b).

$P(L \mid G \cap S)$ was significantly different for small, medium, and large seeds, respectively (Chi-square test for proportions, $\chi^2 = 102.8$, $p < 0.05$) (Table 1).

DISCUSSION

This study reveals that seed size is a life history trait relevant for germination and growth of seedlings in *Cryptocarya alba.* Large seeds germinated in greater numbers compared to the smaller ones. Moreover, seedlings coming from large seeds grew faster and achieved a greater biomass in terms of roots, shoots and leaves. Our results are in agreement with the general assertion that the amount of reserves contained in the cotyledons (a correlate of seed size) is positively related with root length (Harper 1977). This point is

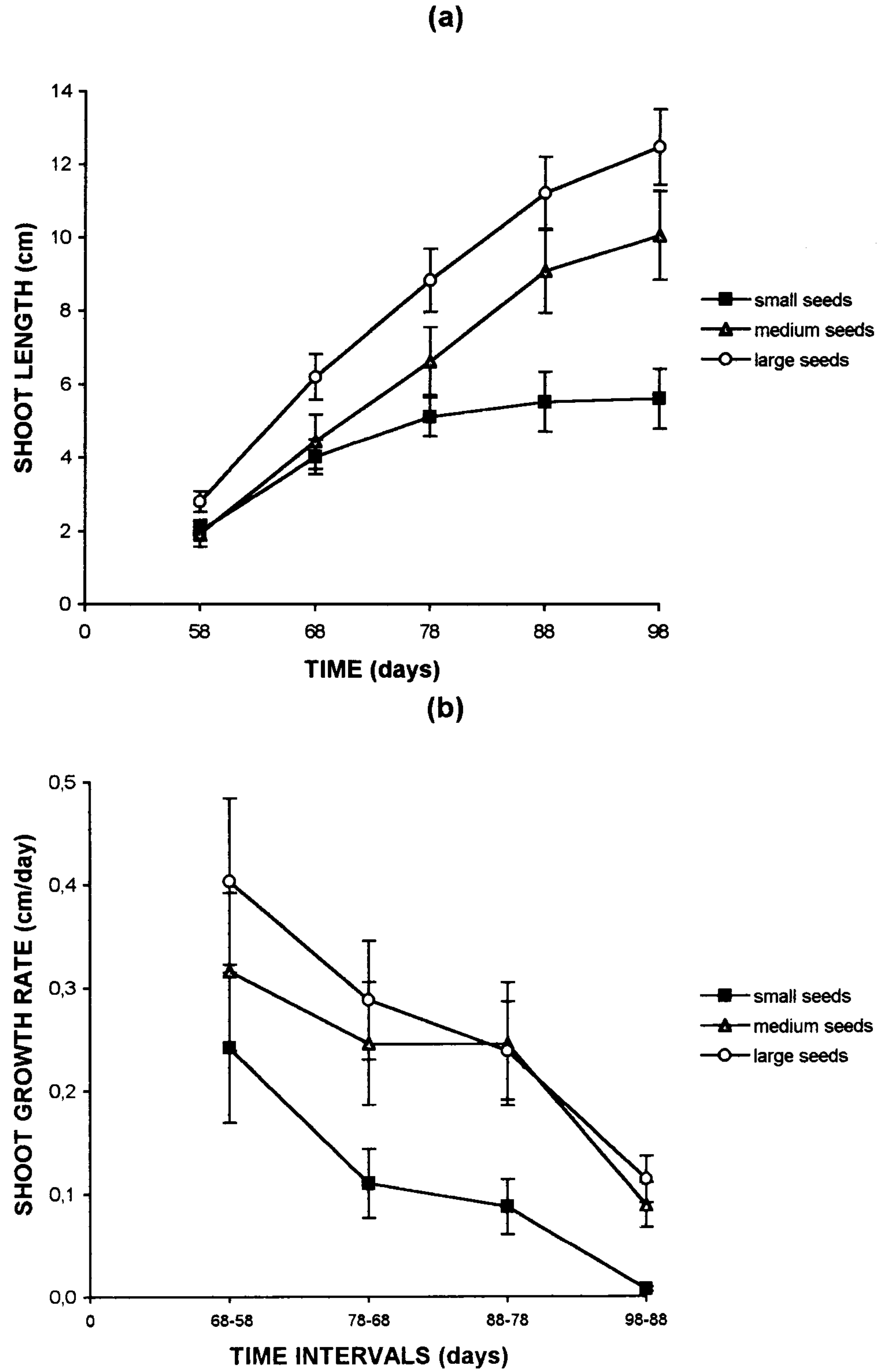

Fig. 3: Shoot length (mean ± 2 SE) (a), and shoot growth rate (mean ± 2 SE) (b), in seedlings coming from small, medium and large seeds in *Cryptocarya alba*.

Longitud de los vástagos (media ± 2 EE) (a), y tasa de crecimiento de los vástagos (media ± 2 EE) (b), en plántulas provenientes de semillas chicas, medianas y grandes en *Cryptocarya alba*.

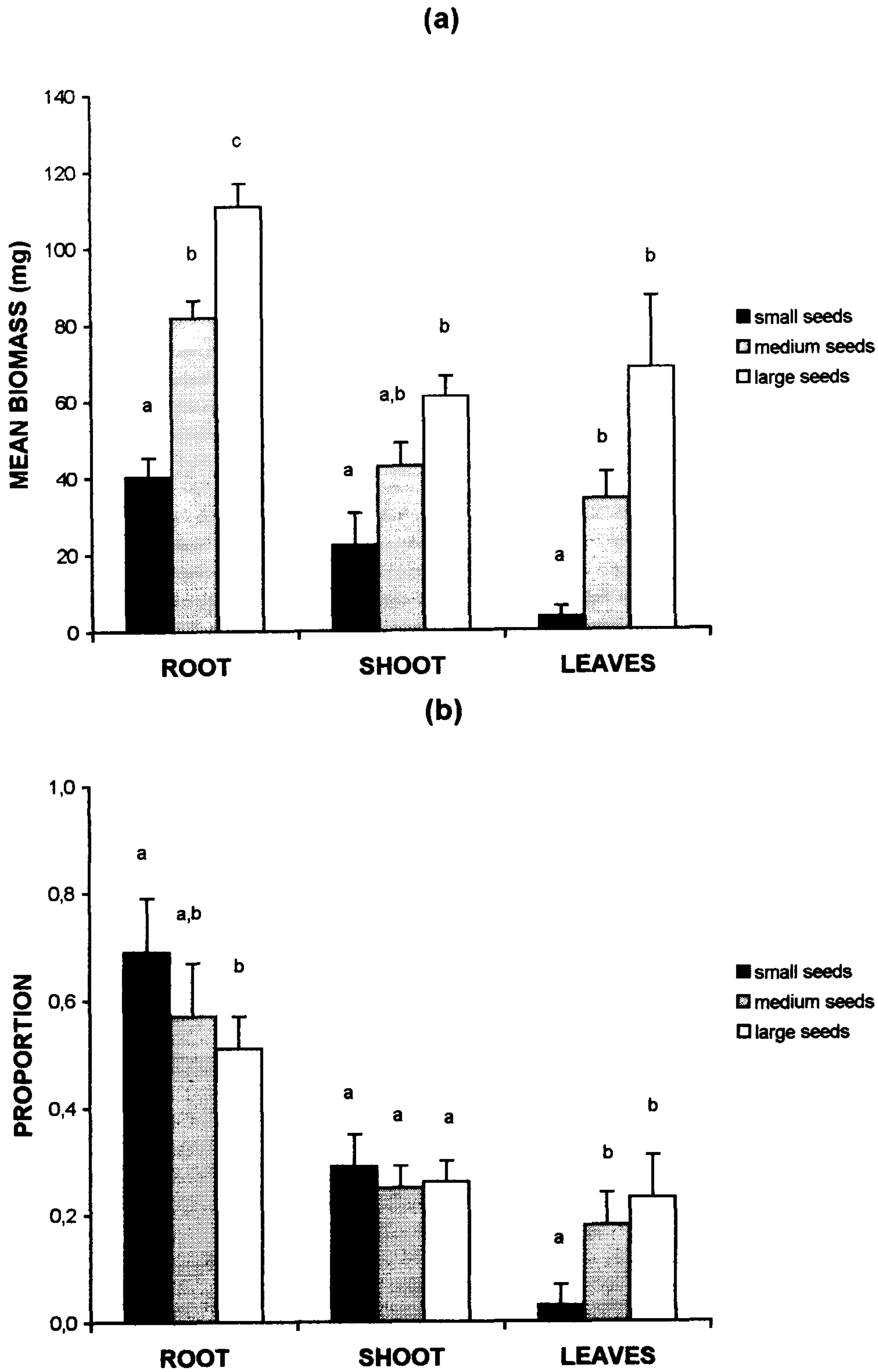

Fig. 4: Root, shoot and leaf biomass (mean ± 2 SE) (a), and biomass allocated to roots, shoots and leaves (mean ± 2 SE) (b), in seedlings coming from small, medium and large seeds in *Cryptocarya alba*. Means with different letters differ significantly.

Biomasa de la raíz, tallo y hojas (media ± 2 EE) (a), y biomasa asignada a raíces, tallos y hojas (media ± 2 EE) (b), en plántulas provenientes de semillas chicas, medianas y grandes en *Cryptocarya alba*. Los promedios con letras diferentes difieren significativamente.

TABLE 1

Final seedling outcome estimated through P(G), P(S), and P(L) in *Cryptocarya alba*. P(G): probability that a seed germinates; P(S): probability that a germinated seed develops a shoot, and P(L): probability that a seedling produces 3 or more leaves at least 1 cm in length each.

Desempeño final de las plántulas estimado a través de P(G), P(S), y P(L) en *Cryptocarya alba*. P(G): probabilidad que una semilla germine; P(S): probabilidad que una semilla germinada desarrolle un vástago, y P(L): probabilidad que una plántula produzca 3 o más hojas de al menos 1 cm de longitud cada una.

Small seeds	Medium seeds	Large seeds
30	28[1]	30
↓	↓	↓
P(G) = 0.43 [a]	P(G) = 0.79 [b]	P(G) = 0.87 [b]
↓	↓	↓
13	22	26
↓	↓	↓
P(S) = 0.69 [a]	P(S) = 0.60 [a]	P(S) = 0.60 [a]
↓	↓	↓
9	13	22
↓	↓	↓
P(L) =0.11 [a]	P(L) = 0.62 [b]	P(L) = 0.77 [c]
↓	↓	↓
1	8	17
$P(L \mid G \cap S) = 0.03$ [a]	$P(L \mid G \cap S) = 0.29$ [b]	$P(L \mid G \cap S) = 0.57$ [c]

Note: Means with different letters differ significantly (Chi-square test for proportions, $p < 0.05$). [1] Two medium sized seeds were lost.

important because seedlings with larger roots are able to compensate for water lost by transpiration (Baker 1972), specially in areas where seedlings must overcome dry seasons such as the Mediterranean region of central Chile (Di Castri & Hajek 1976). Differences observed between seedlings coming from large versus small seeds have profound demographic implications as tiny differences in early stages become disproportionately greater in later ones in terms of plant survival and vigour (Howe & Richter 1982).

Although the biomass of roots, shoots and leaves was always greater in large seeds, there were differences in terms of relative biomass allocation. In fact, large seeds invested proportionally more biomass to leaves whereas small seeds invested proportionally more to roots. The net primary productivity of seedlings is positively correlated with photosynthetic to non-photosynthetic tissue ratios, specially when Photosynthetically Active Radiation intensity is above the leaf light compensation point (Foster 1986). Thus, because seedlings allocate more energy to leaves, those coming from large seeds have higher net primary productivity in comparison to their smaller counterparts. These differences in performance may be crucial in determining which seedlings have a better chance of reaching the canopy in forest gaps. In general, tree species, such as those belonging to Lauraceae, are termed "persistent species" because they germinate in the shade and form a seedling bank on the forest ground "waiting for" the fortuitous appearance of a small treefall gap (Foster 1986). We expect that seedlings coming from large seeds will have a greater ability to grow and become dominant in gaps.

We did not find any other study documenting that small seeds allocate more biomass to roots. We can hypothesise that in small seeds, with scarce reserves in the cotyledons, energy investment to roots allow them to explore a greater volume of soil for water and nutrients.

Substantial differences among seedlings originated from different seed size classes emerged from the comparison of P $(L \mid G \cap S)$. We observed significant differences among P(G) and specially among P(L), but not in P(S). That is, although seedlings coming from small seeds developed shoots in the same proportion than medium and large seeds, their reserves were not sufficient to produce 3 or more leaves.

Our study suggests that seedlings coming from large seeds have enormous advantages over seedlings coming from small seeds. Therefore, seed size will be an important demographic filter at an early phase of the life cycle of *C. alba*. However, Venable & Brown (1988) have suggested that at least theoretically, under favourable conditions of light or humidity, seedlings coming from small and large seeds will not present differences in recruitment, but under unfavourable conditions, seedlings coming from large seeds will show greater recruitment. This is an hypothesis that should be evaluate empirically.

Finally, we observed differences among seedlings coming from different sized seeds even though our experiment was carried out without resource restrictions (water ad libitum and one seed per pot). Others authors (e.g., Dolan 1984, Stanton 1984) did not find differences between seedlings from different seed size when they performed their experiments under similar conditions. We predict that the differences observed in the laboratory with respect to germination, seedling growth and biomass allocation, will increase under fields conditions, where water availability is limiting during at least six months of the year.

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