Patterns of tree seedling mortality in a temperate-mediterranean transition zone forest in Chile

Patrones en la mortalidad de plántulas de especies arbóreas de un bosque de la transición templado-mediterránea de Chile

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ABSTRACT

Seedling mortality in forests is the net result of an array of processes that vary spatially and temporally. We quantified emergence and mortality of seedlings at monthly intervals for two years, in a forest situated in the transition zone between the Mediterranean and temperate regions of Chile. We aimed to determine if survival of species responded differentially to seasonal water availability, to the spatial variation in light availability and to seedling density. The commonest species in the seedling bank were the Mediterranean-climate species *Cryptocarya alba* (61%) and the temperate-climate species *Aextoxicon punctatum* (29%). 279 of the 504 new seedlings that emerged during the two-year study died during the same period, corresponding to 55,4% mortality. Four of the less common species (*Persea lingue, Peumus boldus, Nothofagus obliqua* and *Luma apiculata*) suffered 100 % mortality of new recruits. Mortality of *A. punctatum* showed a marked seasonal pattern, with high mortality during the dry summer months. In contrast, mortality of the Mediterranean-climate species *C. alba* was more evenly distributed throughout the year. Multiple regressions showed that light availability had no significant effect on mortality of *A. punctatum* or *C. alba*. The same analysis revealed that survival of *A. punctatum* was negatively affected by conspecific seedling density, but this density-dependent effect was not found for *C. alba.* Heterospecific density-dependent effects were not found, i.e. mortality of neither species was affected by local density of seedlings of other species. This study shows that spatial and temporal variation in critical factors shapes interspecific variation in seedling mortality in this forest.

KEYWORDS: *Aextoxicon punctatum*, *Cryptocarya alba*, density-dependent mortality, drought tolerance, shade tolerance.

RESUMEN

La mortalidad de las plántulas es el resultado de una gama de procesos y agentes que pueden variar espacial y temporalmente en los ecosistemas forestales. En este estudio cuantificamos la emergencia y mortalidad de plántulas mes a mes, por un período de dos años en un bosque situado en la zona de transición entre la región mediterránea y templada de Chile. Pretendimos dilucidar si las especies sobreviven en forma diferencial a la disminución estacional en la disponibilidad de agua, a la variación espacial en la disponibilidad de luz y a la densidad local de plántulas. Las especies más abundantes en el banco de plántulas son la esclerófila *Cryptocarya alba* (61%) y la especie templada *Aextoxicon punctatum* (29%). Del total de 504 plántulas emergidas durante el estudio, murieron 279, lo que corresponde a un 55,4 %. Cuatro de las especies menos abundantes (*Persea lingue, Peumus boldus, Nothofagus obliqua* y *Luma apiculata*) sufrieron un 100 % de mortalidad de plántulas emergidas durante los dos años. La mortalidad de *A. punctatum* evidenció una marcada estacionalidad, con tasas elevadas durante la estación más seca (verano), pero este patrón fue mucho menos evidente en *C. alba*. Un análisis de regresión múltiple mostró que la luz no afectó la mortalidad de *A. punctatum* ni de *C. alba*. El mismo análisis demostró que existe un efecto densodependiente conespecífico sobre la mortalidad de *A. punctatum,* en contraste con *C. alba,* cuya mortalidad no fue afectada por la densidad conespecífica de plántulas. Efectos densodependientes comunitarios se descartan para ambas especies. La presente investigación muestra que los factores críticos varían espacial y temporalmente determinando diferencias interespecíficas en la supervivencia de plántulas de especies nativas en este tipo de ecosistema.

PALABRAS CLAVE: *Aextoxicon punctatum*, *Cryptocarya alba*, mortalidad densodependiente, tolerancia a la sequía, tolerancia a la sombra.

INTRODUCTION

Seedling mortality results from a range of processes and agents that vary spatially and temporally in the forest ecosystems. Intra and interspecific variation in seedling survival has long-term consequences for forest structure and composition, through its role in shaping forest dynamics (Kobe 1996, Beckage & Clark 2003). Identifying the agents and processes responsible for seedling mortality is therefore fundamental for understanding forest dynamics and for developing criteria for the management, conservation and restoration of forest ecosystems (Clark *et al*. 1999, Clark 2008).

Drought is one of the leading causes of seedling mortality in regions subject to Mediterranean-type climates (Peñuelas *et al.* 1998). Drought can differentially affect species, some possessing adaptations that enable them to tolerate sustained periods of water soil deficit, whereas others succumb rapidly (Caspersen & Kobe 2001, Engelbrecht & Kursar 2003, Moles & Westoby 2004). In the Chilean Mediterranean-temperate transitional zone, precipitation occurs mostly between April and October and a severe summer drought between December and February (Almeyda & Sáez 1958, Di Castri & Hajek 1976). If the tree seedling species of this region differed in their susceptibility to drought, these differences would likely be expressed towards the end of the dry summer, when water is scarcest.

Light availability is probably the biggest single influence on seedling and juvenile tree survival in humid temperate forests (Finzi & Canham 2000, Kobe *et al.* 1995). Although temperate forests often comprise mixtures of species that differ widely in shade tolerance, the survival of most species shows positive relationships with light availability (Kobe *et al.* 1995, Lusk 2002). In Mediterranean-type climates, in contrast, the relationship of survival with light availability can be more complex. The negative impact of drought on seedling growth and survival can be less in the shade than in high light (Sánchez-Gómez *et al.* 2006). It has been suggested that, in dry environments, the negative impact of shade on light availability is more than compensated by the positive impact in reducing heat load and transpiration (Prider & Facelli 2004). The facilitative effects of shade have been documented as a crucial mechanism of regeneration in Mediterranean-type ecosystems (Maestre *et al.* 2003).

Density-dependent seedling mortality has been attributed an important role in tree species coexistence (Connell 1971, Janzen 1970, Webb & Peart 1999). Density-dependent mortality can potentially arise through competition, or through the action of natural enemies that strongly affect the survival of seedlings on the forest floor. It has been proposed that the high diversity of tropical forests is at least partly attributable to species-specific pathogens or predators that selectively kill seeds or seedlings (Janzen 1970, Connell 1971). Doubt has been cast on this hypothesis by evidence that the proportion of species affected by density-dependent mortality is broadly similar in tropical and temperate forests (Lambers *et al.* 2002). To date, however, little or nothing is known about the importance of density-dependent mortality in forests with Mediterranean-type climatic influence.

Here we report a study of seedling mortality in a forest located in the temperate-mediterranean transition zone of south-central Chile. In this region, precipitation occurs mostly between April and October, although the summer drought is less marked than further north (Di Castri & Hajek 1976). The tree assemblage includes species typical of the sclerophyll forest of the Mediterranean-type climate of central Chile (e.g. *Cryptocarya alba* (Molina) Looser, Lauraceae) as well as species more characteristic of the humid temperate forests further south (e.g. *Aextoxicon punctatum* Ruiz et Pav., Aextoxicaceae). We documented emergence and mortality of seedlings during a two-year period, and addressed the following questions: a) Do seasonal patterns of seedling mortality show evidence of differential species responses to water availability? b) Is seedling mortality related to light availability? c) Is there evidence of density-dependent seedling mortality in this forest?

MATERIALS AND METHODS

Study site

The study was carried out in Parque Coyanmahuida (36°49'S, 72°43'W) a forest reserve located in the coast ranges of south-central Chile, 38 km east of the city of Concepción. This reserve lies within the temperate-mediterranean transition zone of south-central Chile (Villagrán & Hinojosa 1997), characterized by cool rainy winters and warm dry summers (Di Castri & Hajek 1976). Mean annual rainfall in Concepción is 1276 mm, although on average only about 64 mm falls during the summer months of December to January. The main tree species present in the forest canopy were *Aextoxicon punctatum, Cryptocarya alba*, *Peumus boldus* Molina (Monimiaceae), *Persea lingue* (Miers ex Bertero) Nees (Lauraceae)*, Luma apiculata* (DC.) Burret (Myrtaceae)*,* and *Citronella mucronata* (Ruiz et Pav.) D.Don. (Icacinaceae), with emergent *Nothofagus obliqua* (Mirb.) Oerst. (Nothofagaceae). Subcanopy and understorey species included *Aristotelia chilensis* (Molina) Stunz (Elaeocarpaceae), *Rhamnus diffusus* Clos (Rhamnaceae), *Azara integrifolia* Ruiz et Pav. (Flacourtiaceae)*, Rhaphithamnus spinosus* (Juss.) Mold. (Verbenaceae) and *Lapageria rosea* Ruiz et Pav. (Philesiaceae) (Gajardo 1994, Luebert & Pliscoff 2006).

Quadrat installation and seedling census

24 permanent $1 m^2$ quadrats were laid out at random intervals between 10 and 20 m apart, on two transects run through the forest understorey. We avoided areas close to walking tracks and forest margins. Within each quadrat, each seedling was identified with a plastic label. Quadrats were revisited at

monthly intervals over a two-year period beginning in September 2003, recording emergence of new seedlings and mortality of all seedlings present.

Measurement of light availability

A pair of LAI-2000 Plant Canopy Analyzers (Li-COR, Lincoln, Nebraska, USA) was used to quantify light availability above each quadrant, in October 2003. The LAI-2000 enables computation of diffuse light availability in an overall field of view of 148°, calculated by referring measurements taken under a canopy with simultaneous measurements taken in an open area (in this case, a field) outside the forest (Fig. 2). Measurements taken with the LAI-2000 have been shown to correlate closely with spatial variation in daily photon flux in forest understories (Machado & Reich 1999), and to accurately predict spatial variation in plant growth (Kobe & Hogarth 2007). Our springtime measurements probably underestimate wintertime canopy openness above quadrats located close to trees of the deciduous *Nothofagus obliqua*. However, these errors are likely to be small, as *N. obliqua* is present as scattered emergent above a canopy of evergreens.

Table I. Repeated measures ANOVA to determine the effects of season on mortality rates of tree species' seedlings.

Tabla I. ANOVA de medidas repetidas para determinar el efecto de la estación del año sobre la tasa de mortalidad de plántulas de especies arbóreas.

Species	Source of variation	SS	df	MS	*F*	*P-value*
Cryptocarya alba	Season	5541.6	7	791.6	1.45	0.188
	Error	80026.9	147	544.4		
Aextoxicon punctatum	Season	50787.9	7	7255.4	11.01	<0.001
	Error	64579	98	659		

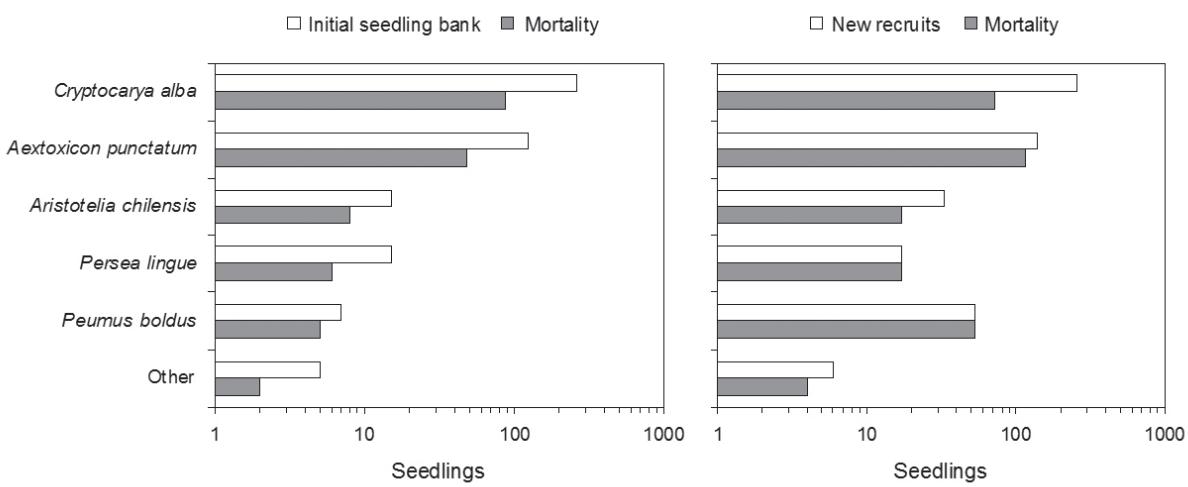

Figure 1. Structure and dynamics of seedlings communities. Obtained from 24×1m^2 quadrats in Coyanmahuida, south-central Chile. Left-hand panel shows composition of seedling bank at the outset, and mortality during the two-year study (Sept. 2003-Sept. 2005). Right-hand panel shows composition of new recruits during the study, and their mortality. "Other" species are *Nothofagus obliqua, Citronella mucronata* and *Luma apiculata.*

Figura 1. Estructura y dinámica de la comunidad de plántulas. Datos obtenidos en 24 cuadrantes de 1m^2 en el Parque Coyanmahuida, centro sur de Chile. El panel de la izquierda muestra la composición del banco de plántulas y su mortalidad durante los dos años de estudio (Sept. 2003-Sept. 2005). El panel de la derecha muestra la composición de las plántulas que emergieron durante el estudio y su mortalidad. "Otras" especies son *Nothofagus obliqua, Citronella mucronata* y *Luma apiculata.*

Table II. Summary of multiple regressions to determine the effects of light, density of conspecific and other species' seedlings on seedling mortality of the two main tree species of Coyanmahuida. Year 1 = Sept 2003-Sept 2004; Year 2 = Oct 2004-Sept 2005; Both years = Sept 2003-Sept 2005.

Tabla II. Resumen del análisis de regresión múltiple para determinar el efecto de la luz, densidad conespecífica de plantas y densidad de plántulas de otras especies sobre la mortalidad de plántulas de las dos principales especies arbóreas de Coyanmahuida. Año 1 = Sept 2003-Sept 2004; Año 2 = Oct 2004-Sept 2005; Ambos años = Sept 2003-Sept 2005.

	Year 1			Year 2			Both years		
(a) *Aextoxicon punctatum*									
Effect	df	F	P	df	F	P	df	F	P
Conspecific density	1	12.23	0.003	1	22.00	0.000	1	23.53	0.000
Other species' density	1	1.42	0.251	1	0.00	0.970	1	1.00	0.324
Light	1	0.81	0.383	1	2.31	0.149	1	1.39	0.246
Error	16			15			35		
(b) *Cryptocarya alba*									
Effect	df	F	P	df	F	P	df	F	P
Conspecific density	1	0.00	0.927	1	1.67	0.212	1	1.33	0.256
Other species' density	1	0.46	0.509	1	0.94	0.345	1	1.22	0.277
Light	1	2.18	0.158	1	0.15	0.703	1	2.01	0.164
Error	17			18			39		

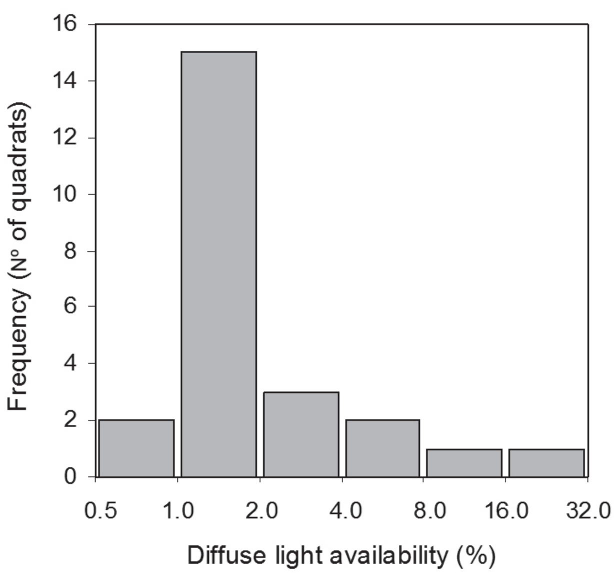

Figure 2. Frequency distribution of diffuse light percentage in 24×1m^2 quadrats, measured in the forest floor. The measurements were making with the LAI-2000 in Coyanmahuida, south-central Chile.

Figura 2. Distribución de frecuencias del porcentaje de luz difusa en 24 cuadrantes, medidos en el piso del bosque. Las mediciones fueron hechas con LAI 2000 en Coyanmahuida, centro sur de Chile.

Data analysis

The data were analysed using JMP statistical software (SAS Institute, Cary, N.C.). The normality of data was assessed using the Komolgorov-Smirnov test; as the assumptions of normality and homogeneity of variance were not met in all cases, mortality and density data were subjected to a log (X+1) transformation (Zar 1996). The light availability data were also subjected to a simple log-transformation. Multiple regression was used to assess the effects of light availability and seedling density on mortality rates of *C. alba* and *A. punctatum*.The explanatory variables were diffuse light availability (%), density of conspecific seedlings, and density of other species' seedlings. This analysis was performed separately for each of the two years, as well as for the whole period (Table II). Repeated measures ANOVA was used to test for seasonal variation in mortality of *A. punctatum* and *C. alba*, as the same 24 quadrants were sampled on each visit. In order to corroborate the occurrence of summer drought during the period of date collected, we averaged mean rainfall data from the two nearest rainfall stations (Fig. 3). These were Las Pataguas (36º29'S; 72º40'W), and Concepción (36º50'S; 73º03'W). Seasons were defined as spring (September-November), summer (December-February), autumn (March-May), and winter (June-August).

RESULTS

Seedling census

Although eight species were present at the outset, the seedling bank was overwhelmingly dominated by the sclerophyll forest species *Cryptocarya alba* (61% of the total seedling bank) and the temperate forest species *Aextoxicon punctatum* (29%). Of the 429 seedlings initially present, 156 (36.4 %) of these died during the two-year period; the mortality rate of *A. punctatum* (38%) was slightly higher than that of *C. alba* (33%; Fig. 1). 504 new seedlings emerged during the study, and 279 of these (55.4 %) died during the same period (Fig. 1). New recruits of *A. punctatum* suffered much higher mortality (82%) than those of *C. alba* (28%). New recruits of four of the less common species (*P. lingue, P. boldus, N. obliqua* y *L. apiculata*) suffered 100% mortality during the two years of the study (Fig. 1).

Seasonal variation in mortality

Mortality of *A. punctatum* showed significant seasonal variation, with mortality rates being far higher in summer than during other seasons (Fig. 3). Mortality of *C. alba*, in contrast, show no marked seasonality. Repeated measures ANOVA confirmed that season was a significant influence on mortality of *A. punctatum*, but not on that of *C. alba* (Table I).

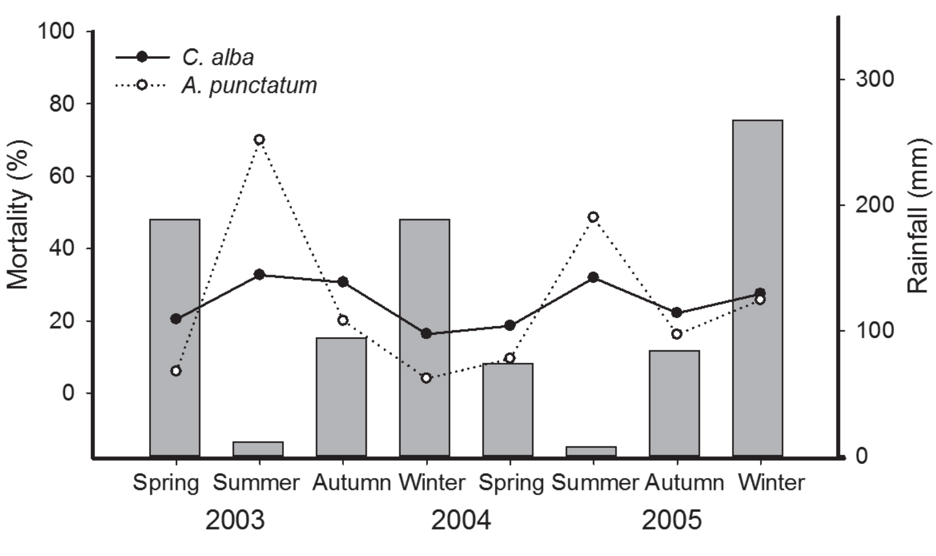

Figure 3. Seasonal pattern of seedling mortality of *Cryptocarya alba* (solid line) y *Aextoxicon punctatum* (dotted line) from September 2003 to September 2005, at Parque Coyanmahuida, south-central Chile. Grey bars show rainfall estimated by averaging figures from nearby meteorological stations at Las Pataguas (36º29'S; 72º40'W), and Concepción (36º50'S; 73º03'W).

Figura 3. Patrón estacional de mortalidad de plántulas de *Cryptocarya alba* (línea continua) and *Aextoxicon punctatum* (línea punteada) desde septiembre del 2003 a septiembre del 2005 en el parque Coyanmahuida, centro sur de Chile. Barras grises muestran el agua caída estimada desde estaciones meteorológicas cercanas en Las Pataguas y Concepción.

Effects of light and seedling density

Diffuse light availability at most quadrats was < 2% (Fig. 2). Multiple regression showed that mortality of *A. punctatum* across the 24 quadrants was significantly positively correlated with conspecific seedling density. This result was found consistently, whether data from the two years were analysed separately, or together (Table II). However, mortality of *A. punctatum* was not influenced by density of other species' seedlings. Mortality of *C. alba* was not influenced by either conspecific or heterospecific seedling density. The same analysis showed that light availability had no effect on mortality rates of either species, once the effects of seedling density were controlled for.

DISCUSSION

Like Kobe (1996), who found that juvenile survival was a good predictor of overstorey composition in several forests in the eastern USA, we found that the commonest species in the forest canopy at Coyanmahuida (*Cryptocarya alba*) is also the species with the highest seedling survival (Fig. 1). With only eight species, the seedling bank of this forest is floristically poorer than those of low-altitude temperate rainforests further south (Figueroa & Lusk 2001, Lusk *et al.* 2006), although similar to the seedling bank diversity of some montane temperate forests (Lusk 1995). However, the dominance of *C. alba* followed by *A. punctatum* at Coyanmahuida is similar to the composition of other forests in the coast ranges at similar latitudes (Bustamante *et al.* 2005).

The two dominant species showed contrasting seasonal patterns of seedling mortality (Fig. 3). The high mortality of *A. punctatum* during the dry summer months suggests that this species is less tolerant of drought than its associate *C. alba*, and this is consistent with the relative distributions of the two species. *C. alba* is abundant and widespread in the Mediterranean-climate regions of central Chile, whereas *A. punctatum* is mainly a tree of the temperate forests further south, although it also occurs locally in humid gullies and coastal fog forest further north (e.g. Del-Val *et al.* 2006). Our results also might indicate that interannual variation in the severity of summer drought could influence coexistence of sclerophyll and temperate forest species in south-central Chile. Although *A. punctatum* seedlings suffer high mortality most years, unusually rainy summers might occasionally permit higher survival of this species.

Mortality of seedlings of neither of the dominant species was significantly influenced by light availability (Table II). *Aextoxicon punctatum* is considered one of the most shade-tolerant species of the region (Donoso 1989, Figueroa & Lusk 2001), as its seedlings survive in the shadiest understorey microsites of the Valdivian rainforest (Lusk *et al.* 2006). Less is known for certain about the light requirements of *C. alba,* although this species is also considered to be relatively shade-tolerant (Armesto & Pickett 1985). However, in temperate forests, it is common to find that seedling survival responds positively to light availability, even in shade-tolerant species (Coates 2000, Kobe *et al.* 1995). In Mediterranean-type regions, in contrast, the impact of drought on seedlings is sometimes less under shade than in the open (Sánchez-Gómez *et al.* 2006). The lack of correlation of survival with light availability in our study might reflect a similar interaction between the effects of drought and shade.

The present study shows that density-dependent seedling mortality may contribute to tree species coexistence in this forest in the Mediterranean-temperate transition zone of south-central Chile. Density-dependent seedling mortality has been widely-documented in tropical and temperate forests (Lambers *et al.* 2002), but we are not aware of previous reports from regions with Mediterranean climatic influence. The only density-dependent effect that we found, involved conspecific interactions in one of the dominant species, *A. punctatum* (Table II). The lack of evidence for heterospecific effects suggests that competition between seedlings is unlikely to be the main mechanism of density-dependent seedling mortality in this forest. The correlation of *A. punctatum* mortality with conspecific seedling density is therefore more likely to reflect the action of pathogens or herbivores that selectively attack this species. Although pathogen or herbivore activity can be determined by inherent preferences for certain species, there is also some evidence that drought-stressed plants are more susceptible to attack (McDowell *et al.* 2008). One possibility is that *A. punctatum*'s vulnerability to drought stress renders its seedlings susceptible to pathogens or pest attack during the summer months. Aguilera (2004) isolated *Phytophthora* and several fungal and bacterial pathogens from the roots of *A. punctatum*, and speculated that these are likely to have a major impact on seedlings, although no mortality data were presented. Del-Val & Armesto (2010) reported that small mammals were responsible for about 30% of *A. punctatum* seedling mortality at subtropical and temperate sites, but did not examine density-dependent effects.

Our study points to drought and density-dependent mortality as key factors shaping patterns of seedling recruitment in this forest in south-central Chile. These findings may inform forest restoration programs in a region that has undergone widespread recent forest clearance and fragmentation (Bustamante *et al.* 2005). The differential response of the two dominant species to summer drought also points to likely changes in the composition of the forest at Coyanmahuida, as climate change models predict declining precipitation in the region (Vera *et al.* 2006).

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REFERENCES

Aguilera, L.E. 2004. Microorganismos fitopatógenos asociados al bosque de Olivillo (*Aextoxicon punctatum Ruiz et Pav.*) en el Parque Nacional Bosque Fray Jorge, IV Región, Chile. In: Historia Natural del Parque Nacional Bosque Fray Jorge (eds F. A. Squeo, J. R. Gutiérrez and I. R. Hernández), pp. 255-264. Ediciones Universidad de La Serena, La Serena, Chile.

Almeyda, E. & F. Sáez 1958. Recopilación de datos climáticos de Chile y mapas sinópticos respectivos, Ministerio de Agricultura, Santiago, Chile.

Armesto, J.J. & S.T.A. Pickett. 1985. A mechanistic approach to the study of succession in the chilean matorral. Revista Chilena de Historia Natural 58: 9-17.

Bustamante, R.O., J.A. Simonetti, A.A. Grez & J. San Martín. 2005. Fragmentación y dinámica de regeneración del bosque Maulino: diagnóstico actual y perspectivas futuras. In: Historia, Biodiversidad y Ecología de los Bosques Costeros de Chile, pp. 529-539. Editorial Universitaria, Santiago de Chile.

Beckage, B. & J.S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. Ecology 84:1849-1861.

Caspersen, J.P. & R.K. Kobe. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos 92: 160-168.

Clark, J.S. 2008. Beyond neutral science. Trends in Ecology and Evolution 24: 8-15.

Clark, J.S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. MacLachlan, J. Mohan & P. Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86:1-16.

Coates, K.D. 2000. Conifer seedling response to northern temperate forest gaps. Forest Ecology and Management 127: 249-269.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Dynamics of Populations (eds P. J. Den Boer and G. Gradwell) pp. 298-312. PUDOC, Wageningen.

Del-Val, E. & J.J. Armesto. 2010. Seedling mortality and herbivory damage in subtropical and temperate populations: testing the hypothesis of higher herbivore pressure toward the tropics. Biotropica 42 (2): 174-179.

Del-Val E., J.J. Armesto, O. Barbosa, D.A. Christie, A. Gutiérrez, C.G Jones, P.A. Marquet & K.C. Weathers. 2006. Rain forest islands in the Chilean semiarid region: fog-dependency, ecosystem persistence and tree regeneration. Ecosystems 9: 598-608.

Di Castri, F. & E.R. Hajek. 1976. Bioclimatología de Chile. Universidad Católica de Chile, Santiago, Chile. 129 pp.

Donoso C. 1989. Antecedentes básicos para la silvicultura del tipo forestal siempreverde. Bosque 10: 37-53.

Engelbrecht, B.M. J. & T.A. Kursar. 2003. Comparative drought resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136: 383-393.

Figueroa J.A. & C.H. Lusk. 2001. Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. New Phytologist 152: 483-489.

Finzi, A.C. & C.D. Canham 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management 131: 153-165.

Gajardo, R. 1994. La vegetación natural de Chile. Clasificación y distribución geográfica. Editorial Universitaria, Santiago de Chile. 165 pp.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical rainforests. The American Naturalist 104: 501.

Kobe, R.K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecological Monographs 66: 181-201.

Kobe, R.K. & L.J. Hogarth. 2007. Evaluation of irradiance metrics with respect to predicting sapling growth. Canadian Journal Forest Research 37: 1203-13.

Kobe, R.K., S.W. Pacala, J.A. Silander & C.D. Canham.1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5: 517-532.

Lambers, J.H.R., J.S. Clark & B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417: 732-735.

Luebert, F. & P. Pliscoff. 2006. Sinopsis Bioclimática y Vegetacional de Chile. Editorial Universitaria, Santiago de Chile. 316 pp.

Lusk, C.H. 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. Journal of Vegetation Science 6: 249-256.

Lusk, C.H. 2002. Leaf area accumulation helps juvenile evergreen trees tolerate shade in a temperate rainforest. Oecologia 132: 188-96.

Lusk, C.H., R.L. Chazdon & G. Hofmann 2006. A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. Oikos 112: 131-7.

Machado, J.L. & P.B. Reich. 1999. Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. Canadian Journal of Forest Research 29: 1438-1444.

Maestre, F.T., J. Cortina, S. Bautista & J. Bellot. 2003. Does *Pinus halepensis* facilitate the establishment of shrubs in Mediterranean semi-arid afforestations? Forest Ecology and Management 176: 147-60.

McDowell, N., W.T. Pockman, C.D. Allen, D.D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D.G Williams & E.A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologyst 178: 719-39.

Moles, A.T. & M. Westoby. 2004. What do seedlings die from and what are the implications for evolution of seed size? Oikos

106: 193-199.

Peñuelas, J., I. Filella, J. Llusia, D. Siscart & J. Piñol. 1998. Comparative field study of spring and summer leaf gas exchange and photobiology of the mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. Journal of Experimental Botany 49: 229-238.

Prider, J.N. & J.M. Facelli. 2004. Interactive effects of drought and shade on three arid zone chenopod shrubs with contrasting distributions in relation to tree canopies. Functional Ecology 18: 67-76.

Sánchez-Gómez, D., F. Valladares & M.A. Zavala. 2006. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. New Phytologyst 170: 795-806.

Vera, C., G. Silvestri, B. Liebmann & P. González. 2006. Climate change scenarios for seasonal precipitation in South America from IPCC-AR4 models. Geophysical Research Letters 33.

Villagrán, C. & F. Hinojosa. 1997. Historia de los bosques de Sudamérica II. Fitogeografía. Revista Chilena de Historia Natural 70: 241-267.

Webb, C.O. & D.R. Peart. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. Ecology 80: 2006-2017.

Zar, J. 1996. Biostatiscal Analysis. New Jersey, USA. Third edition. Prentice Hall. 662 pp.

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