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1 Does site quality affect the additive basal area phenomenon?: results from Chilean old-growth
2 temperate rainforests.

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Draft

12 Abstract

13 Complex old-growth forests with large emergent trees may support more basal area-BA than
14 those without these trees. The so-called additive basal area phenomenon occurs when the
15 presence of these emergent trees does not affect the basal area (BA) of the canopy trees, i.e. BA
16 of emergent and canopy trees add up. We studied two old-growth forests in south-central Chile
17 with similar species composition and structure but contrasting soil quality. We sampled 57 1,000
18 m² plots in a relatively high-quality site (Quillaiepe) and 65 in a relatively low-quality site
19 (Yaldad), and evaluated total stand BA, BA of emergent trees, BA of canopy trees, and the
20 influence of the BA of emergent trees on total and canopy BA. Quillaiepe accumulated on average
21 50% higher BA than Yaldad. The additive BA effect only occurred on the high quality site
22 Quillaiepe. A more detailed analysis showed that canopy associates were differentially affected in
23 terms of BA depression with increasing BA of emergent trees in each site. The relative
24 competitive ability of canopy species, as affected by their ecological traits and geographical
25 distribution, presumably explain if BA of individual species or functional groups are depressed
26 by the BA of emergents. Above- and below ground resource partitioning may be decisive
27 mechanisms affecting the occurrence of additive BA accumulation in forest stands. *Key words:*
28 Canopy stratification, competition, emergent trees, *Nothofagus*, resource use complementarity.
29

30 Introduction

31 Several studies have demonstrated that multi-stratified old-growth forest stands can
32 develop more biomass or basal area than pure stands when species occupy different canopy
33 strata, i.e., in stands with a rich vertical stratification (Enright 1982; Lusk 2002; Donoso and
34 Lusk 2007). This apparent complementarity can occur when different strata or functional groups
35 in the vertical profile (i.e., canopy segregation in emergent, upper main canopy, lower main
36 canopy, below main canopy and understory (see Veblen et al. 1980)) have a more efficient
37 resource use through this vertical arrangement, which has been considered a key aspect of
38 resource-use differentiation in forest stands with complex structures (Terbough 1985; Lusk and
39 Ortega 2003). One straightforward form to assess this resource-use complementarity is if there is
40 an independent relationship between the basal area of emergent and canopy tree species in old-
41 growth forests. This phenomenon among forest ecologists has been called the “additive basal
42 area-ABA” effect (e.g., Enright 1982; Lusk 2002; Donoso and Lusk 2007).

43 The first formal test of this phenomenon was reported by Enright (1982), who found that
44 basal area of forest stands with emergent *Araucaria hunsteinii* trees was greater than that of
45 adjacent stands without these trees. In fact, the basal area of the canopy species (mid- and shade-
46 tolerant tree species) did not vary much with or without the emergent *Araucaria* trees. A similar
47 effect was documented by Ogden (1985) for the emergent conifer *Agathis australis* in New
48 Zealand. After these works, both authors mentioned that this may be a global ecological rule (cf.
49 Enright and Ogden 1995). More recently, works have studied these patterns in stratified old-
50 growth forests with an emergent canopy tier dominated by Podocarps in New Zealand (Lusk
51 2002), by *Nothofagus dombeyi* in Chile (Donoso and Lusk 2007), and conifers in Japan (Ishii and
52 Asano 2010). Besides, this phenomenon has been reported also in stratified second-growth
53 temperate forests in the northern (Kelty 1989) and southern (Lusk and Ortega 2003) hemispheres,
54 where upper canopy species do not depress the basal area of the understory shade-tolerant
55 species.

56 Researchers have developed different approximations to explain the mechanisms behind
57 this phenomenon. Enright (1982), Ogden (1985), Enright and Ogden (1995) and Lusk (2002)
58 argued that resource-use complementarity (e.g., light and nutrients) is a plausible mechanism to
59 explain the phenomenon, although some authors have considered size-asymmetric competition
60 for light as the most important mechanism governing the ABA phenomenon in mesic sites (Kelty
61 1989; Lusk and Ortega 2003)., Stratified profiles with light-demanding and fast growing species
62 occupying the emergent tier, and slow growing shade-tolerant species occupying the lower tiers,
63 might outyield forest stands without this vertical structure, and this occurs through
64 complementary use of light (Kelty 1989; Lusk and Ortega 2003; Donoso and Lusk 2007; Ishii
65 and Asano 2010). Also competition and mortality may occur within each stratum and not among
66 strata, and mortality of upper canopy trees may generate the release of resources and thus
67 increase the growth of the canopy species (interspecific growth facilitation; Soto et al. 2010).
68 Finally, from a disturbance ecology point of view, Enright and Ogden (1995) and Lawes et al.
69 (2006) suggested that the lack of frequent large-scale disturbances (e.g. return point interval
70 between disturbances) throughout stand succession, and also the longevity of some emergent
71 trees, are responsible for the occurrence of this phenomenon. Overall, these studies suggest that
72 multiple factors may occur simultaneously to affect the ABA phenomenon in temperate forests.

73 In spite of a number of studies about the ABA phenomenon, insights about the
74 mechanisms acting from belowground resources could expand and improve the comprehension
75 of the effects of resource-use complementarity and biomass production in complex old-growth
76 forests (Kelty 1989; Moreno-Chacon and Lusk 2004). In that way, Moreno-Chacon and Lusk
77 (2004) found that vertical stratification of root systems from different functional groups (e.g.,
78 emergent and canopy tree species) could explain the largest aboveground production in deep
79 soils in old-growth forests (e.g. at least 80 cm in depth). They reported that the fine roots of
80 emergent *Nothofagus* trees occupied a shallower soil layer than canopy tree species, which in
81 general have more pivotal or deeper root systems. Moreover, they postulated that belowground

resource-use complementarity could help to reduce the competition between emergent trees with their canopy associates, promoting the ABA phenomenon. Overall, in addition to competition for light, belowground competition could also play an important role in explaining the occurrence of the ABA phenomenon, and whether there is a threshold in site quality below which the BA of emergent tree depresses the BA of the canopy tier.

In this study, we tested two highly similar old-growth forests of the Evergreen forest type of south-central Chile in terms of structure and composition, with similar climate but on soils of different quality. For this purpose we sampled two old-growth forests in different phytogeographical regions (Veblen et al. 1983). One forest is located in Quillaie (Andes Cordillera) in a relatively high-quality site within the region of the Valdivian Temperate Rainforests (VTR, 42°S), and the other in Yaldad (Chiloé Island) in a relatively low-quality soil within the region of the North-Patagonian Temperate Rainforests (NPTR, 44°S). The vertical component of these forests is characterized by the two emergent and shade-intolerant hardwood evergreen trees *Nothofagus nitida* and *Weinmannia trichosperma*, which have their crowns above the main canopy tier dominated by mid- and shade-tolerant tree species (*Saxegothaea conspicua*, *Drimys winteri*, *Laurelia philippiana* and *Amomyrtus luma*). Having the same emergent tree species in both forests is relevant since crown traits of these species is the principal influence on biomass accumulation of the overtopped canopy trees (Enright and Ogden 1995). In this case these two pioneer tree species are relatively long lived and have a sparse canopy architecture which ensures a proper amount of light reaching the main canopy tier of more shade tolerant tree species (Enright and Ogden 1995). In this study we hypothesized that basal area of the emergent *N. nitida* and *W. trichosperma* trees do not depress the basal area of its canopy associates in the high-quality site, but it does in the low-quality site. Based upon results from the present study and a similar one in the northern distribution of the VTR (Donoso and Lusk 2007), we discuss possible mechanisms that presumably affect the relative competitive ability of canopy tree species and eventually the occurrence of the ABA phenomenon.

Methods

Study area and site quality features

The studied forests are located in the transitional zone between two of the main phytogeographical regions described by Veblen et al. (1983) for Chilean temperate rainforests (Fig. 1). One forest is located in the Andes foothills of south-central Chile (Quillaipe; 41°33'S, 72°40'W) within the southern limits of the VTR (42°S), and the other forest is in the southeastern part of the Chiloé island (Yaldad; 43°03'S, 73°44'W) within the northern limits of the NPTR(44°S). However, both forests correspond to the evergreen forest type, and more specifically to the subtype with emergent trees (Donoso 1993). These stratified forests are the result of long periods of time without large-scale disturbances affecting these forests, which have allowed the pioneer species to emerge above the canopy of late-successional species. Although large-scale and stand-replacing disturbances are common in the Andes, at lower elevations (e.g. foothills and mid elevations) these disturbances are less common and there are more shade-tolerant species as compared to higher elevations. Coastal or low-elevation forests are dominated by gap dynamics (i.e., large –scale disturbances are uncommon) (Veblen 1985). Several studies have suggested that coastal evergreen old-growth forests have remained largely free of stand-disrupting disturbances (*sensu* Donoso et al. 1985, Gutiérrez et al. 2004). Pioneer species in these regions include mostly *N. dombeyi*, *N. nitida* and *W. trichosperma* (*N. nitida* usually replacing *N. dombeyi* in more poorly drained soils). These are long-lived species that can reach emergent positions if time allows. Many shade-tolerant and midtolerant species occupy the main canopy, either below the emergent tier if it is present or dominating the upper canopy tier. Most are also long-lived species (Table 1), and include especially the conifer *S. conspicua*, and the hardwoods *D. winteri*, *L. philippiana* and *A. luma*, among other minor ones (Donoso et al. 1985; Gutiérrez and Huth 2012; Bannister and Donoso 2013).

Particularly, in this study both forests have an emergent canopy tier with the evergreen hardwood trees *N. nitida* (*Nothofagaceae*) and *W. trichosperma* (*Cunoniaceae*), below which the main tree canopy is dominated by the midtolerants *S. conspicua* (*Podocarpaceae*) and *D. winteri* (*Winteraceae*) and the shade-tolerants *L. philippiana* (*Monimiaceae*) and *A. luma* (*Mirtaceae*), although the latter is marginal in Quillaipé. In Quillaipé trees in the emergent tier reach up to 40 m, and those of the canopy tier 25-30 m, and in Yaldad emergent trees reach up to 32 m above a canopy tier of 20-25 m in height. These stratified forests have the typical reverse J-shaped diameter distribution of complex uneven-aged forest structures (e.g. O'Hara 2014). The stand structure of the two studied forests is shown in appendix S1.

The climate at the latitudes of the forests studied is humid temperate with strong oceanic influence (di Castri and Hajek 1976). Quillaipé has a mean annual precipitation range between 2,000 to 3,000 mm, a mean annual temperature around 11°C (the warmest month is January with 15 °C and coldest July with 7 °C, with a threshold minimum temperature of -10°C (Schlatter et al. 1995)). The soil is derived from modern volcanic ashes, deposited on basaltic or granitic rocks and sometimes on fluvioglacial sand and gravel in the Andes foothills (Tosso 1985). The terrain is composed of undulated hillocks to abrupt hills at an elevation between 300-500 m a.s.l. The soils are deep (> 2 m), with a rapid internal drainage (Schlatter et al. 1995). They have low P, B, Mg and K availability, and high P fixation due to high levels of active Al (Schlatter et al. 1995). The main limiting factor of this soil is the rapid surface drying in warm months due to high volume of pores and low bulk density (Tosso 1985; Schlatter et al. 1995).

Yaldad has a mean annual precipitation of 2105 mm/yr, without dry periods (Bannister and Donoso 2013). The mean annual temperature is between 9.1 to 10.8 °C, the mean temperature of the warmest month is 16°C (January) and that of the coldest month 5°C (July), with a minimum absolute temperature of - 4 °C (Schlatter et al. 1995). The soil corresponds to recent volcanic ashes above fluvio-glacial deposits that followed glacier retreat during the last ice age in the Pleistocene (Denton et al. 1999), and they have developed a hardpan layer of ferrous

oxides (~30–60 cm deep). These soils have poor drainage, high acidity, and high accumulation of organic matter, a high C/N ratio, and acid humus with a moderate degree of downwashing of organic matter into the mineral substratum (Bannister and Donoso 2013). The terrain is undulate to flat, with some scatter hillocks, at elevations < 100 m a.s.l., and the main soil limiting factor to forest development is rooting depth, in addition to a superficial water table that causes waterlogging conditions in flat or relatively flat terrains (Bannister and Donoso 2013).

Overall, differences in site are mainly reflected in the soil characteristics (richer in Quillaípe), in the height of the emergent and canopy trees (higher in Quillaípe) and partially in the greater relative importance in basal area of species adapted to eutrophic/mesotrophic sites in Quillaípe (Table 2).

Forest sampling and measurements

The data base was obtained from two evergreen old-growth forests with no apparent recent human disturbance. In Quillaípe we sampled 57 plots, and in Yaldad 65 plots. Emergent trees of *N. nitida* or *W. trichosperma* were present in 54 and 42 plots, respectively. The sample units were 1,000 m² (50 by 20 m) in size, with a systematic sampling along parallel transects. In each plot all trees > 5 cm in diameter at breast height (1.3 m; DBH) were sampled and species recorded. The vertical canopy position for each tree was assigned according to the classification by Veblen et al. (1980): emergent, upper main canopy, lower main canopy, below main canopy and understory.

Data management and statistical analysis

To assess the effect of ABA phenomenon we grouped the forests into emergent trees and canopy trees. The analysis was made in two parts. First, to evaluate the effects of site quality (i.e., two classes) on 1) total stand basal area, 2) basal area of emergent trees, and 3) basal area of canopy trees (grouped and by species) we performed the non-parametric Mann-Whitney *U*-test

for paired samples (Dytham 2003), using all the plots measured in each site. Second, to evaluate the influence of the basal area of emergent trees on total basal area and basal area of canopy tree species (excluding emergent tree species) we used simple linear regression (SLR). This analysis was conducted only with plots that had emergent trees, which corresponded to 54 in Quillaiepe and 42 in Yaldad, as mentioned above. The lack of emergent trees in some plots may be explained by the fact that there are gaps, localized areas with younger cohorts, and stochastic factors. By using only plots with emergent trees we secure that the data base is not including plots that represent these mentioned conditions within the matrix of the old-growth forest, which could alter the more straightforward analysis that only includes plots with emergent trees, as it has been done in other similar studies (e.g., Lusk 2002, Donoso and Lusk 2007). For SLR we tested normality of the data with the Shapiro-Wilk's test, and to evaluate homoscedasticity we used the Levene's test (Dytham 2003). All analyses were performed using R (R Development Core Team 2015).

Results

Structural differences between canopy groups

Structural differences between canopy groups were found in the two sites evaluated (Fig. 2). A significant difference in total basal area between the high-quality site (Quillaiepe) and the poor-quality site (Yaldad) was found ($U=332$, $P < 0.001$). The high-quality site accumulated on average 50% more basal area, which was significantly higher than the basal area in the low-quality site ($77.3 \pm \text{SD } 21.4 \text{ m}^2 \text{ ha}^{-1}$ vs. $53.5 \pm \text{SD } 15.6 \text{ m}^2 \text{ ha}^{-1}$; Table 2). The maximum value reached in the high-quality site was $118.9 \text{ m}^2 \text{ ha}^{-1}$, while it was only $83.7 \text{ m}^2 \text{ ha}^{-1}$ in the low-quality site. On the other hand, minimum values registered were 42.4 and 23.8 for the high- and the low-quality sites.

The basal area of the canopy species was significantly higher in the high-quality site ($49.9 \pm \text{SD } 14.4 \text{ m}^2 \text{ ha}^{-1}$ vs. $33.2 \pm \text{SD } 13.5 \text{ m}^2 \text{ ha}^{-1}$ in the low-quality site; $U=340$, $P < 0.001$). The maximum basal areas for the canopy tier were close to $80 \text{ m}^2 \text{ ha}^{-1}$ in the high-quality site and to $60 \text{ m}^2 \text{ ha}^{-1}$ in the low-quality site (Fig. 2 and Table 2). The basal area of emergent trees was also significantly higher in high-quality site ($U=715$, $P = 0.02$), with average basal areas of $27.4 \text{ m}^2 \text{ ha}^{-1}$ (SD 16.5) in the high-quality site and $20.3 \text{ m}^2 \text{ ha}^{-1}$ (SD 15.7) in low-quality site (Table 2). The maximum values reached in basal area for the emergent tier were 79.0 in the high-quality site and $56.0 \text{ m}^2 \text{ ha}^{-1}$ in the low-quality site (Fig. 2 and Table 2).

Effect of the basal area of emergent trees on total and canopy.

Increasing basal area of emergent trees was significantly related to increasing total basal area at both sites (Fig. 3). However, while the basal area of emergent trees in the high-quality site did not have a significant effect on the basal area of canopy trees ($r^2 = 0.002$, $P = 706$), in the low-quality site the increasing basal area of emergent trees depressed the basal area of canopy trees ($r^2 = 0.192$, $P = 0.003$) (Fig. 3). A significant slope was fitted for the regression model for the low-quality site ($\beta_1 = -0.37$, $P < 0.05$), but the slope was not significant for the regression model in the high-quality site ($\beta_1 = -0.01$; $P > 0.05$). Further details about model fitting and statistics can be seen in appendix S2.

Basal area of emergent tree species differentially affected the basal area of individual canopy species. Significant depressions ($P < 0.05$) in basal area occurred for *D. winteri* in the high-quality site and for both *L. philippiana* and *A. luma* in the low-quality site (Fig. 4). Basal area of *S. conspicua* was not significantly affected by basal area of emergent tree species in either site (Fig 4).

Discussion

In this study we evaluated whether the ABA effect occurred in two contrasting old-growth forests in terms of site quality, especially in regards to soil depth and fertility. The two sites were similar in species composition and stand structure, with an emergent tier of *N. nitida* and *W. trichosperma* above a canopy tier dominated by *L. philippiana*, *D. winteri*, *S. conspicua* and *A. luma*. The identical species composition of the emergent tier is an important variable since it ensures similar effects of this layer on the amount of light reaching the main forest canopy of more shade tolerant tree species (Enright and Ogden 1995). Although the proportion of each of the emergent species differed in each site, with more basal area of *N. nitida* in Quillaiepe and more of *W. trichosperma* in Yaldad (Table 2), their similar sparse canopy architectures provide enough confidence on the fact that the emergent tier generates a similar light interception to the lower canopy tiers. The high-quality site (Quillaiepe, within the Valdivian Temperate Rainforests Region in the Andes) had greater total basal area than the low-quality site (Yaldad, within the North Patagonian Rainforests Region in the Chiloé Island). In Quillaiepe increasing basal area of the emergent trees did not affect the accumulation of basal area among canopy tree species, which remained nearly constant with variable levels of basal area of emergent trees, while in Yaldad there was a negative relationship between basal area of each canopy tier, i.e., the basal area of canopy tree species was depressed by increasing basal area of the emergent tree species (Fig. 3). Therefore, this study supports our hypothesis that basal area of the emergent trees does not depress the basal area of its canopy associates in a high-quality site, but it does in a low-quality site.

There is also evidence that in other sites of relatively high quality among Chilean temperate rainforests the ABA phenomenon occurs. The ABA effect was reported in a large tract of old-growth forests forest with emergent *Nothofagus dombeyi* trees in the Andes of south-central Chile (Donoso and Lusk 2007). Also in an old-growth forest nearby Quillaiepe the ABA effect occurred, but we did not use this site in the present study since it has an additional tree species (*Eucryphia cordifolia*) that shares both the dominant and emergent canopy tiers (i.e., the

composition and canopy architecture of the emergent tier is different). From these studies it is possible to suggest that in stratified Andean forests from 39-42°S forests, which can be considered sites of good quality that support forests of high productivity (Donoso 1993), the ABA effect occurs. There are no previous studies or reports on competition between tree canopies farther south, where soils are even shallower and very nutrient poor (e.g. Innes 1992).

In spite of the differences in terms of ABA phenomenon in both sites, the exploration of the relationship of the BA of single tree species with the basal area of emergent trees showed that *D. winteri* had a depressed BA in the high-quality site, and both *L. philippiana* and *A. luma* in the low-quality site, while *S. conspicua* did not have any significant relationship between its basal area and that of the emergent trees in either site. Interestingly, in the Andean location farther north studied by Donoso and Lusk (2007), *S. conspicua* had its BA depressed, and *L. philippiana* did not, with increasing BA of the emergent *N. dombeyi* in this high-quality site. These differing effects of the basal area of the emergent canopy tier upon canopy trees presumably occur by a combination of species' traits and their natural ecological distributions. Both *L. philippiana* and *A. luma* are shade-tolerant tree species, the former adapted to eutrophic sites and the latter to mesotrophic sites, while both *D. winteri* and *S. conspicua* are midtolerant, the former adapted to oligotrophic sites and the latter to mesotrophic sites (Table 1). These species, like any species, perform better when growing in their preferred sites (ecological optimum) within their geographical distributions. Following the silvics of the major canopy species in the present study (Donoso 2006, Lusk et al. 1997) *S. conspicua* is within its ecological optimum, *D. winteri* and *A. luma* are in the northern margins of their ecological optimum in the Andes (Quillaipé), and *L. philippiana* is in the southern margin of its ecological optimum in Yaldad. Farther north in the study by Donoso and Lusk (2007), *L. philippiana* grows within its ecological optimum, while *S. conspicua* is in the northern tail of its natural distribution (Donoso et al. 1986), i.e. in the margin of its ecological optimum. Overall, the mechanism that eventually leads to the ABA effect is that the most important canopy species in a given ecosystem have a relatively high competitive

ability, which occurs within the region of their ecological optimum, in addition to having sufficient light that penetrates through the sparse and light canopies of emergent trees in forests with a rich vertical stratification. When site conditions become stressful, either because canopy species have a reduced competitive ability due to low-quality soils (*L. philippiana* and *A. luma* in Yaldad) or to less favorable climatic conditions within their natural distribution (*D. winteri* in Quillaipé and *S. conspicua* in the study by Donoso and Lusk (2007)), the ABA effect does not occur.

Several studies in high-quality sites have shown a strong complementary relationship between emergent trees with canopy associates (e.g., Enright 1982; Ogden 1985; Lusk 2002; Donoso and Lusk 2007). The present study suggests, however, that in low-quality sites the ABA phenomenon may not occur due to a strong belowground competition (size-symmetric competition) for canopy species better adapted to more fertile sites. Interestingly, this also suggests that if low-quality sites are dominated by tree species adapted to these sites, as it happens farther south in Chile with *Podocarpus nubigena* (e.g., Innes 1992), size asymmetric competition for light could become also the major determinant of the occurrence of the ABA phenomenon, as long as pioneers are able to reach emergent positions in the canopy. In low-quality sites strong intraspecific competition between functional groups could be explained by size-symmetric competition for belowground resources (Schwinning and Weiner 1998; Moreno-Chacon and Lusk 2004). For instance, below-ground resource-use partitioning may be influenced by interactions of functional groups. Tree species root traits (i.e., shallower or pivotal root systems) have a major effect on soil space partitioning among functional groups (Kelty 1989; Moreno-Chacon and Lusk 2004). In low-quality sites the interspecific competition for below-ground resources between functional groups might be intense, given the poor nutrient pool, as in soils with shallow rooting depth such as in Yaldad (Bannister and Donoso 2013). This competition for below-ground resources is greater for species adapted for fertile site conditions,

in this case especially for the eutrophic and deep-rooted *L. philippiana* in Yaldad, and leads to an overall canopy BA depression with increasing BA of the emergent tree species.

The old-growth successional stage in temperate forests is known for its large biomass accumulation (Keith et al. 2009), which reaches its maximum when scattered pioneer emergent species remain alive in the forest and above the canopy tier (*sensu* Borman and Likens 1979). This is usually a transient forest successional stage (Lusk 2002), since in the long-term pioneers are only able to remain in the forest as long as major disturbances allow them to persist in the system (e.g. Donoso and Lusk 2007). During this stage the ABA phenomenon may occur, albeit some times only to a certain limit or threshold of emergent basal area (Donoso and Lusk 2007; Lusk 2002), allowing larger biomass accumulation in these forests with complex forest structures as long as forest species are well adapted to local soil fertility conditions, thus facilitating resource-use complementarity (nutrients, water and light). These complex structures may increase productivity (Danescu et al. 2016; Donoso and Lusk 2007). For ecological (e.g., carbon storage, biodiversity) and productive (in biomass or volume) reasons, it seems interesting to conduct additional research in sites of differing quality and tree species of varied functional groups with contrasting ecological traits and site adaptability, which would aid in clarifying site-species interactions that determine the occurrence of the ABA phenomenon in temperate forests with complex structures.

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474 **Table 1.** Some autoecological features of the studied species of the evergreen old-growth forests.

Species	Family	Position in vertical profile	Tolerance to shade	Soil fertility requirements **	Life span (years)	Max height (m)	Max DBH (cm)	References*
<i>Nothofagus nitida</i>	Nothofagaceae	Emergent	Intolerant	Mesotrophic Oligotrophic	350	40	200	1, 2, 5, 7
<i>Weinmannia trichosperma</i>	Cunoniaceae	Emergent	Intolerant	Oligotrophic	400-730	40	197	1, 2, 3, 4, 7, 8
<i>Drimys winteri</i>	Winteraceae	Main canopy	Midtolerant	Oligotrophic	230+	30	104	1, 3, 4, 10
<i>Saxegothaea conspicua</i>	Podocarpaceae	Main canopy	Midtolerant	Mesotrophic	750	27	200	1, 5, 6, 7, 8
<i>Laureliopsis philippiana</i>	Monimiaceae	Main canopy	Tolerant	Eutrophic	657	30+	121	5, 6, 7, 8, 9, 10
<i>Amomyrtus luma</i>	Mirtacea	Main canopy Lower canopy	Very tolerant	Mesotrophic	200-300	20+	50	5, 6, 7, 8, 9

475 * 1. Donoso 1993; 2. Donoso et al. 1985; 3. Innes 1992; 4. Lusk 1999; 5. Donoso 2006; 6.
476 Gutiérrez and Huth 2012; 7. Bannister and Donoso 2013; 8. Lusk et al. 1997; 9. Armesto and
477 Fuentes 1988; 10. Soto and Donoso 2006; 11. Veblen et al. 1996.

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Table 2. Major dasometric characteristics (mean $\pm$ standard deviation, minimum and maximum) of the forests of Quillaipé and Yaldad for emergent and canopy species.

Species	Quillaipé			Yaldad		
	QSD*	Basal area $\pm$ SD**	%	QSD*	Basal area $\pm$ SD**	%
	(cm)	(min-max)		(cm)	(min-max)	
<i>N. nitida</i>	68.6	22.1 $\pm$ 15.7 (0-66.1)	28.6	62.9	8.3 $\pm$ 9.9 (0-38.6)	15.5
<i>W. trichosperma</i>	71.4	5.2 $\pm$ 7.8 (0-35.1)	6.7	70.7	12.0 $\pm$ 13.0 (0-49.5)	22.4
Mean emergent trees (min-max)	68.2	27.4 $\pm$ 16.5 (0.6-79.0)	35.3	66.8	20.3 $\pm$ 15.7 (0.4-56.0)	37.9
<i>Drimys winteri</i>	22.7	12.7 $\pm$ 8.5 (0.4-33.5)	16.4	35.8	12.6 $\pm$ 7.8 (0.4-28.9)	23.5
<i>Saxegotaea conspicua</i>	36.2	14.1 $\pm$ 8.5 (0.7-35.5)	18.2	62.0	10.1 $\pm$ 15.9 (0.8-62.6)	18.8
<i>Laureliopsis philippiana</i>	29.6	13.2 $\pm$ 10.5 (0.7-64.5)	17.1	34.6	4.9 $\pm$ 14.5 (0.1-41.1)	9.1
<i>Amomyrtus luma</i>	7.4	9.9 $\pm$ 5.0 (3.2-15.3)	12.8	19.1	5.6 $\pm$ 5.3 (0-25.7)	10.5
Mean of canopy species (min-max)	32.0	49.9 $\pm$ 14.4 (18.5-76.6)	64.6	37.8	33.2 $\pm$ 13.5 (9.8-62.8)	61.9
Mean per stand (min-max)	30.8	77.3-21.4 (42.5-118.9)	100	47.5	53.5 $\pm$ 15.6 (23.8-83.7)	100

*QSD: Quadratic Stand Diameter or the diameter of the tree of mean basal area. ** SD: standard deviation.

Figure legends

Fig. 1. Location of the old-growth forests studied in the high-quality site (Quillaipe) and the low-quality site (Yaldad) in southern Chile.

Fig. 2. Box-plot comparisons of basal areas for all species and within functional groups (emergent tree species and canopy tree species) at a high-quality site (Quillaipe) and low-quality site (Yaldad).

Fig. 3. Simple linear regression lines for total basal area (white dots) and basal area of canopy tree species (black dots) as a function of the basal area of emergent trees.

Fig. 4. Simple linear regression lines fitted for basal area of dominant canopy tree species as a function of basal area of emergent trees. Results of r^2 and p -values given in the right side of each graph for the high-quality site (above) and low-quality site (below).

499 **Fig. 1.**

500

501 Fig. 2.

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504 Fig. 3.

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507 **Fig. 4.**

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1 SUPPORTING INFORMATION

2 Appendix 1

3

4 Diameter distributions (with 10-cm intervals) for canopy tree species (white bars) and emergent tree
5 species (inserted graphs).

6

7 **Appendix 2**

8 Summary of the simple linear regressions (SLR) fitted on the effect of emergent basal area on 1) canopy,
9 and 2) total basal areas for each site condition. $\hat{\beta}_0$ is the intercept and $\hat{\beta}_1$ is the slope of the SLR, r^2 is
10 the coefficient of determination, and SEE is the standard error of estimation.

Site quality	Location	Response canopy layer	n	$\hat{\beta}_0$	$\hat{\beta}_1$	r^2	F-value	SEE
High	Quillaipe	Canopy	54	48.250***	-0.006ns	0.000	0.003ns	12.717
		Total	54	39.258***	0.961***	0.623	85.827***	13.463
Low	Yaldad	Canopy	42	37.862***	-0.376**	0.192	9.510**	12.287
		Total	42	37.868***	0.624***	0.396	26.26***	12.28

11 ns: not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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