


RESEARCH PAPER

Does water availability regulate biomass partitioning between trunk and branches?

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ABSTRACT

- The extent to which a vertical trunk is differentiated from its branches is a key trait for the architecture of trees and may affect interspecific relationships.
- In this study, we analysed the effect of soil water availability on biomass partitioning for *Nothofagus pumilio* by means of a nursery experiment. Juvenile trees were subject to three irrigation conditions: no irrigation, intermediate irrigation and high irrigation. Irrigation conditions emulated the mean precipitation of the most representative environments inhabited by *N. pumilio*.
- Changes in soil water availability modified the biomass partitioning patterns of trees. In comparison to the other two conditions, high irrigation caused: (i) a higher ratio of biomass partitioning to stems than roots; (ii) more trunk growth in relation to its branches; and (iii) more photosynthetic organs relative to the aboveground biomass. Trunk size relative to that of its most recent branches was not increased by water availability.
- Water availability may play a significant role in the capacity of *N. pumilio* for space occupation due to the effects on axis differentiation.

INTRODUCTION

One of the features that define the architecture of a plant is the extent of differentiation among the axes that build up the plant's branching system. Such differentiation is a key determinant of the ecological role of the plant in its environment (Poorter *et al.* 2006; Charles-Dominique *et al.* 2015). In the case of trees, the differentiation of the trunk, or vertical axis, from its branches is the main determinant of their architecture (Hallé *et al.* 1978) and modulates the dominance–suppression relationships between individuals (Charles-Dominique *et al.* 2012; Puntieri *et al.* 2013). Trees with a clear differentiation between trunk and branches may show faster height growth and would thus be able to reach the forest canopy earlier than trees of similar biomass but with a poorly differentiated vertical axis (Steconci *et al.* 2010; Hérault *et al.* 2011). Such differentiation may be numerically evaluated through the relationship between the size of branches and that of their bearing trunk, using biomass or other related variables such as stem diameter (Puntieri *et al.* 2013).

It has been shown that tree architecture may exhibit intraspecific variations between individuals growing under different environmental conditions (Hallé *et al.* 1978; Passo *et al.* 2002; Vennetier *et al.* 2013; Magnin *et al.* 2014). However, scientific evidence concerning the actual factors involved in architectural plasticity is lacking. Better knowledge on those factors involved in intraspecific architectural plasticity may improve our understanding of the effects of climate variations on plant structure, as well as plant–plant interactions. Because of the importance of water as a factor frequently limiting plant

growth (*e.g.*, Singer *et al.* 2012; Brunner *et al.* 2015), water availability could be considered as one important environmental factor modulating architectural traits in trees. Plant plasticity in response to changes in water availability is a central issue in ecological and physiological studies (Reynolds *et al.* 2004; Martínez Pastur *et al.* 2007; Lambers *et al.* 2008; Padilla *et al.* 2009; Peri *et al.* 2009), but information concerning the effects of water availability on the architectural plasticity of woody plants is scarce.

One of the perspectives employed in the scientific evaluation of the effects of resource availability on plant growth is that of the functional partitioning theory, which proposes that plants should allocate resources to increase their uptake of the resource that is most limiting to growth (Poorter *et al.* 2012). In environments where the dry period of the year matches the growing season, between-year changes in soil water availability due to variations in precipitation can have significant effects on resource partitioning (Reynolds *et al.* 2004; Padilla *et al.* 2009; Martínez Pastur *et al.* 2011). Plants would respond to variations in water availability by shifting the allocation of resources to different organs so as to maximise growth rate (Poorter & Nagel 2000 and references therein), which influences carbon sequestration and cycling (Binkley *et al.* 2004). However, most of the studies in support of this view have focused on annual plants and grasses (Sher *et al.* 2004; Maestre & Reynolds 2007). There is limited information about the effects of different water availability on the resource partitioning of woody plants beyond the seedling stage and under natural growth conditions. In woody plants, water resources can affect compartmentalisation and biomass partitioning not only between

aboveground and belowground organs, but also among the axis categories that make up aboveground and belowground branching systems (e.g., Singer *et al.* 2012; Brunner *et al.* 2015), thus playing a role in axis differentiation. Such differential partitioning of resources among axis categories, would allow a plant to adapt to new environmental conditions and modulate dominance–suppression relationships among plants (Charles-Dominique *et al.* 2012). For instance, those individuals that grow with higher soil water availability could dominate the tree canopy faster, as they would proportionally allocate more biomass to the trunk with respect to the branches.

In the present study we experimentally evaluated the effect of soil water availability on the biomass partitioning between stem and roots, and the differentiation of the trunk relative to branches for *Nothofagus pumilio* (Poepp. et Endl.) Krasser (known as 'lenga'), a tree species widely distributed in the temperate Andean forests of southern South America. Through controlled irrigation, we emulated the variations in water supply that normally occur in the most representative environments inhabited by *N. pumilio* (dry, mesic and moderately wet sites). Based on previous studies from temperate and mesic regions, we may predict that *N. pumilio* trees would allocate more biomass to stems relative to roots as water availability increases (Poorter & Nagel 2000; Lencinas *et al.* 2007; Padilla *et al.* 2009). Regarding axis differentiation, there is no experimental background on how water availability affects the architecture of *N. pumilio* trees. A previous study on *N. pumilio* indicates that trunk length and volume are higher in wetter areas such as valley bottoms or sites with abundant precipitation than in drier and more exposed areas (González *et al.* 2006; Stecconi 2006). It has also been pointed out that trunk forking through the development of co-dominant distal branches, which is related to the loss of trunk differentiation, is promoted in *N. pumilio* trees under drier or deeply shaded conditions (Stecconi 2006; Stecconi *et al.* 2010). We hypothesise that water availability plays a significant role in the partitioning of resources among axes in this species, increasing the size of the trunk relative to that of its branches.

MATERIAL AND METHODS

Study species

Nothofagus pumilio grows in the Patagonian Andes between 35°35' S and 55°31' S along diverse environmental conditions (González *et al.* 2006). At the southern end of its distribution, mean annual temperature is around 6 °C and precipitation is evenly distributed throughout the year; in more northern regions of its range, rainfall is concentrated in autumn–winter and mean annual temperature is close to 12 °C at lower elevations (Villalba *et al.* 1997; Conti 1998). The present study was carried out at 41° S where the total annual precipitation decreases along a west-to-east gradient, reaching 4,000 mm in western, Chilean areas, and around 500 mm in the eastern border limiting the Patagonian steppe (Conti 1998). However, at this latitude most *N. pumilio* is distributed between 800 and 1,800 mm isohyets (De Fina 1972; González *et al.* 2006). The altitudinal range of *N. pumilio* at this latitude (between 1,000 and 1,800 m a.s.l.) encompasses significant variations in temperature and precipitation (Rusch 1993; Villalba *et al.* 1997). *N. pumilio* grows on different soil types, but predominantly on

those of volcanic origin (trumaos; Gerding & Thiers 2002). The morpho-architectural variations of this species could be related to phenotypic (Barrera *et al.* 2000; Stecconi *et al.* 2010) and/or genetic factors (Premoli *et al.* 2004, 2007). Spontaneous regeneration of *N. pumilio* is commonly observed in canopy gaps (González *et al.* 2006).

Experimental design

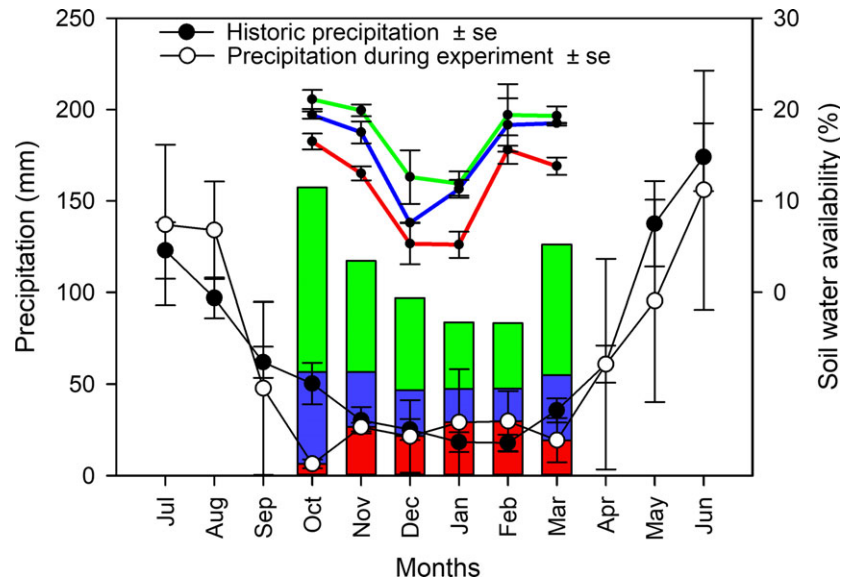
The study was conducted on 5-year-old *N. pumilio* plants derived from seeds collected from different natural populations in the Chubut Province of Argentina (42°50'–44°53' S, 71°10'–71°40' W). These specimens, about 90 cm tall and 12 mm in diameter (Table 1), had been raised in pots at the tree nursery of the Instituto Nacional de Tecnología Agropecuaria, INTA, Bariloche (41°07' S, 71°14' W, 790 m a.s.l.). This site is located near the eastern limit (dry) of the natural range of this species. We selected an area of 13 m² located under the canopy of 7-m tall juvenile and adult *N. nervosa* and *N. obliqua* trees that were at least about 5 m from one another. This canopy provided an intermediate level of shading (canopy opening between 44% and 46% for all treatments was determined using hemispherical photographs analysed with the GLA program), in an attempt to emulate those canopy conditions under which *N. pumilio* regenerates in native forests. Precipitation in the area is similar to that recorded for areas at the same latitude where natural regeneration of *N. pumilio* occurs (Heinemann *et al.* 2000). Six 1.2 m × 1.8 m plots were established in a row. The plots were separated from each other and from the surrounding soil with phenolic panels that were buried 80 cm in the ground. Each panel was placed protruding 10 cm above ground level to prevent water flow between plots. Soil characteristics in the plots were similar to those derived from volcanic ash deposition (N: 0.24%; Organic matter: 5.7%; P: 10 mg kg⁻¹; K: 244 mg kg⁻¹; Electric conductivity: 0.6 ds m⁻¹; pH-H₂O: 6.2; pH-sodium fluoride: 9.7; Ferrari 2010). Ninety specimens of *N. pumilio* without obvious signs of damage were selected and planted in the plots in winter 2009. In each plot, 15 randomly selected individuals of *N. pumilio* were planted in five rows with three individuals each (minimum distance between trees = 30 cm).

In October 2010 three water supply regimes were established. Each condition was assigned to two non-contiguous plots (*i.e.*, 30 plants per treatment). These conditions were as follows: (I) no irrigation (or control); water supply depended exclusively on precipitation; (II) intermediate irrigation, precipitation during the experiment supplemented by an amount of water equivalent to the mean local precipitation; and (III) high irrigation, precipitation during the experiment supplemented by twice the mean local precipitation (Fig. 1). Conditions II and III emulated, respectively, precipitation in mesic and moderately wet sites during the growing period of *N. pumilio*

Table 1. Initial traits of the *Nothofagus* surveyed for the three treatments. Values represent mean ± 1 SE. N = 30 for each treatment.

treatment	height (cm)	diameter (mm)
no irrigation	94.8 ± 5.8	12.1 ± 0.5
intermediate irrigation	94.2 ± 7.6	11.9 ± 0.5
high irrigation	91.1 ± 6.6	12.1 ± 0.6

Fig. 1. Precipitation, water supply and soil water availability of the study system. Monthly total precipitation from INTA-Bariloche weather station: over the period 1981–2009 (continuous black line and black dots, mean \pm SE) and over treatment period 2010–2012 (dashed black line and white dots, mean \pm SE) are indicated. Colour bars show mean water supply (as equivalent of rainwater) for each treatment (red: no irrigation, blue: intermediate irrigation, green: high irrigation). The curves of soil water availability are indicated for the period in which water was supplied.



(October–March). To estimate the amount of water to be added in conditions II and III, we used the mean precipitation record from the weather station at INTA-Bariloche over the last 30 years (~ 800 mm annual precipitation, *i.e.*, a relatively dry site for *N. pumilio*). From 2010 to 2012, plants were irrigated through the growing season (6 months every year) at 14- and 7-day intervals for conditions II and III, respectively, so that, by the end of the growing season, they had received approximately 200 and 400 mm more water than plants in condition I (Fig. 1). To check whether the water supply treatments were actually modifying water availability, predawn leaf water potentials (obtained with a pressure chamber, PMS 1000; PMS Instruments, Corvallis, OR, USA) were measured for the three treatments in the period of greatest drought in the growing season. These water potentials (no irrigation: -1.8 MPa, intermediate irrigation: -0.96 MPa, high irrigation: -0.57 MPa), agreed with bibliographic records for the same species under different water regimes (Peri *et al.* 2009).

Measurements

In May 2012 (after complete leaf shedding), two growth seasons after establishing the irrigation experiment, all plants were harvested. The roots were dug up carefully with spades, rakes and brooms, so as to minimise damage to fine roots. The annual shoots that were developed on the trunk of each plant in the 2010–2011 and 2011–2012 growth seasons were identified using morphological markers widely used in *Nothofagus* spp.: cataphyll scars and main branch positions (Barthélémy *et al.* 1999). For the trunk annual shoot developed in 2010–2011, the number of leaves (counted based on scars left by the leaf petiole on the stem after leaf abscission) and the axillary production (presence or absence of branch) at each node were recorded (Fig. 2a). Basal stem diameters were measured for the most distal shoot of the trunk and each of the most recently developed branches (those extended in 2011–2012) using digital calipers (Fig. 2a). For the belowground structure, we measured lengths and basal diameters of at least ten secondary roots (*i.e.*, those derived directly from the major root; Fig. 2a);

each major root had 14.5 ± 0.1 (mean \pm SE) secondary roots. In two secondary roots per plant, we measured the number of tertiary roots on a 10-cm long distal segment (Fig. 2d).

To obtain a proxy for soil water availability, we took one sample per plot every week during the experimental period (about 10 cm below ground level). For each sample, we calculated the gravimetric water content (%) corresponding to each treatment by measuring the weight of a soil sample before each watering, and re-measuring its weight after drying the sample at 105°C for 48 h.

The extent of differentiation of the trunk distal end relative to its branches was evaluated with two variables. The first one took into account the size of all branches arising from the trunk in the 2011–2012 growth period, relative to the size of the trunk's distal shoot developed in the same period. This variable (relative size of summed branches, RSB_{sum}) was calculated for each tree with the equation (Fig. 2b i):

$$RSB_{sum} = \frac{\sum \text{diameter lateral branches}}{\text{diameter of trunk apex}}$$

The second variable was computed as the ratio between the size of the largest branch (in terms of stem diameter) developed from the trunk in 2011–2012, and the basal stem diameter of the trunk's distal shoot (RSB_{max} ; Fig. 2b ii):

$$RSB_{max} = \frac{\text{largest branch diameter}}{\text{diameter of trunk apex}}$$

These two variables would provide different perspectives on trunk differentiation, despite the fact that high values of both RSB_{sum} and RSB_{max} would indicate low differentiation of the trunk relative to its branches. High RSB_{sum} values would indicate the development of a large branching system in relation to the trunk apex (*i.e.*, the trunk's annual shoot), whereas high values of RSB_{max} would, unlike RSB_{sum} , reflect a tendency towards the formation of a branch, which, judging by its size would compete with the trunk apex for dominance.

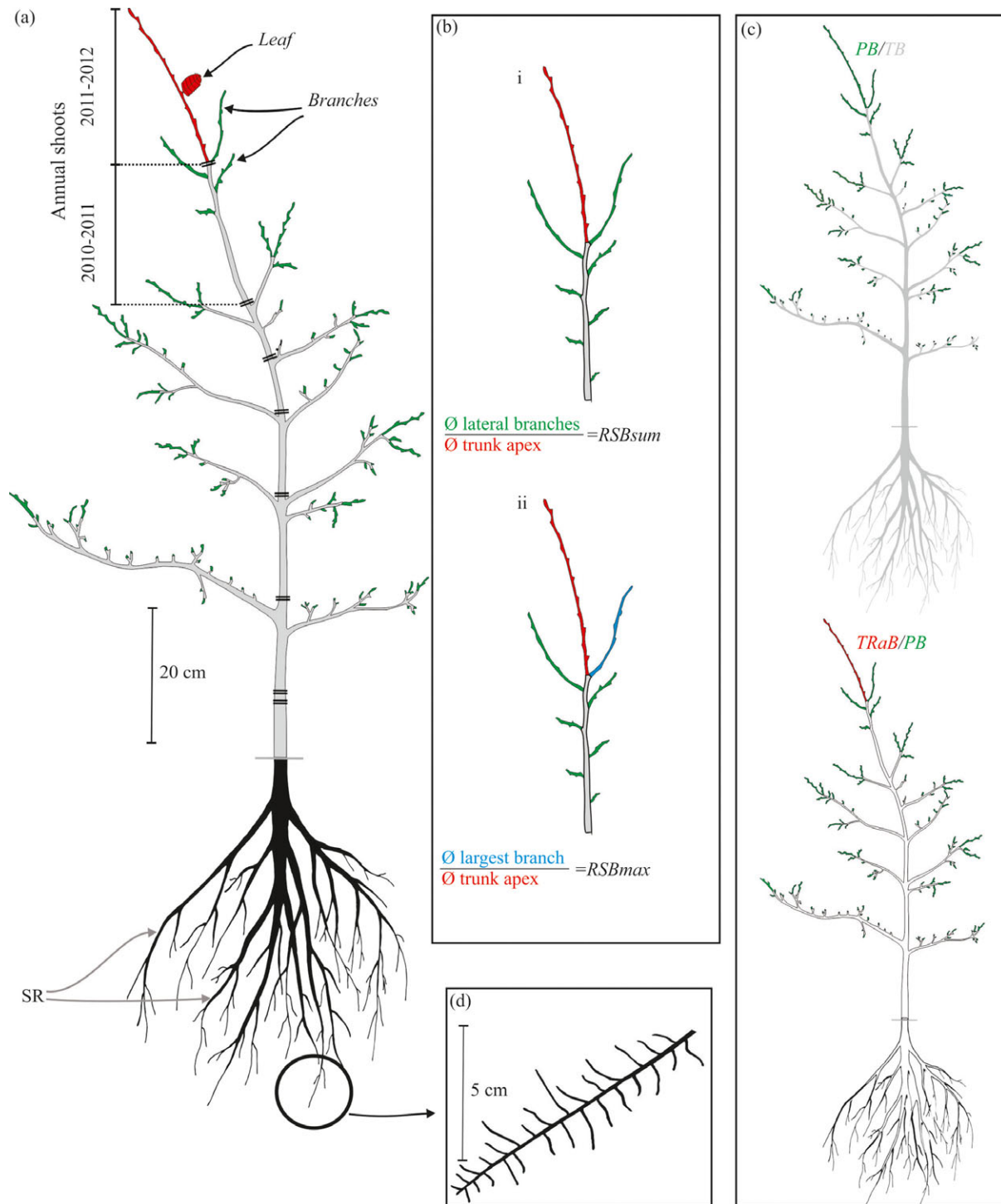


Fig. 2. a: Diagram of a juvenile *Nothofagus pumilio* tree similar to those used in this experiment. b: Details of a parent shoot of the trunk (grey) with a recent trunk shoot in distal position (red) and a simultaneously developed set of branches (green and blue); RSB_{sum} : ratio between the sum of diameters of all branches arising from the parent trunk shoot and diameter of the distal trunk shoot developed in the same period; RSB_{max} : ratio between diameter of the lateral branch with the largest diameter (blue) and diameter of the distal trunk shoot. c: PB/TB : relationship between total primary growth biomass and total plant biomass; $TRaB/PB$: relationship between trunk apex and primary growth biomass. d: Detail of a branched secondary root. Double horizontal black lines in (a) indicate the limits of inter-annual annual shoots. SR: secondary roots.

Each plant was divided in the following compartments: (i) annual shoot of the trunk developed in the 2011–2012 growth season, (ii) all annual shoots of the 2011–2012 growth season

excluding that of the trunk, (iii) all aboveground axes excluding shoots extended in the 2011–2012 growth season, and (iv) roots (Fig. 2). Each compartment was dried at 60 °C to

constant weight. We obtained the following dry biomass compartments: $TRaB$ = trunk apex biomass (*i.e.*, biomass of annual shoot developed in 2011–2012), PB = primary growth biomass, which included all shoots developed in the 2011–2012 season, AB = aboveground plant biomass, BB = belowground biomass (root biomass), and TB = total plant biomass. In this study ‘compartmentalisation of the dehydrated biomass’ is used with reference to the absolute amount of dry biomass in each type of organ, and ‘partitioning’ to the amount of biomass present in one or more organs in relation to the total biomass of the plant or the biomass in all other compartments. The following ratios were computed: BB/AB : biomass partitioning to roots relative to the stem; PB/TB : biomass partitioning to primary growth in 1 year relative to total plant biomass; $TRaB/PB$: biomass partitioning to the trunk primary growth in 2011–2012 relative to the biomass assigned to the entire primary growth in the same period (Fig. 2c).

Statistical analyses

The RSB_{sum} , RSB_{max} , root, compartmentalisation and biomass partitioning variables were compared between the three irrigation conditions using one-way ANOVA (with water availability as fixed factor), followed by *a posteriori* comparisons with Holm-Sidak tests. Due to non-homoscedasticity of the data, RSB_{sum} was evaluated using the `varIdent` function from the `nlme` package in R (R Development Core Team 2014), followed by Tukey tests. The relationships BB/AB , PB/TB and $TRaB/PB$ were log-transformed to adjust data to normal distributions. A 5% error probability was adopted in all comparisons.

RESULTS

The RSB_{sum} was significantly higher for plants in condition III than for those in conditions I and II ($F = 17.3$, $P < 0.001$); the frequency distribution of this variable was notably right-skewed for condition III, but not for the other two conditions (Fig. 3a). RSB_{max} was similar between conditions in both mean and distribution outline ($F = 2.5$, $P = 0.09$; Fig. 3b). The most vigorous branch was similar to or slightly smaller than the trunk apical shoot, which resulted in high frequencies of RSB_{max} of between 0.8 and 1.1. The number of leaves in the trunk apical shoot was lower for individuals in conditions I and II than for those in condition III. The frequency distribution for the number of leaves per trunk shoot was more right-skewed in plants under condition III than under conditions I and II (Fig. 3c).

The biomass of shoots developed in the 2011–2012 growth season (*i.e.*, primary growth) increased with water supply, both for the trunk ($TRaB$) and for the whole tree (PB ; Fig. 4a,b). In contrast, total aboveground biomass (AB) and belowground biomass (BB) were not affected by water supply (Fig. 4c,d). The $TRaB/PB$ ratio was higher for individuals under high than low water supply (Fig. 4e). The PB/TB ratio increased with water supply (Fig. 4f). BB/AB was higher for plants in condition I than in conditions II and III (Fig. 4g).

The length and diameter of secondary roots were maximum in plants of condition III, intermediate in plants of condition II, and minimum in those of condition I (Fig. 5a,b). Secondary roots of non-irrigated plants developed more tertiary branches

at their distal end than those of plants that received additional water supplies (Fig. 5c).

DISCUSSION

Resource partitioning and trunk differentiation in woody plants

Morphological differentiation between axes is a key determinant of tree architecture and affects use of the aerial space by the crown (Hallé *et al.* 1978; Barthélémy & Caraglio 2007). In particular, the development of a clearly differentiated vertical axis or trunk in many tree species contributes to establish size hierarchies among trees in a population or community (Stevens & Perkins 1992). Axis differentiation is considered as linked to variations in resource allocation to the structural units that make up plant axes (Charles-Dominique *et al.* 2012). However, there is no general agreement as to how axis differentiation should be numerically evaluated. In this study, we employed two approaches for such evaluation. The first one focused on the compartmentalisation of primary growth in different types of axes at the whole plant level, whereas the second focused on the size of the distal branches relative to the size of their bearing trunk shoot. In turn, for the latter approach we proposed two quantitative relationships by considering either the summed size of all branches arising from the trunk, or only the size of the largest branch developed from the trunk.

Our analysis based on primary growth at a whole plant level supports the idea that a larger water supply during the growth season increases the size of the trunk relative to that of all other tree axes. As different water conditions did not affect tree biomass, the effect of water supply on trunk differentiation at the whole plant level may not be linked to a possible allometric relationship between trunk size and plant size. Similar observations have been recorded in other species subject to different water availability regimes within the same (Lencinas *et al.* 2007) and other habitats (Padilla *et al.* 2009; Pizarro & Bisigato 2010).

The results of the present study based on the distal part of the trunk show that the summed size of the distal branches of the trunk relative to the size of the distal trunk shoot (*i.e.*, high value of RSB_{sum}) was higher in plants under the highest water supply than in those under low or intermediate water supply. It is noteworthy that the dispersion of RSB_{sum} was also higher in the former than in the other two conditions. Such differences in RSB_{sum} among conditions would have a morphogenetic basis. In *N. pumilio*, each newly extended shoot includes a set of leaves that had remained as leaf primordia in winter buds until spring, *i.e.*, preformed leaves (on average 16 leaves for the trunk of juvenile trees; Souza *et al.* 2000). Sometimes, simultaneous differentiation and extension of additional leaves – known as neoformed leaves – take place after preformation extension in late spring or early summer (Barthélémy *et al.* 1999). As the number of preformed leaves in *N. pumilio* winter buds is defined in the autumn preceding bud break (Souza *et al.* 2000), and the watering treatments started at the beginning of the 2010–2011 growth season, in spring, plants under all three water conditions must have had similar average numbers of preformed leaves. Consequently, differences in number of leaves of the distal trunk shoot and RSB_{sum} linked to the level of water availability should be linked to variations

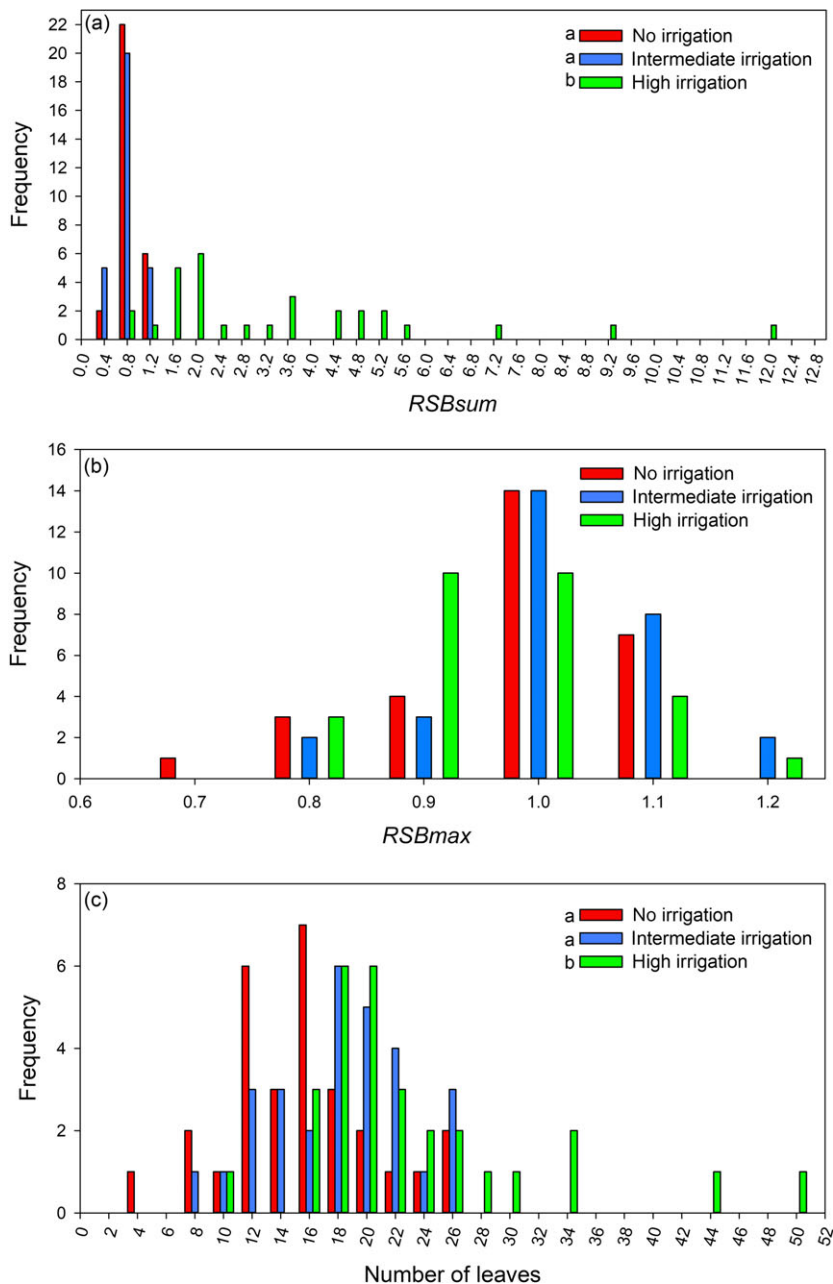


Fig. 3. Relative frequency distribution of: a: relative size of branches (RSB_{sum}), b: relative size of largest branch (RSB_{max}) and c: number of leaves produced by the trunk distal shoot. Different lowercase letters to the left of each legend reference indicate that the mean values are statistically different ($P < 0.05$).

in the development of neoformed organs, both in the distal trunk shoot and in the distal trunk branches. Further support for this idea is provided by the higher degree of skewness of the number of leaves of trunk shoots and RSB_{sum} in plants under high water supply, as the number of neoformed organs developed by annual shoots of woody species usually exhibits a more skewed and scattered distribution than the number of preformed organs, as neoformation proceeds in a step-wise fashion (Guédon *et al.* 2006). It is interesting to notice that both the RSB_{sum} and the number of leaves of the distal trunk shoot were similar between plants with intermediate and low water availability, which suggests that a threshold level of water availability should be reached for the neoformation process to be triggered. The development of neoformed leaves at the distal end of the trunk (including the distal trunk shoot and distal

branches) could be beneficial in terms of light interception. Thus, our results provide support for the long-standing but little supported idea that neoformation is an opportunistic strategy to take advantage of unforeseen favourable conditions for growth (Sabatier *et al.* 1999; Guédon *et al.* 2006).

Contrary to our expectations, trunk forking (measured by RSB_{max}) did not decrease with increasing water supply. Apparently, more water supply favours, to a similar extent, the development of the shoot engaged in trunk length growth, and that of the most vigorous distal branch, so that the co-dominance between these two axis types is kept constant. It has been observed that trunk forking in *N. pumilio*, as in other *Nothofagus* species, increases with tree age (Barthélémy *et al.* 1999) and also depends on light conditions (Steconni *et al.* 2010); for instance, trunk forking is more frequent in understorey than in

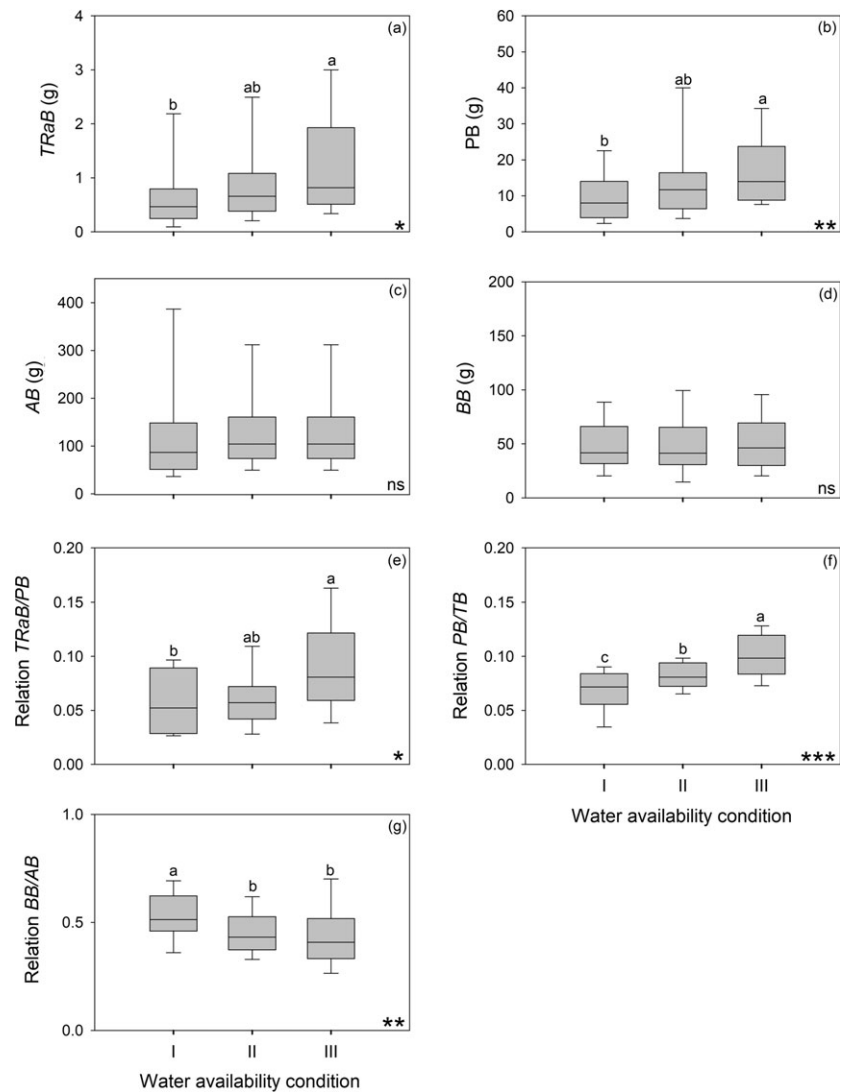


Fig. 4. Effect of soil water availability on compartmentalisation and partitioning of biomass in *Nothofagus pumilio* according to water availability condition: I without irrigation, II intermediate irrigation, III high irrigation (see text for details). $TRaB$ trunk apex biomass, PB primary growth biomass, AB total aboveground biomass, BB total belowground biomass, TB total biomass. Statistical differences between treatments are indicated with different letters and significance levels in the lower right corner of each graph (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns $P > 0.05$). Box and whiskers represent 10th, 25th, median, 75th and 90th percentiles.

gap-dwelling trees (Puntieri *et al.* 1999; Stecconi *et al.* 2010). A similar pattern has been observed for other tree species (Delagrè *et al.* 2006; Charles-Dominique *et al.* 2012; Puntieri *et al.* 2013). It may be proposed that light would be a key factor in the differentiation between the trunk and its most distal branches. Other environmental factors positively correlated with light availability, *e.g.*, exposure to wind, snow accumulation and soil erosion, may have a counteracting effect on trunk differentiation (Villalba *et al.* 1997; Wardle 1998); the genetic composition of trees that establish under different sets of environmental conditions could also play a role in intraspecific architectural variations (Premoli *et al.* 2004, 2007).

Resource partitioning and water supply

In woody species growing under markedly seasonal climates, such as *N. pumilio*, it is possible to differentiate the annual shoots that are formed in a particular year as a result of primary growth (Passo *et al.* 2002; Magnin *et al.* 2014). In *N. pumilio*, as in other deciduous species, primary growth in one growth season provides the origin for all the leaves present

in the plant in that period. Consequently, the dry weight of shoots developed in the most recent growth season may be used as an estimate of the photosynthetic activity in that season, and the PB/TB ratio can be interpreted as a measure of the relative biomass partitioning to leaves. This is supported by a number of studies showing that the allometric relationship between leaf mass and stem + root mass does not change with plant size (Poorter & Nagel 2000). In this sense, the high correlation between $TRaB$ and number of leaves per trunk shoot found here ($r = 0.70$, $P < 0.001$) provides support for this idea. Following these assumptions, our results would indicate that low water availability limits the development of leaves, and therefore the evaporative area of *N. pumilio* trees. However, measurements of leaf area and biomass in plants under different water treatments would be necessary in order to provide robust evidence for this idea. Thus, the PB/TB ratio supports the functional equilibrium theory proposed by Poorter & Nagel (2000), which predicts larger relative biomass allocation to the photosynthetic system when water is not the limiting factor.

In our study, neither above- nor belowground biomass in *N. pumilio* trees was affected by water availability, which

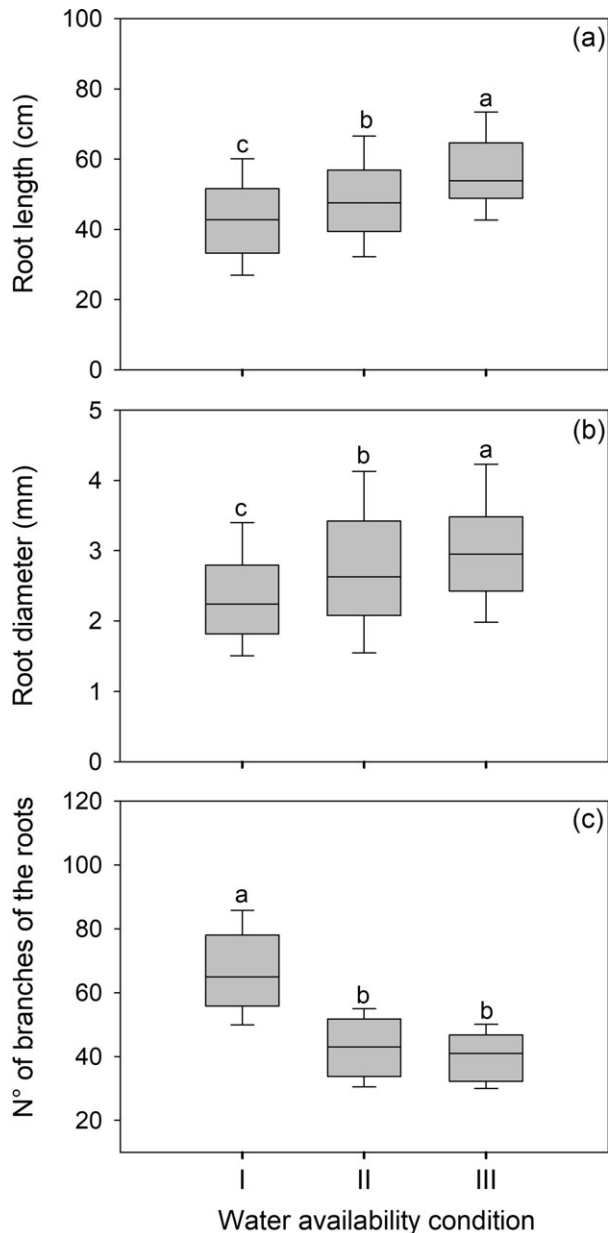


Fig. 5. Effect of soil water availability (conditions I, II and III) on length (a), diameter (b) and number of distal branches (c) of *Nothofagus pumilio* secondary roots. Statistical differences between water availability conditions are indicated with different letters on top of the bars. $P < 0.001$ for all comparisons. Box and whiskers represent 10th, 25th, median, 75th and 90th percentiles.

could be related to the inertial effect of similar growth conditions for the 5-year period prior to the experiment. However, and despite this inertial effect, biomass partitioning to roots relative to stems (BB/AB) was larger in plants growing

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with lower water availability, in agreement with many previous studies (Poorter & Nagel 2000; Ammer 2003; Padilla *et al.* 2009; Poorter *et al.* 2012; Brunner *et al.* 2015). For other species of *Nothofagus* from Patagonia it has been observed that plants allocated more biomass to roots than to shoots when site quality was low in terms of water (Gargaglione *et al.* 2010) and nutrient availability (Peri *et al.* 2006; Agüero *et al.* 2014). On the other hand, the interaction between water and light availability, may impose some limitations to the resource partitioning of *N. pumilio* (Lencinas *et al.* 2007). Seedlings of *N. pumilio* may increase their photosynthesis rates with canopy opening as long as water is not limiting. When light increases and soil moisture becomes a limiting factor (predawn leaf water potential less than -1.7 MPa), the photosynthetic response of *N. pumilio* seedlings is reduced (Peri *et al.* 2009). In this sense, it could be expected that biomass partitioning to shoots with respect to roots, and to the trunk apex with respect to other axes, increases with light availability as long as water is not a limiting factor.

In the present study secondary roots of *N. pumilio* were shorter and thinner, but had more branches in plants subject to lower water supply. Shorter and more branched roots would increase the absorption capacity of water and nutrients in the soil volume that is already occupied by the plant, with a reduced cost in terms of root mass per unit area (Chapin *et al.* 1987; Wright & Westoby 1999; Lambers *et al.* 2008). This may indicate that the response of *N. pumilio* to water shortages involves more intensive soil exploitation rather than extensive soil exploration.

CONCLUSIONS

Our results show significant architectural changes in *N. pumilio* trees after 2 years of experimental conditions with different water availability. Soil water levels as high as those in *N. pumilio* wet forests contribute to increase: (i) biomass partitioning to stems relative to roots, (ii) primary growth of the trunk relative to other axes, and (iii) primary growth of all stems relative to total biomass. Although the level of differentiation of the trunk apex relative to its distal branches seems to be rather reduced when water availability is high, the development of larger shoots at the distal end of the trunk would provide better conditions for future growth in a competitive environment.

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