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Allometric relations for biomass partitioning of *Nothofagus antarctica* trees of different crown classes over a site quality gradient

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ABSTRACT

Data on tree biomass are essential for understanding the forest carbon cycle and plant adaptations to the environment. We determined biomass accumulation and allometric relationships in the partitioning of biomass between aboveground woody biomass, leaves and roots in *Nothofagus antarctica*. We measured above- and belowground biomass of *N. antarctica* trees across different ages (5–220 years) and crown classes (dominant, codominant, intermediate and suppressed) in three site qualities. The biomass allocation patterns were studied by fitting allometric functions in biomass partitioning between leaves (M_L), stem and branches (M_S) and roots (M_R). These patterns were tested for all pooled data and according to site quality and crown classes. Biomass accumulation varied with crown class and site quality. The root component represented 26–72% of the total biomass depending on age and site. *N. antarctica* scaling exponents for the relationships M_L *vs.* M_S, M_A *vs.* M_R, and M_S *vs.* M_R were close to those predicted by the allometric biomass partitioning model. However, when biomass allocation was analyzed by site quality the scaling exponents varied following the optimal partitioning theory which states that plants should allocate more biomass to the part of the plant that acquires the most limiting resource. In contrast, the crown class effect on biomass partitioning was almost negligible. In conclusion, to obtain accurate estimations of biomass in *N. antarctica* trees the allometric approach appears as an useful tool but the site quality should be taken into consideration.

1. Introduction

Nothofagus antarctica (ñire) is one of the most common native species of the Patagonian forest (Argentina) that extends from 46° to 56°S. It grows on a variety of sites and reaches heights up to 20 m on the best sites (Donoso et al., 2006), but on poorly drained or drier sites near Patagonian steppe, it grows as a shrubby 2–3 m tall tree (Veblen et al., 1996). Patagonian forests occupied by ñire have been used for wood extraction (firewood, poles) and in silvopastoral systems, where natural pastures grown under the tree canopy are grazed by cattle and sheep (Peri, 2005).

Data on tree biomass are essential for evaluating carbon sequestration and cycling (Brown and Lugo, 1982; Dixon et al., 1994; Binkley et al., 2004), plant adaptations to the environment (Bradshaw, 1965; West-Eberhard, 2003) and also for studying impacts of silvicultural practices on forest productivity (Johnson and Todd, 1998; Santa Regina, 2000). Many factors like tree age, crown class (i.e. dominant, suppressed and intermediates) and site quality may influence tree biomass accumulation (Wang et al., 1996; Binkley, 2004; Peri et al., 2006; Castilho et al., 2006). While age and site effects have been more studied (i.e., Wang et al., 1996; Rapp et al., 1999) not many studies have quantified the crown class effects on biomass accumulation, in spite of large differences found between dominant and suppressed trees. For example, Peri et al. (2006) reported a series of functions for total biomass accumulation in *N. antarctica* where the total biomass of dominant 160 years old trees grown on a medium quality site was 336 kg tree^{-1}, whereas suppressed trees only had 47 kg tree^{-1}. Also, Le Goff and Ottorini (2001) reported large differences in belowground biomass accumulation between crown classes of *Fagus sylvatica*. Belowground components are not often evaluated due to the great complexity in extracting and studying roots, especially for large individuals. However, roots may account for a significant proportion of tree biomass and carbon storage (Kurz et al., 1996; Cairns et al., 1997; Peichl and Arain, 2007). Another important aspect of forest ecology is biomass allocation, which examines how plants distribute their resources to different plant organs (stems, leaves, and roots). Some authors (i.e., Huxley and Teissier, 1936; Hunt,

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1990; Müller et al., 2000) postulated that consistent allometric relationships exist among the different organs of the plant. According to this theory, biomass allocation is mainly governed by the size of the plant and is determined by a power function of the form $Y_1 = \beta Y_2^{\alpha}$, where Y_1 and Y_2 are interdependent variables (i.e. stem mass and root mass), β is the allometric constant, and α is the scaling exponent. This exponent, also named the allometric coefficient (Hunt, 1990), determines how the root-to-shoot ratio changes with plant size. When $\alpha = 1$ the model describes an isometric relation, i.e. one that plots as straight line on both linear and logarithmic axes, and when $\alpha \neq 1$ the model describes an allometric relation, i.e., one that plots as a linear function only on logarithmic axes. Later, Niklas and Enquist (2002) postulated "the canonical rules" to explain general allocation patterns in plants. These rules predict that, after the logarithmic transformation of biomass data ($\log Y_1 = \log \beta + \alpha \log Y_2$), the standing leaf biomass scales as 3/4—power of stem (or root) biomass ($\alpha = 0.75$) and that the stem scales isometrically ($\alpha = 1$) with respect to roots (West et al., 1997; Niklas and Enquist, 2002; Enquist and Niklas, 2002). An important characteristic of these scaling relationships is that they appeared to be insensitive to environmental conditions such as latitude, precipitation and temperature (Cheng et al., 2007). The only parameter which varies according to the species is β, which permits to estimate the absolute biomass of different tree components (Enquist and Niklas, 2002). However, while these rules have been derived from a large compendium of standing tree biomass, Robinson (2004) postulated that they are not universally applicable and that there is a large discrepancy between measured and predicted root biomass in forests ecosystems. Another popular theory for biomass allocation is the "optimal partitioning theory" which postulates that the environmental conditions are the major determinants of the root-to-shoot ratio (Thornley, 1972; Bloom et al., 1985). According to this theory, plants preferentially allocate biomass to the organ that is harvesting the most limiting resource. This means that, depending on the environment where plants grow, biomass allocation will favor leaves and branches if light becomes more limiting and will favor roots if nutrients or water becomes limiting. This prediction would represent an apparent contradiction to the allometric theory, which states that the root-to-shoot ratio is mainly regulated by the total size of the plant, following a scale relationship characteristic of each species (Müller et al., 2000). For many species, the root-to-shoot allometric coefficient predicts that small plants, either because they are young or they are under the influence of any factor that limits growth, have a greater proportion of roots than older or non-stressed plants.

On the other hand, research efforts focused towards predicting belowground biomass based on aboveground components will help to uncover the common gap in ecological studies of lack of root biomass data. In this sense, allometrics would be a useful tool to predict belowground biomass from aboveground data. In this context, we studied the biomass accumulation and allocation of *N. antarctica* to answer three main questions: (i) does *N. antarctica* follow allometric patterns of biomass allocation? (ii) Do these patterns follow the canonical rules proposed by Niklas and Enquist (2002)? (iii) Do the crown class and site quality influence on the biomass allometric patterns? To answer these questions, the aim of this study was to evaluate the allometric theory across an age sequence of individual *N. antarctica* trees of different crown classes grown in a site quality gradient in the Southern Patagonia forests.

2. Methods

2.1. Study area

This study was carried out in pure stands of *N. antarctica* of the Southern West Patagonia forest, Argentina. Three different site qualities (i.e., site classes) from these forests were selected following the Lencinas et al. (2002) classification. High, medium and low qualities were represented by site classes III, IV and V respectively, according to the classification from these authors. For site class III (SC III) (51°13′21″S, 72°15′34″W), the total height of dominant mature tree (*H*) reached 10 m; in site class IV (SC IV) (51°34′S, 72°14′W), H reached 7.8 m and site class V (SC V) (51°40′59″S, 72°15′56″W) represented a marginal site which was drier, exposed to strong winds and with rocky soils, where *H* reached 5.3 m. Regional climate is cold temperate. Climatic characteristics from each site were derived from the WorldClim data set (Hijmans et al., 2005) (Table 1). The SC III has the highest mean annual precipitation (563 mm/yr) and the lowest mean annual water deficit (−422.4 mm/yr). In the other extreme, the worst site class (SC V) has the lowest annual precipitation (335 mm/yr), the highest evaporation value (1512.4 mm/yr) and consequently, the highest mean annual water deficit (−1177.4 mm/yr) (Table 1). For soil analysis, at each site class 30 bulked soil sample cores were taken at random from different depths (Table 1). All sites had around 50% of sand and the maximum rooting depth ranged from 0.6 m in the SC III to 0.5 m in SC V (Table 1). Soil nutrient concentrations were similar between sites with exception of P and Mg which were higher in SC IV and Ca in SC III (Table 1).

Table 1
Climate and soil characteristics from sites of high, medium and low qualities (SC III, IV and V, respectively) studied for *N. antarctica* stands.

Soil characteristics	Site class III Mean annual *T*: 5.9 °C Annual pp: 563 mm Evaporation: 985.4 mm/yr MAWD: −422.4 mm/yr[a]			Site class IV Mean annual *T*: 5.4 °C Annual pp: 422 mm Evaporation: 1210.1 mm/yr MAWD: −788.1 mm/yr			Site class V Mean annual *T*: 5.0 °C Annual pp: 335 mm Evaporation: 1512.4 mm/yr MAWD: −1177.4 mm/yr		
Depth (cm)	5–20	20–40	40–60	1–5	5–20	40–60	1–5	5–20	40–50
Clay (%)	8.0	8.2	14.5	–	20	20	–	26.0	25.0
Silt (%)	36.2	35.9	24.7	–	30	60	–	22.5	19.9
Sand (%)	55.8	55.9	60.8	–	50	20	–	51.5	55.1
pH	4.8	4.8	4.6	6.1	4.8	4.8	5.6	4.7	4.5
Resistance (ohm cm)	7695	10,764	13,226	4170	8800	5810	5430	7690	10,445
N total (ppm)	5985	3320	2272	8670	880	460	5190	2810	1890
P trough (ppm)	23.5	10.7	10	129	12	6	66	25	6
K ($\text{cmol}^+ \text{kg}^{-1}$)	0.37	0.2	0.4	4.2	0.3	0.1	1.3	0.9	0.5
Ca ($\text{cmol}^+ \text{kg}^{-1}$)	21.4	16.3	12.6	10.6	4.2	8.0	6.3	2.3	2.1
Mg ($\text{cmol}^+ \text{kg}^{-1}$)	5.0	2.5	1.7	52.4	11.3	20.7	24.6	8.5	5.1

[a] MAWD: mean annual water deficit.