Axis Differentiation in Two South American *Nothofagus* Species (Nothofagaceae)

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An analysis was carried out on the length, diameter and number of leaves, and the ratios between these variables for current-year growth units (sibling growth units) derived from different nodes of previous-year growth units (parent growth units) of young *Nothofagus dombeyi* and *Nothofagus pumilio* trees. Changes in sibling growth unit length, diameter, and number of leaves with position on the parent growth unit were assessed. In both species, sibling-growth unit morphology varied according to both the axis type of the parent growth unit and the position of the sibling growth unit on its parent growth unit. For the largest parent growth units, the length, diameter and number of leaves of their sibling growth units decreased from distal to proximal positions on the parent growth unit. Distal sibling growth units had a more slender stem and longer internodes than proximal sibling growth units. Sibling growth units in equivalent positions tended to have a more slender stem for *N. dombeyi* than for *N. pumilio*. Long main-branch growth units of *N. pumilio* had longer internodes than those of *N. dombeyi*; the converse was true for shorter growth units. The growth unit diameter/leaf number ratio was consistently higher for *N. pumilio* than for *N. dombeyi*. *Nothofagus pumilio* axes would go through a faster transition from an 'exploring' morphology to an 'exploiting' morphology than *N. dombeyi* axes. Within- and between-species variations in growth unit morphology should be considered when assessing the adaptive value of the branching pattern of plants. © 2003 Annals of Botany Company

Key words: Architecture, axis differentiation, branching pattern, growth unit, morphogenetic gradients, *Nothofagus dombeyi*, *Nothofagus pumilio*, tree.

INTRODUCTION

Plants may be regarded as modular organisms consisting of linear sequences of nodes and internodes. Much of the inter-specific variation in the aerial structure of plants relates to the branching pattern resulting from the specific way in which old structural units generate new ones. Because of its involvement in the display and function of leaves, the branching pattern is regarded as relevant for the adaptation of plants to different conditions (Horn, 1971; Brunig, 1976; Pickett and Kempf, 1980; Watkinson, 1988). Most studies on branching patterns have focused on the role of environmental factors on these patterns. A number of studies on the branching pattern of perennial herbs have dealt with the morphological features of their component structural units, such as branching frequency, number of leaves and internode length (Sutherland and Stillman, 1988; Watkinson, 1988, and references therein). On the contrary, branching patterns of woody plants have mostly been described, partly because of their complexity, from a broader scale, without delving into the morphological features of their structural units (e.g. Pickett and Kempf, 1980; Steingraeber and Waller, 1986; Bertram, 1989; Harris and Bassuk, 1993).

A more botanically minded perspective of branching patterns integrates plant morphology and ontogeny (Hallé *et al.*, 1978; Barthélémy *et al.*, 1989, 1997). In this approach, structural units derived from the activity of primary meristems are identified and differentiated according to the position on the plant of the meristem concerned and the ontogenetic stage of the plant. In many plants with rhythmic growth each structural unit resulting from an uninterrupted event of primary growth may be termed 'growth unit' (GU; Caraglio and Barthélémy, 1997). An annual shoot, i.e. the axis portion extended in 1 year, may consist of one or more than one GU. Under this perspective, the most important sources of inter-species differences in branching pattern are the time at which GUs develop from a particular portion of an axis, and the relationships between the position of a GU and its size and form (Caraglio and Barthélémy, 1997). Systematic variations in the size of GUs simultaneously formed from a common parent GU (here-after referred to as 'sibling GUs') have been described either qualitatively (e.g. Parker and Johnson, 1987; Caraglio and Barthélémy, 1997; Thiébaut *et al.*, 1997) or quantitatively (e.g. McCurdy and Powell, 1987; Costes *et al.*, 1992; Honda *et al.*, 1997; Hatta *et al.*, 1999; Stecconi *et al.*, 2000; Sabatier and Barthélémy, 2001) for some woody species. Within-species variations in the morphology of GUs depending on their architectural position and the

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developmental stage of their bearing plant have led to the idea that plants consist of different types of axes and then to the concept of 'axis differentiation' (Hallé *et al.*, 1978). The more differentiated an axis, the more limited the morphology of the GUs it would be able to develop. The effects of environmental factors on GU morphology would be limited by the differentiation level of the axis concerned (see Remphrey and Powell, 1984; de Reffye *et al.*, 1991*a*, *b*, 1997, 1999). For a small number of tree species, the endogenous rules of the growth and branching of different axis types have been deeply investigated, enabling the development of the precise mathematical models and computer simulations of trees now being applied in forestry, agronomy and fruit production (Godin *et al.*, 1999; Godin, 2000; Seleznyova *et al.*, 2002; Heuret *et al.*, 2003). The application of this approach to the study of branching patterns may help to relate axis differentiation to the functional properties of GUs. Moreover, our understanding of the adaptive value and evolution of branching patterns may be largely improved by comparing the branching patterns of related species. The latter may only be achieved with the support of previous knowledge of the types of axes each of the species to be compared is able to develop (e.g. Grosfeld, 2002; Heuret, 2002).

The basic morphology of GUs of *Nothofagus* species has been investigated in recent years (Puntieri *et al.*, 1998, 2000, 2002; Souza *et al.*, 2000; Stecconi *et al.*, 2000). However, within- and between-species variations in the morphology and branching pattern of GUs of saplings of these species had not been reported so far. In the present study the branching patterns of two *Nothofagus* (Nothofagaceae) species are compared from this perspective. For sibling GUs, the length, basal diameter and number of leaves (i.e. size descriptors) and the ratios between these parameters (i.e. form descriptors) after extension were analysed. The effects are assessed of (*a*) the size and position on the tree of the parent GUs and (*b*) the position on their parent GUs of the sibling GUs on sibling-GU size and form.

MATERIALS AND METHODS

Study species and sampling sites

Nothofagus dombeyi (Mirb.) Oersted and *N. pumilio* (Poepp. et Endl.) Krasser are among the most important tree species of southern South America in terms of forest area (Veblen *et al.*, 1996). The evergreen *N. dombeyi* is a tall tree (up to 40 m high) which forms dense stands in the most humid areas of the northern-central Andes of Patagonia, between 400 and 1200 m altitude and between 39°25′ and 45°40′S (Correa, 1984). *Nothofagus pumilio* is a winter-deciduous species which may reach 35 m in height at low altitude (between sea level and ~1600 m, depending on the latitude). It adopts a bushy form at the high-altitude timberline along the Andes from northern (38°S) to southern Patagonia (55°S). Extensive abutting between *N. dombeyi* and *N. pumilio* forests occurs but mixed stands with both species are uncommon (Donoso, 1994).

Plants of both species have a stage of fast height growth between about 5 and 30 years after emergence (Barthélemy

et al., 1999), with a well-defined, vigorous vertical axis or trunk (Fig. 1). Axes derived from the trunk show a high degree of variation in size. In order to analyse the architecture of these species at this stage of development, a categorization of axes other than the trunk has been proposed (Barthélemy *et al.*, 1999; Puntieri *et al.*, 1999; Fig. 1): (*a*) main branches are slanted or horizontal axes formed at the distal end of trunk GUs; (*b*) secondary branches are horizontal axes which derive from the distal end of main-branch GUs as well as from intermediate nodes of trunk GUs; (*c*) short branches are horizontal or slanted axes derived from the proximal end of trunk and main-branch GUs and from any positions on secondary-branch GUs. All of these types of axes extend by means of the production of an annual shoot consisting on one GU. The production of a second GU in an annual shoot of these axes may occur after the traumatic death of the apex (Puntieri *et al.*, 1998). The apex of a GU may persist after GU extension. Far more commonly, apex death occurs after GU extension; axis growth in the following year takes place through the development of a relay GU derived from one of the most distal axillary buds of the previous year's GU. On each GU of both species, each of the one to four most proximal nodes bears a cataphyll and each of the other nodes (which vary in number from 2 up to about 30) bears a green leaf. Internodes between cataphylls are usually very short (<1 mm), whereas those between green leaves vary in length from <1 mm to 30 mm. Most usually a GU only develops branches 1 year after its extension and these branches derive from the axillary buds of green leaves. The present study concerned main branches (MB), secondary branches (SCB) and short branches (SHB). Trunk GUs were not included in the present study because of their high morphological variability in *N. dombeyi* (Puntieri *et al.*, 1998).

For each species, 52 trees were randomly selected from a population of homogeneous, healthy and unshaded trees in north-western Patagonia, Argentina. Tree height, basal diameter and age (determined by counting annual shoots along the trunk) are described in Table 1. In this region, precipitation is mainly in autumn and winter (Conti, 1998). Soils derive mostly from volcanic ash (Scoppa, 1998). *Nothofagus dombeyi* trees were sampled from a population located along 1000 m of roadside between the localities of San Carlos de Bariloche and Villa Mascardi (41°10′S, 71°10′W, 850 m altitude), where mean annual precipitation reaches about 1000 mm (Conti, 1998). The population sampled is a natural regeneration of the mixed *Austrocedrus chilensis* (Cupressaceae)–*N. dombeyi* forest present in this area before road construction. The *N. pumilio* trees selected were growing in large gaps within a 10 ha site at Cerro Otto, San Carlos de Bariloche (41°09′S, 71°10′W, 1350 m altitude), where adult *N. pumilio* trees were scattered. Precipitation in this area reaches 800 mm (Conti, 1998). The sampling sites were about 20 km apart. It was considered that the sampled trees were, for each species, representative of young trees growing in full-sun conditions.

For each axis type (i.e. MB, SCB and SHB) of each tree, one annual shoot consisting of one GU extended in the 1996–97 growing season was collected in April 1998
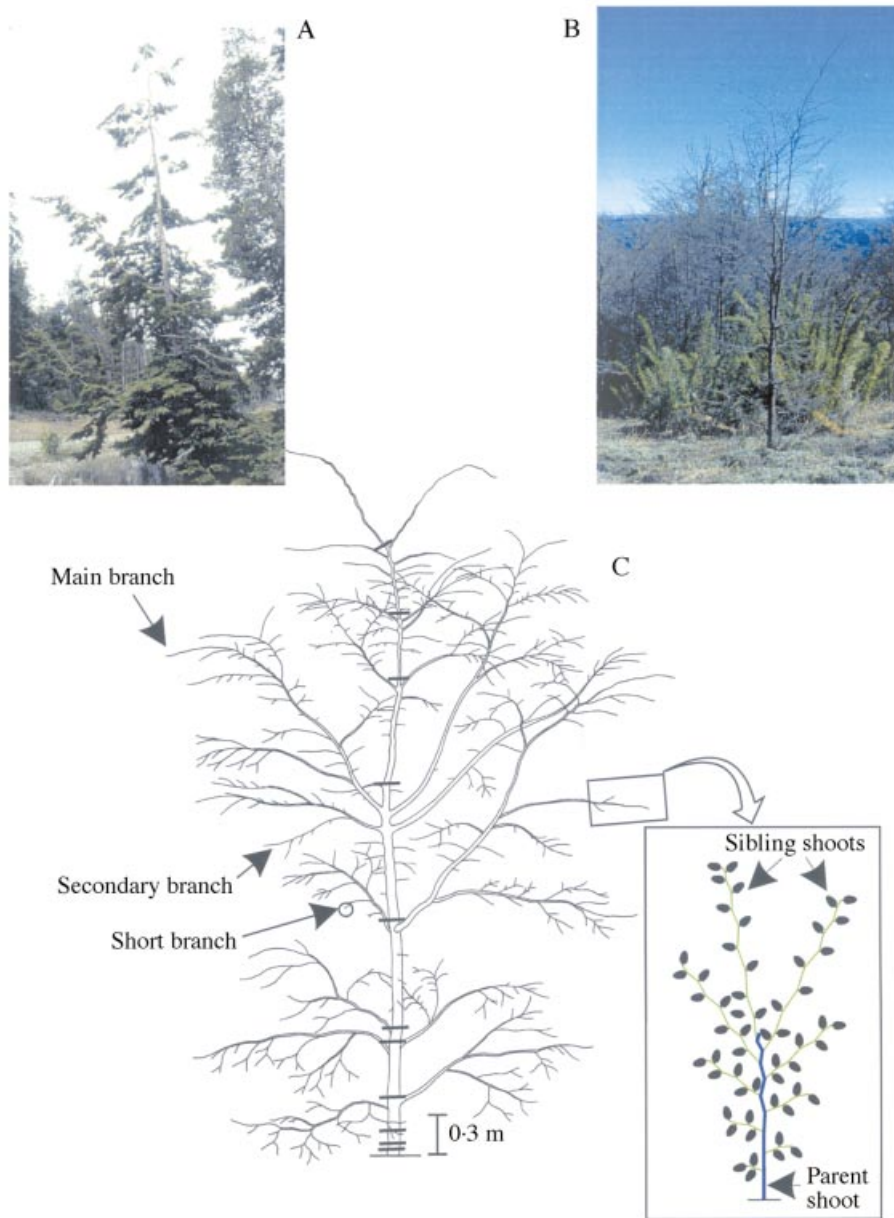
FIG. 1. Young trees of *N. dombeyi* (A) and *N. pumilio* (B) such as those selected for the present study. C, Diagrammatic representation of a *Nothofagus* tree in which main branches, secondary branches and short branches are indicated. Thick horizontal lines on the tree trunk indicate limits between two successive annual growth units. A parent growth unit (green stem) and its sibling growth units (green stem with black leaves) are shown in the detail.

(Fig. 1). By the time of sampling, each of these GUs (parent GUs) was bearing a set of sibling GUs extended in the 1997–98 growing season. In order to homogenize the sample, only parent GUs derived from axillary buds, with a dead apex and devoid of intra-annual branches were included in this study. Only GUs positioned between 1 and 2 m high in the trees and without evident damage by herbivores were chosen. These restrictions in GU selection were considered necessary in view of previous results on GU growth and size variability (see Puntieri *et al.*, 1998).

By the time of sampling, the size of each parent GU and each of their sibling GUs was measured in terms of stem length, basal stem diameter and number of leaves. Length was measured to the nearest millimetre with a measuring tape and diameter was measured to the nearest 0·1 mm with digital callipers. Because of the relatively invariable number of cataphylls per GU (two or three for *N. dombeyi* and four for *N. pumilio*; Barthélémy *et al.*, 1999; Puntieri *et al.*, 2000, 2002; Souza *et al.*, 2000) and the consistently short internodes separating them, irrespective of GU size, only

TABLE 1. *Mean, standard error (s.e.), maximum (max.) and minimum (min.) height, basal diameter (diameter) and age of* Nothofagus dombeyi *and* N. pumilio *trees selected for the present study*

	Mean	s.e.	Max.	Min.
N. dombeyi				
Height (m)	4·2	0·1	5·3	3·4
Diameter (mm)	66·3	2·0	95	37
Age (years)	12·6	0·2	15	10
N. pumilio				
Height (m)	4·1	0·1	5·7	3·0
Diameter (mm)	69·8	1·8	103	33
Age (years)	14·9	0·2	20	12

n = 52 for each species.

green leaves were considered in the number of leaves per GU. The ratios length : diameter (= stem slenderness), length : number of leaves (= internode length) and diameter : number of leaves were computed as measures of GU form.

Statistical analyses

Parent-GU size and form descriptors were compared between species for each axis type by means of one-way ANOVA on log-transformed data (Sokal and Rohlf, 1981). To compare the size and form of sibling GUs, a mean value for each variable was obtained for the sibling GUs in ranges of five node ranks counted from the 6th node (on a proximal-to-distal basis) on the parent GU (the five most proximal nodes usually do not develop branches in these species). The resulting ranges of node ranks and their representation for each axis type of each species were as follows: 6–10, all axis types of both species; 11–15, MB and SCB of both species, SHB of *N. dombeyi*; 16–20, MB and SCB of both species; 21–25, MB of both species, SCB of *N. dombeyi*; 26–30, MB of *N. dombeyi*. Comparisons among sibling GUs in different positions within each species and axis type were performed with one-way ANOVA (Sokal and Rohlf, 1981).

To quantify the rate of change in sibling GU length, diameter and number of leaves along each parent GU, the slope of the least-squares regression line relating the magnitude of each of these variables (dependent variable) to the rank number of the sibling GU (independent variable; rank number = 1 for the most proximal branch) was computed for each parent GU with at least three sibling GUs. All sibling GUs developed from node rank 6 upwards were considered in line-fitting. In some cases somewhat better fittings were reached with second- or third-order polynomials or power functions, but it was considered that the low degree of improvement achieved did not justify the subsequent increase in the number of terms and/or the complexity of the function. Linear regressions were always significant and judged appropriate given the wide range of sizes of the parent GUs. Regression slopes were averaged for each axis type of each species, separating parent GUs

according to their size assessed by their number of nodes (6–10, 11–15, 16–20, 21–25 and 26–30 nodes). Mean slopes were compared between parent GUs of different size for each species and each axis type with one-way ANOVA followed by *a posteriori* Tukey–Kramer tests. Comparisons between species and parent GU sizes were performed for each axis type by means of two-way ANOVA (GLM procedure for unbalanced designs; Sokal and Rohlf, 1981). In the latter case, only parent-GU sizes represented in both species were compared for each axis type.

RESULTS

Size and form of parent GUs

For both species, parent GU length, diameter and number of leaves decreased following the sequence: MB, SCB and SHB (Table 2). Parent GU length and number of leaves were higher for *N. dombeyi* than for *N. pumilio* for each axis type. Parent GU diameter was similar for both species in the case of MB and SCB. SHB were significantly thicker for *N. pumilio* than for *N. dombeyi*. For each axis type, the stem of *N. dombeyi* GUs was more slender than that of *N. pumilio* GUs (more notably so in the case of SHB). Internode length was significantly higher for *N. dombeyi* than for *N. pumilio* in the case of SCB and SHB and similar for both species in the case of MB. The diameter : number of leaves ratio was significantly higher for *N. pumilio* than for *N. dombeyi* for all three axis types (Table 2).

Size and form of sibling GUs

Variation according to position on the parent GU. In the case of MB of both species and SCB of *N. dombeyi*, the length, diameter and number of leaves of sibling GUs increased from proximal (6–10) to intermediate (16–20) positions on the parent GU and tended to be constant between intermediate and distal positions (Fig. 2; Table 3). A similar pattern of variation was found for stem slenderness and internode length of the same GUs (Fig. 3A and B; Table 3). The ratio between stem diameter and number of leaves of sibling GUs tended to decrease from proximal to distal positions on the parent GUs for MB and SCB of *N. dombeyi* and MB of *N. pumilio* (Fig. 3C; Table 3)

For SCB of *N. pumilio* and SHB of *N. dombeyi*, sibling GU length, diameter and number of leaves did not vary with sibling GU position on the parent GU. Stem slenderness, internode length and the diameter/number of leaves ratio did not vary significantly for SCB sibling GUs of *N. pumilio* (Fig. 3; Table 3).

All parent GUs of SHB of *N. pumilio* developed only one sibling GU derived from their most distal node.

Inter-species differences in sibling-GU size and form. MB sibling GUs of both species in similar position on the parent GU were similar in terms of length; those of *N. pumilio* tended to be thicker and to have fewer leaves than those of *N. dombeyi* (Fig. 2). MB sibling GUs of *N. dombeyi* were more slender than those of *N. pumilio*, whereas internode length (except in the most proximal positions) and the

TABLE 2. *Morphological traits of parent growth units of main branches (MB), secondary branches (SCB) and short branches (SHB) of* Nothofagus dombeyi *and* N. pumilio *trees.*

	Nothofagus dombeyi			Nothofagus pumilio			
	Mean	s.e.	*n*	Mean	s.e.	*n*	*F*-test
Length (mm)							
MB	241·1	18·4	42	143·9	8·8	51	25·4***
SCB	100·8	5·5	50	53·1	5·1	52	42·3***
SHB	26·4	1·8	50	3·4	0·3	51	158·1***
Diameter (mm)							
MB	4·42	0·20	42	4·71	0·18	51	0·8 ns
SCB	2·48	0·07	52	2·63	0·08	52	0·2 ns
SHB	1·47	0·03	50	1·65	0·04	51	17·4***
No. of leaves							
MB	18·1	1·0	42	11·8	0·6	51	32·0***
SCB	11·9	0·4	50	6·9	0·4	52	74·3***
SHB	6·4	0·3	50	3·0	0·0	51	125·9***
Stem slenderness (length: diameter)							
MB	5·27	0·28	42	3·03	0·11	51	63·2***
SCB	3·96	0·16	50	1·90	0·15	52	92·3***
SHB	1·72	0·08	50	0·20	0·01	51	343·1***
Internode length (length: no. of leaves)							
MB	1·30	0·05	42	1·22	0·04	51	2·0 ns
SCB	0·84	0·03	50	0·71	0·04	52	5·5*
SHB	0·40	0·01	50	0·11	0·01	51	253·7***
Diameter: no. of leaves							
MB	0·26	0·01	42	0·42	0·02	51	72·1***
SCB	0·22	0·01	50	0·39	0·01	52	131·0***
SHB	0·24	0·01	50	0·57	0·01	51	823·0***

Mean, standard error (s.e.) and sample size (*n*) are indicated.
The results of inter-species comparisons are indicated (*F*-tests).
***, $P < 0.001$; *, $P < 0.05$; ns, $P > 0.05$.

diameter : number of leaves ratio were higher for *N. pumilio* than for *N. dombeyi* (Fig. 3).

In the case of SCB and SHB, the length and number of leaves of sibling GUs were higher for *N. dombeyi* than for *N. pumilio* for all positions; the converse was true for the diameter (Fig. 2). Sibling GUs of SCB and SHB of *N. dombeyi* were more slender and had longer internodes than their respective counterparts of *N. pumilio* in similar parent-GU positions (Fig. 3A and B). The diameter : number of leaves ratios of SCB and SHB were notably higher for *N. pumilio* than for *N. dombeyi* (Fig. 3C).

Slope of sibling-GU size variation with position on the parent GU. In the case of MB of each species, the slope of change in sibling-GU length was significantly higher for parent GUs with less leaves than for those with more leaves (Fig. 4; Table 4). Similar tendencies were found for the diameter and number of leaves of MB, but differences among means were not significant. For MB, between-species differences in the slope of change among sibling GUs (when considering the effect of parent GU size) were significant only in the case of diameter (*N. pumilio* > *N. dombeyi*; Fig. 4; Table 4). With regards to SCB, the slopes of change in length, diameter and number of leaves were significantly higher for smaller than for larger parent GUs of *N. pumilio* and did not vary significantly with parent GU size in the case of *N. dombeyi*. The slopes of change in length, diameter and, more notably, in number of leaves of

SCB sibling GUs were, on average, higher for *N. dombeyi* than for *N. pumilio*. For SHB of *N. dombeyi*, the slopes of change in length, diameter and number of leaves did not vary with parent GU size.

The slope of change in sibling GU length differed among axis types for both species (*N. dombeyi*: MB > SC > SHB, $F = 13.6$, $P < 0.001$; *N. pumilio*: MB > SC, $F = 22.3$, $P < 0.001$); similar differences were found for the slopes of change in diameter and number of leaves for *N. pumilio* ($F = 38.5$, $P < 0.001$ and $F = 28.3$, $P < 0.001$, respectively) but not for *N. dombeyi* ($F = 1.5$, $P > 0.2$ and $F = 2.5$, $P > 0.05$, respectively).

DISCUSSION

GU size and size variation in Nothofagus *trees*

In young *N. dombeyi* and *N. pumilio* trees the size (in terms of length, diameter and number of leaves) of a GU relates to the type of parent axis and the position on the parent GU of the node of origin of the sibling GU. In the case of MB of both species and SCB of *N. dombeyi*, the size of sibling GUs tends to increase from proximal to intermediate and distal positions along parent GUs (Fig. 5; see also following section). On the contrary, hardly any variation in sibling GU size is found for SCB of *N. pumilio* and SHB of *N. dombeyi*. SHB of *N. pumilio* develop only one distal sibling GU (see following section).
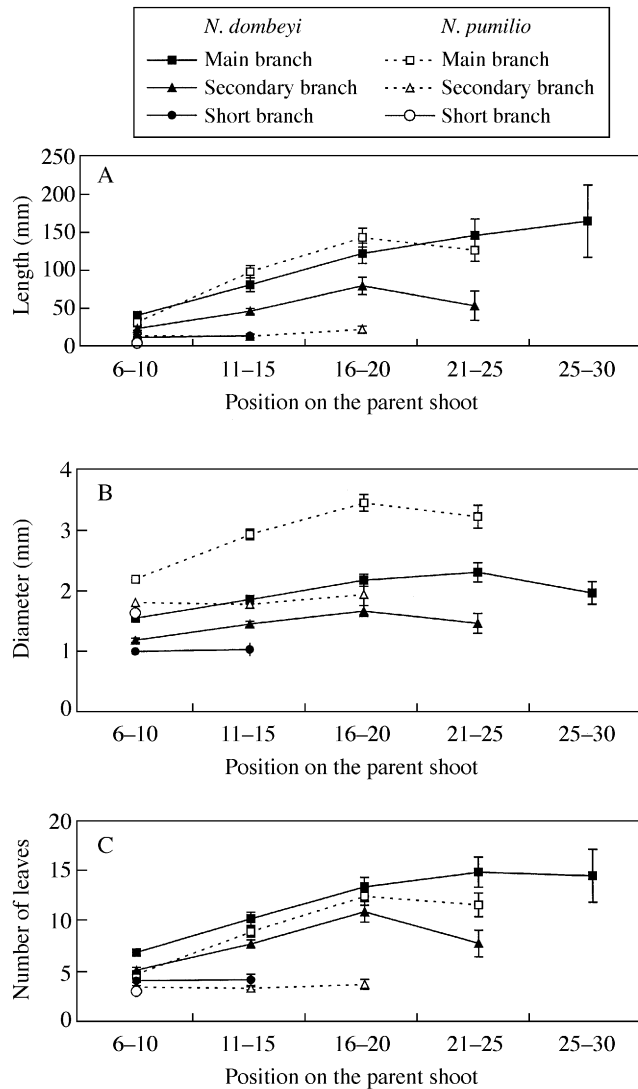
FIG. 2. Mean (±1 s.e.) length (A), basal diameter (B) and number of leaves (C) of sibling growth units of *N. dombeyi* (closed symbols) and *N. pumilio* (open symbols) developed in different positions on their parent growth units and grouped according to the rank number of the parent growth unit nodes (counted from the parent growth unit's proximal end) from which sibling growth units derived. Data corresponding to parent growth units of main branches, secondary branches and short branches are shown separately.

For both species, the length, diameter and number of leaves of sibling GUs at any given position on the parent GU decrease from MB to SCB and SHB. Likewise, stem slenderness and internode length of sibling GUs are higher for MB than for SCB and higher for these than for SHB. These results comply with those on other tree species studied so far, for which stem slenderness and internode length were found to be positively correlated to GU length (Costes *et al.*, 1992; Costes and Guédon, 1997; Nicolini, 1998). The diameter : number of leaves ratio decreased as the diameter and number of leaves of the sibling GU increased, but its variation with respect to the type of axis depended on the species considered (see below).

TABLE 3. *Results of one-way ANOVA comparisons (F, Fisher's statistic; P, probability of error) of morphological traits between sibling growth units in different positions on their parent growth units, for each species (N. dombeyi and N. pumilio) and axis type*

Axis type	N. dombeyi		N. pumilio	
	F	P	F	P
Length				
MB	13·4	***	38·3	***
SCB	21·9	***	0·7	ns
SHB	0·5	ns	-	-
Diameter				
MB	10·4	***	34·3	***
SCB	13·3	***	0·5	ns
SHB	0·2	ns	-	-
No. of leaves				
MB	14·7	***	38·1	***
SCB	22·2	***	0·3	ns
SHB	0·0	ns	-	-
Stem slenderness				
MB	15·2	***	42·8	***
SCB	30·1	***	1·2	ns
SHB	0·5	ns	-	-
Internode length				
MB	9·0	***	40·7	***
SCB	16·2	***	2·3	ns
SHB	1·2	ns	-	-
Diameter: no. of leaves				
MB	8·2	***	28·5	***
SCB	4·9	**	0·2	ns
SHB	0·0	ns	-	-

MB, main branches; SCB secondary branches; SHB, short branches.
***, $P < 0.001$; **, $P < 0.01$; ns, $P > 0.05$.

The close relationship between axis type and the size and form of sibling GUs supports the idea of axis differentiation in trees (Sabatier and Barthélémy, 1995, 1999; Barthélémy *et al.*, 1997). Among the axis types included in the present study, MB could be considered the least specialized type of axis for both species, since GUs within a broad range of sizes may derive from a MB. On the same grounds, SHB may be described as the most specialized type of axis since their production is limited to short GUs (Figs 2 and 3).

The slope of change in sibling GU size along a parent GU depends, for each species, on both the axis type concerned and the size of the parent GU. MB GUs exhibit, on average, sharper differences in sibling GU size than SCB GUs (Fig. 4). For MB, the slope of change in sibling GU length tends to be inversely related to the size of the parent GU from which the sibling GUs derived. Differences in the size of GUs derived simultaneously from a common parent GU have been explained by alluding to patterns of resource allocation (Küppers, 1994; Pallardy *et al.*, 1995), sometimes shown to be controlled by the parent GU's distal end (Brown *et al.*, 1967; Cline, 1997; Cook *et al.*, 1999; Wilson, 2000). Under this perspective, in young *N. dombeyi* and *N. pumilio* trees, the proportional allocation of resources to distal rather than proximal sibling GUs would be higher for MB than for SCB and would tend to be higher for smaller
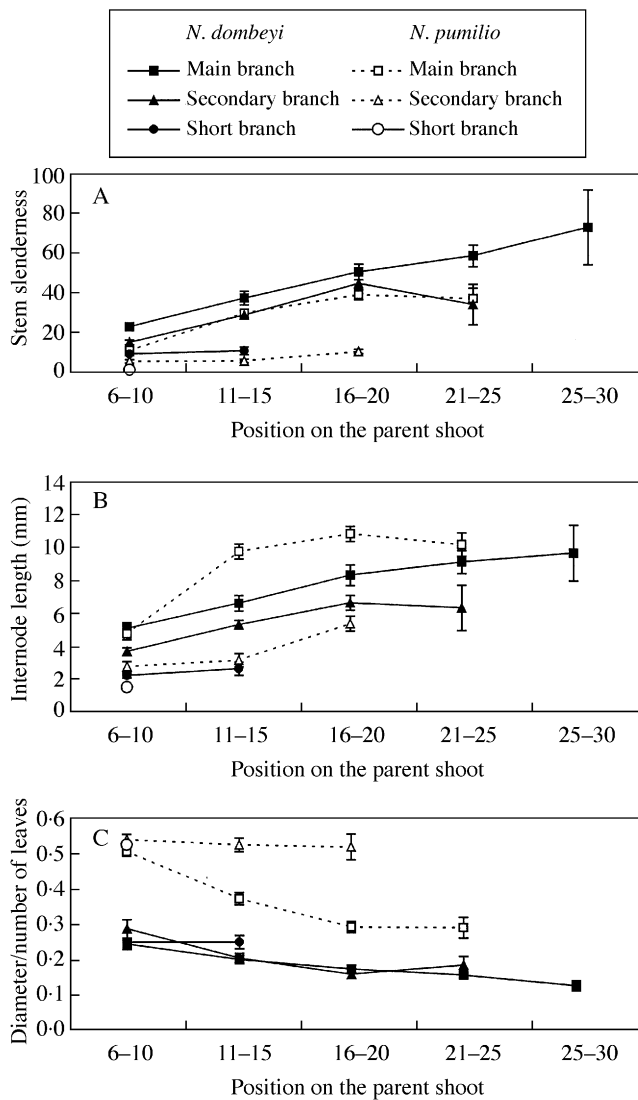
FIG. 3. Mean (± 1 s.e.) stem slenderness (length : diameter; A), internode length (length : number of leaves; B) and diameter : leaf number ratio (C) for sibling growth units of *N. dombeyi* (closed symbols) and *N. pumilio* (open symbols) developed in different positions on their parent growth units. Other details as in Fig. 2.

than for larger parent GUs of the same axis type (especially for *N. pumilio*).

Variation in the pattern of branch development according to axis type and size may have evolved as a way of achieving high levels of light interception in relation to the biomass of the GU. This may be exemplified by comparing the branching patterns of a long GU and a short GU of a MB. The long GU may be assumed to reach a more peripheral position within the crown than the short GU (Fig. 5). By developing several long sibling GUs with long internodes and a slender stem close to its distal end (i.e. a low slope of variation in sibling GU length, as observed here for *Nothofagus*), the long MB GU would increase the volume reached by the tree crown without extensive overlapping with other MB. The short MB GU, on the other hand, would

be more benefited by developing a long sibling GU only at its distal end (resulting in a higher slope of change in sibling GU length), as long proximal sibling GUs would be likely to overlap with other GUs. In the case of even less peripheral (shorter) SCB and SHB, light interception in relation to the biomass of the GUs produced would be increased by decreasing the proportional investment in support organs (i.e. a stem short and narrow relative to its number of leaves) in all positions (Fig. 5).

Differences between species

Young trees of *N. pumilio* and *N. dombeyi* differ with regards to some morphological features of their GUs. The dimension of GUs which differs most notably between these species, irrespective of the type of axis considered, is stem diameter after extension: it is notably higher (40 % on average) for *N. pumilio* than for *N. dombeyi* for GUs of any given length or number of leaves. The difference in GU diameter between species determines the higher GU slenderness and lower diameter : number of leaves ratio for *N. dombeyi* than for *N. pumilio* for each axis type and position of the sibling GU on its parent GU. This difference between species could be related to different cross-sectional areas of transport tissues. The higher average leaf size (J. Puntieri, unpublished data), nutrient content and nitrogen-resorption (Mazzarino *et al.*, 1998; Diehl *et al.*, 2003) for *N. pumilio* than for *N. dombeyi* might also imply higher metabolic requirements per leaf for the former species which would demand a larger area of conducting tissues. Anatomical and physiological comparative studies would be needed to assess these hypotheses.

Although *N. pumilio* forests are usually at higher altitudes than those of *N. dombeyi*, both species are subjected to snowfalls in winter. Stem flexibility is one of the morphological features which increase the capacity of stems to withstand snow weight without breaking (Givnish, 1995; Payette *et al.*, 1996; Valinger and Fridman, 1997). Having a flexible stem in a region with winter snowfalls would represent a more beneficial trait in an evergreen species than in a winter-deciduous species. The development of a more slender stem in GUs of the evergreen *N. dombeyi* than in the winter-deciduous *N. pumilio* would support this idea, in case a positive relationship between stem slenderness and flexibility were demonstrated for these species.

Nothofagus pumilio and *N. dombeyi* differ in several aspects of their GU morphology relative to the type of axis from which the GU derives: (*a*) internodes are longer for *N. pumilio* than for *N. dombeyi* in the case of MB GUs but the opposite is true for SCB and SHB; (*b*) SCB of *N. pumilio* resemble SHB rather than SCB of *N. dombeyi* with respect to length and number of leaves; (*c*) the differences in the slope of change in length, diameter and number of leaves among sibling GUs both between MB and SCB parent GUs with a similar number of nodes and between SCB parent GUs with a different number of nodes, are more notable in *N. pumilio* than in *N. dombeyi* (Figs 4 and 5); (*d*) morphological variation among SHB GUs of *N. pumilio* is very low (i.e. these GUs consist of three leaves, very short internodes and develop a single distal branch; Figs 2, 3 and 5). In
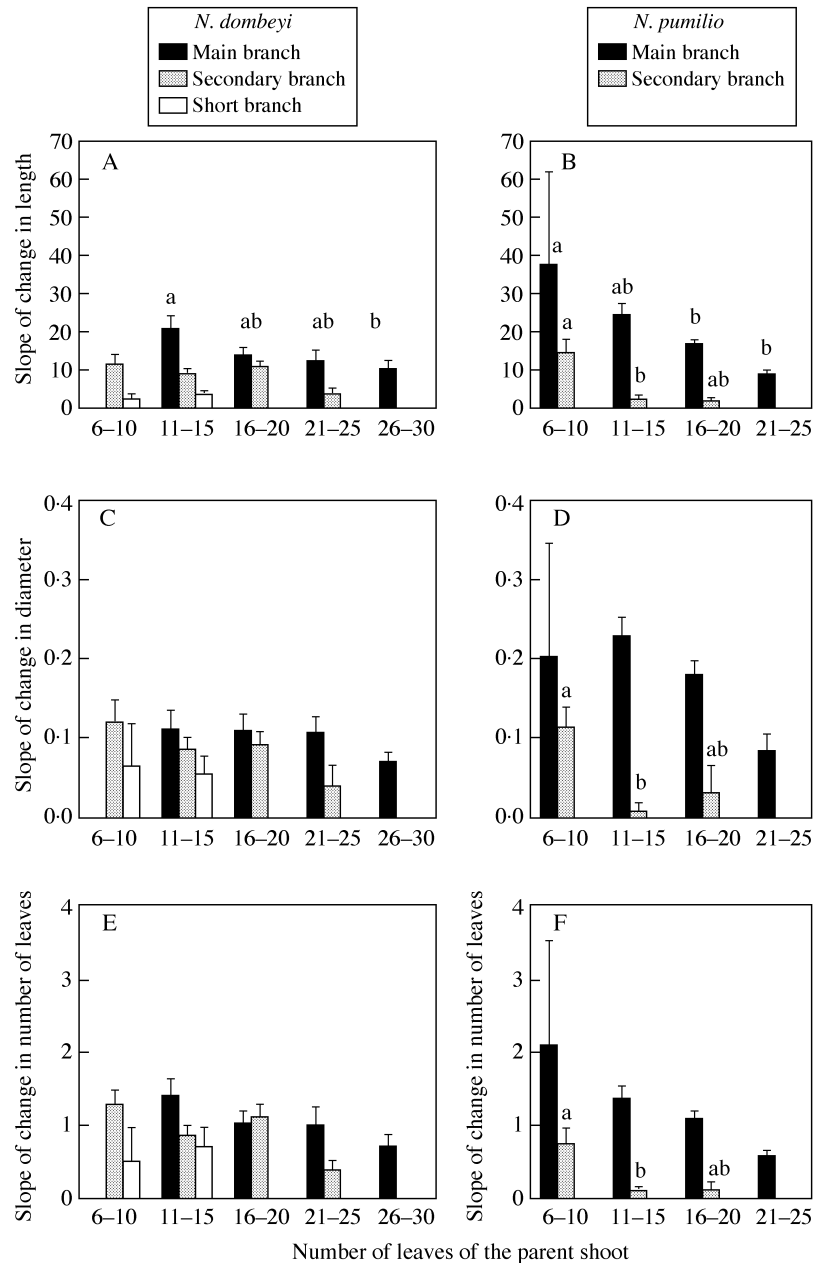
FIG. 4. Mean (+ 1 s.e.) slope of change in sibling-growth unit length (A and B), diameter (C and D) and number of leaves (E and F) for sibling growth units developed from main-branch (black bars), secondary-branch (shaded bars) and short-branch (white bars) parent growth units of *N. dombeyi* (A, C and E) and main-branch (black bars) and secondary-branch (shaded bars) parent growth units of *N. pumilio* (B, D and F). Results for parent growth units with different number of nodes (6–10 nodes, 11–15 nodes, 16–20 nodes, 21–25 nodes and 26–29 nodes) are shown separately. The means of bars of the same species and axis type with different letters on top differ significantly ($P < 0.05$) from each other (Tukey–Kramer tests; see Table 4 for ANOVA comparisons).

addition, SHB of *N. pumilio* have a turned-up distal end and their leaves re-arranged in a tristichous-like display (Puntieri *et al.*, 1999). This specialized axis type of *N. pumilio* trees, also observed in the related species *Betula papyrifera* (Macdonald and Mothersill, 1983) and *Fagus sylvatica* (Nicolini and Chanson, 1999), seems not to have an equivalent axis type in young *N. dombeyi* trees. These results suggest a sharper gradient from less differen-

tiated to more differentiated axes in *N. pumilio* than in *N. dombeyi*. The development of a specialized SHB in *N. pumilio* trees would allow light exploitation with low investment in support tissues and low overlapping among leaves. On the other hand, the less specialized, relatively long SHB of *N. dombeyi* seems more suitable for light exploration, at the cost of increasing the extent of overlapping between neighbour branches (see Küppers,

TABLE 4. *Results of comparisons of the slope of change in length, diameter and number of nodes between parent growth units of different size for each axis type of* N. dombeyi *and* N. pumilio *by means of one-way ANOVAs, and between species and parent growth unit sizes (in terms of number of nodes) for each axis type by means of two-way ANOVAs (species ×* *size : species × parent growth unit size interaction)*

| | | One-way ANOVA | | | | Two-way ANOVA | | | | | |
| | | *N. dombeyi* | | *N. pumilio* | | Species | | GU size | | Species × size | |
Slope of change in	Branch type	F	P	F	P	F	P	F	P	F	P
Length	MB	3·6	*	3·8	*	0·0	ns	6·9	**	0·4	ns
	SCB	1·8	ns	6·8	**	4·4	*	6·9	**	3·0	ns
	SHB	1·0	ns	–	–	–	–	–		–	
Diameter	MB	0·8	ns	1·8	ns	5·2	*	2·5	ns	2·2	ns
	SCB	1·1	ns	9·7	***	5·0	*	7·5	**	2·0	ns
	SHB	0·0	ns	–	–	–	–	–		–	
No. of leaves	MB	2·5	ns	2·7	ns	0·9	ns	4·8	*	0·7	ns
	SCB	2·5	ns	5·1	*	20·6	***	6·0	**	0·5	ns
	SHB	0·1	ns	–	–	–	–	–		–	

For each comparison, the value of Fisher's statistic (*F*) and the probability of error (*P*) are indicated.
MB, main branches; SC, secondary branches; SHB short branches.
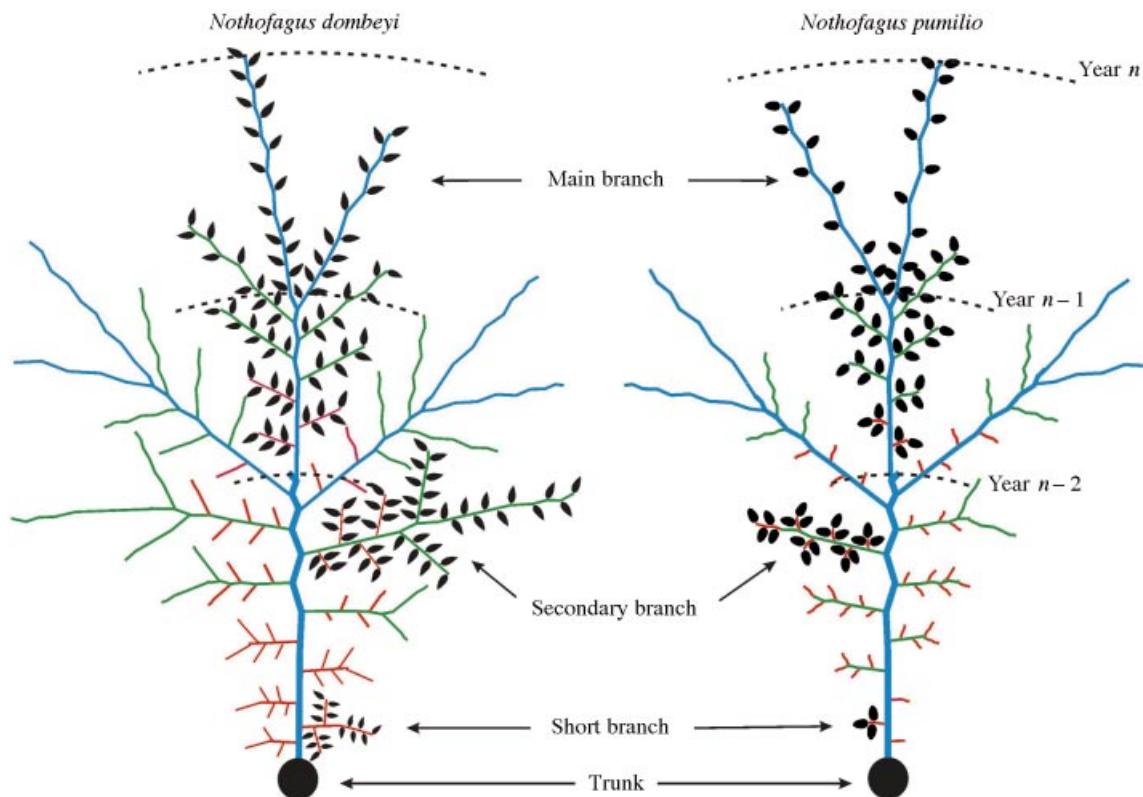*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns, $P > 0.05$.

FIG. 5. Diagrammatic representation of a plan view of a 3-year-old main branch of *N. dombeyi* and *N. pumilio* and all growth units derived from them. Growth units of different axis types are differentiated by colour: main branch, blue; secondary branch, green; short branch, red. Leaves have been drawn on those growth units derived from a main branch, a secondary branch and a short branch of each species. Limits between main branch annual growth units are indicated by dashed arcs. See text for details.

1994; Cao, 1995). Since the leaves of *N. dombeyi* are retained at least for 2 years, the development at the centre of the crown of SHB with internodes as short as those of SHB of the deciduous *N. pumilio* would imply very high levels of leaf overlapping.

CONCLUSIONS

The identification of biologically meaningful structural units of each plant species is fundamental for the study of their branching patterns. A deep knowledge of the restric-

tions imposed by the species' endogenous developmental rules on the size and form of such units is necessary before assessing the role of environmental factors on the branching pattern of a species or comparing branching patterns between species or between populations of the same species (see Watson *et al.*, 1995). The differences pointed out here between the size and form of GUs and the branching patterns of *N. dombeyi* and *N. pumilio* could be considered valid for young individuals growing under optimal conditions. Similar information is not available for other populations of the same species. However, partial data sets from other studies on *N. pumilio* (Passo *et al.*, 2002) and *N. dombeyi* (Puntieri *et al.*, 2002) suggest that the main results would have been similar had the study been performed on other populations of young trees. Variations in the branching pattern of these species for older trees or trees growing under stressful conditions ought to be addressed.

ACKNOWLEDGEMENTS

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