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► **To cite this version:**

Javier Puntieri, Javier Grosfeld, Marina Stecconi, Cecilia Brion, María Marta Azpilicueta, et al.. Shoot development and dieback in progenies of *Nothofagus obliqua*. *Annals of Forest Science*, 2007, 64 (8), pp.839-844. 10.1051/forest:2007068 . hal-00884140

HAL Id: hal-00884140

<https://hal.science/hal-00884140v1>

Submitted on 11 May 2020

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Shoot development and dieback in progenies of *Nothofagus obliqua*

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(Received 29 December 2006; accepted 23 May 2007)

Abstract – Shoot growth and dieback were compared among progenies of nursery-grown seedlings of *Nothofagus obliqua* belonging to seven progenies of the same provenance (Quila-Quina, Argentina). First-year shoots consisted of one growth unit (GU) and second-year shoots of one or two GUs. The probability of development of two GU was similar for all progenies. Progenies were different in terms of shoot size, terminal bud abscission, the extent of shoot dieback after shoot extension and the node of origin of the relay shoot on the first shoot. Plants with a second-year shoot consisting of two GUs had a thicker stem and more nodes than those with single-GU shoots. The selection of *N. obliqua* seed trees based on architectural traits suitable for forestry development at specific sites must contemplate variability among progenies and their probabilities of successful development under different conditions.

shoot dieback / growth unit / plant architecture / progeny / *Nothofagus*

Résumé – Développement et dépérissement des pousses de descendance de *Nothofagus obliqua*. La croissance et le dépérissement des pousses ont été comparés entre sept descendance de *Nothofagus obliqua* élevées en pépinière et issues d’une même provenance (Quila-Quina, Argentine). Les pousses de la première année n’étaient formées que d’une seule Unité de Croissance (UC) tandis que les pousses de deuxième année étaient constituées d’une ou deux UCs. La probabilité de développement d’une deuxième UC était constante quelle que soit la descendance. Les descendance ont montré des différences en termes de taille de pousse, d’abscission du bourgeon terminal, d’étendue de dépérissement des UC en fin d’extension et vis-à-vis du nœud d’origine de la pousse relais sur la pousse de première année. Les plantes avec une pousse de seconde année comportant deux UC avaient une tige plus épaisse et avec plus de nœuds que celles avec des pousses à une seule UC. La sélection, basée sur des traits architecturaux, d’arbres de *N. obliqua* issus de graines, pour qu’elle soit adaptée à la foresterie, doit prendre en compte la variabilité entre descendance et leurs probabilités de réussite et de bon développement sous des conditions diverses.

dépérissement des pousses / unité de croissance / architecture des plantes / descendance / *Nothofagus*

1. INTRODUCTION

Trees may respond to different environmental conditions through morphological and/or physiological mechanisms [5, 12]. The knowledge of genetic components involved in these responses is useful especially in the case of valuable forestry tree species. The South American deciduous species *Nothofagus obliqua* (Mirb.) Oerst. and *N. alpina* (Poepp. et Endl.) Oerst. (Nothofagaceae) are considered suitable broadleaf alternatives to conifers for timber production in temperate regions due to their timber quality and growth rate, as shown in forestries established in Europe in the second half of the 20th century [6, 7, 33]. Both species, but especially *N. obliqua*, suffer from the death of distal shoot segments (*shoot dieback*), allegedly after frost damage [6]. Selection programs on *N. obliqua* aimed at improving productivity have been de-

veloped only in recent years [13] and plants from different geographical areas and/or mother trees have been genetically characterised [11, 18]. Nonetheless, the possible relationships between the genetic structure of *N. obliqua* plants and their susceptibility to the factor/s causing dieback have not been investigated so far. The architectural analysis (sensu Hallé et al.) [14] of genetically identified progenies may help to visualize the link between genetic and developmental traits and to contribute in the selection of seed trees for forestry establishment.

Nothofagus obliqua has a relatively wide ecological amplitude and a large natural distribution area (about 1000 km latitudinally and 200 km longitudinally; from 33° S to 41° 30' S in Chile and from 36° 49' S to 40° 11' S in Argentina). However, its current distribution is highly fragmented as a consequence of glaciation events, volcanism and, more recently, human intervention [10]. Its fruits have a poor dispersal capacity, which restricts genetic interchange among populations and increases the risk of genetic losses after local deforestation [8, 10]. In

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order to examine the morpho-architectural variability of *N. obliqua* populations from Argentina, a common garden plantation of provenances was established [28]. The results of this trial indicated that some traits are influenced by provenance, e.g. the size of the first-year shoot (an annual shoot is defined as an axis segment developed in one growing season) and the development, in the following years, of annual shoots consisting of two or three growth units (GU; defined as an axis segment resulting from an uninterrupted extension event). On the contrary, provenances overlapped notably regarding other traits such as the extent of shoot dieback after extension as well as the size reached by one- and two-year-old plants [28]. The present study reports the results of a progeny trial established at the same time and in the same nursery as the aforementioned provenance trial. We tested the hypothesis that seedlings of half-sib progenies within a provenance would display different shoot growth and dieback in their first two growing seasons.

2. MATERIALS AND METHOD

2.1. Experimental design

Achenes were manually collected from seven *N. obliqua* trees at the natural forest of Quila-Quina, the southernmost population of this species in Argentina (40° 10' 40" S, 71° 26' 37" W; 983 m s.n.m.). The sampled trees were at least 100 m apart from other *N. obliqua* trees. Due to the small size (~ 1 cm long) and disperse location of fruits in each tree, accessibility to fruit-bearing branches was decisive for tree selection. Achenes were sown in containers in September 2000 (early spring) and, after the development of the first green leaves, seedlings were installed directly on soil in the tree nursery belonging to the "Unidad de Genética Forestal" of INTA EEA Bariloche (Argentina; 41° 07' 15" S, 71° 15' 06" W; 770 m s.n.m.), about 150 km south of Quila-Quina. The nursery soil was made by mixing the natural soil of the site (volcanic ash and fluvial deposits) with fine-grained forest debris. Irrigation was provided daily. No artificial light sources were used. The nursery is surrounded by 20–30 m tall trees located about 10 m from the nursery borders, which reduced the hours of direct sunlight on the nursery.

Differences among the seven progenies in fruit availability and seedling mortality after germination conditioned the numbers of seedlings available for this study. In each of three independent blocks, 15 to 20 seedlings per progeny were arranged in rows within one plot (thus, a total of 45 to 60 seedlings per progeny were included). Distance between blocks was 50 cm and that between neighbour seedlings 15 cm. One row of *N. obliqua* seedlings not included in the experiment was established around each block, so as to minimize border effects. The plot of plants of each progeny was randomly placed within each block (randomized complete blocks design). This arrangement, rather than a completely random distribution of plants within each block, was chosen in order to facilitate the identification of progenies, some of which were to be included in a longer-term field experiment after this trial.

2.2. Measurements on seedlings

The vertical axis or trunk of all plants was measured in spring 2002, after the completion of two growing seasons: 2000–2001 and

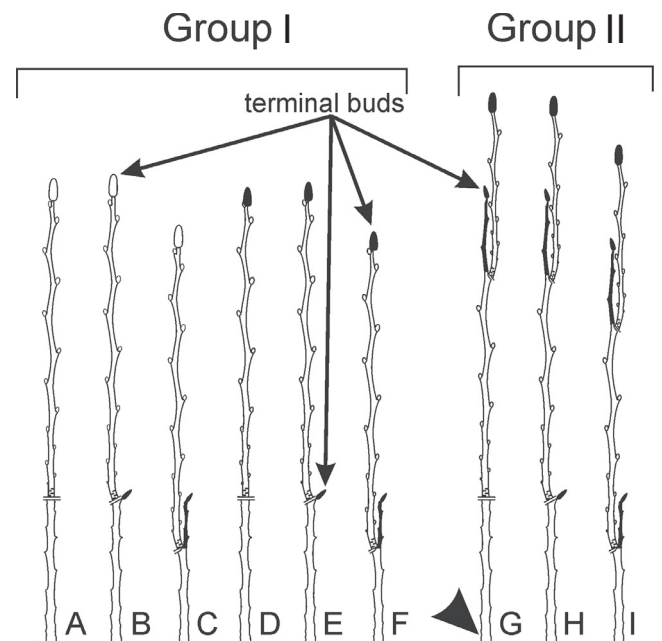


Figure 1. Diagrammatic representation of the most common structural types of the vertical axis of two-year old *N. obliqua* seedlings. (A-F): Group I, the second shoot consists of one growth unit. (G-I): Group II, the second shoot consists of two growth units (leaves and lateral branches not drawn). (A, D and G): the second-year shoot derived from the first shoot's terminal bud. (B, E and H): the second-year shoot derived from an axillary bud after the abscission of the first shoot's terminal bud. (C, F and I): the second-year shoot derived from an axillary bud after terminal bud abscission and dieback. Stem segments and terminal buds that persisted after extension are white-filled and dead stem segments black-filled. Arrowhead: position of the cotyledonary node. = Limit between first-year and second-year shoots. A series of short black dashes represents the sequence of short internodes at the base of each growth unit.

2001–2002. For each plant, shoots and GUs were identified non-destructively using morphological criteria [2, 25]. In *N. obliqua*, the limit between two GUs of a shoot is clearly recognized by the presence of a set of 2 to 5 short internodes (< 1 mm in length) between two sets of longer internodes (> 5 mm in length; Fig. 1).

Each plant's basal diameter was measured to the nearest 0.1 mm with a digital calliper at the cotyledon level. The number of nodes bearing green-leaves was used as a measure of size for first-year and second-year GUs of each plant. Cataphyll-bearing nodes at shoot bases were not considered as they are separated by very short internodes, so that their counting on standing plants is inaccurate. In this, like in other *Nothofagus* species, a terminal bud may develop after GU extension. However, the death of a GU's terminal bud occurs frequently, leaving a recognizable scar on the stem [28]; throughout this text, this condition will be described as *terminal bud abscission*. The death of distal nodes and internodes of a GU may occur together with terminal bud abscission, a condition referred to here as *dieback*. Since no pruning was applied to the plants, the dead segment of each GU was standing at the time of measurement (Fig. 1). For each GU of each plant we registered the presence of a terminal bud and, in case dieback occurred, the number of dead distal nodes/internodes after extension. The node of the first shoot from which the second-year

trunk shoot developed was also recorded (counted from the cotyledonary node). In case the first-year shoot's terminal bud persisted and gave rise to the second-year trunk shoot (Figs. 1A, 1D and 1G), the position of the latter shoot was quantified by adding 1 to the number of nodes of the first-year shoot.

The following descriptors were compared between progenies for first-year GUs: (1) proportion of seedlings with terminal bud abscission, (2) total number of nodes, (3) the ratio [number of dead distal nodes] / [total number of nodes], henceforth termed *dieback fraction* (*DF*), (4) the ratio [second-shoot position] / [(total number of nodes of the first shoot) – (number of dead nodes of the first shoot)], hereafter termed *second shoot position* (*SSP*). For second-year shoots comparisons among progenies included: the proportion of plants with two GUs and descriptors (1) to (3). Variables concerning the number of nodes of second-year shoots were compared separately for the first and the second GUs and for the sum of both GUs.

Two measures of plant size after two growing seasons were compared among progenies: diameter at the cotyledon level and number of nodes (adding the total number of nodes of first and second shoots and subtracting the numbers of dead nodes of each of these shoots).

2.3. Data analyses

Plants with 1-GU second shoot (297 plants, all progenies pooled) will be referred to as group I plants, and plants with 2-GUs second shoot (43 plants) as group II plants (Fig. 1). The proportion of first-year and second-year GUs with terminal bud abscission and the proportion of second-year shoots consisting of two GUs were compared among progenies by means of χ^2 tests [30]. Comparisons among progenies regarding terminal bud abscission were only performed on group I plants due to the relatively low numbers of group II plants.

Differences among progenies were assessed through analysis of variance (ANOVA), including progeny and block as random factors [20, 30]. A 95% significance level was adopted in all comparisons.

3. RESULTS

3.1. First-year shoots

For group I plants, the percentage of first-year shoots with terminal bud abscission differed among progenies (between 53 and 94%; $\chi^2 = 26.8$, $p < 0.001$). In the case of group II, this percentage ranged between 33% and 100% for the different progenies. Similar percentages of group I (83.5%) and group II (72.1%) plants (all progenies pooled) had a first-year shoot with terminal bud abscission ($\chi^2 = 2.8$, $p > 0.05$).

For the first-year shoot, significant differences among progenies were detected for the total number of nodes, the *DF*, and the *SSP* (Tab. I). On average, the first shoot of group II plants had more nodes than that of group I plants (Figs. 2A and 2B).

When considering the seedlings of all progenies, first-year shoots with a terminal bud ($N = 53$) had a similar number of nodes than those with terminal bud abscission and no dieback ($N = 173$; $F = 1.1$, $p > 0.05$; three-way ANOVA, including progeny and block as random factors; after pooling all progenies and groups I and II).

Table I. Mean squares (MS) and Fisher's *F*-test for the effect of progeny (seven levels) after two-way analysis of variance (block effect not shown) on the following variables of first-year and second-year shoots and two-year plants: number of nodes per GU (nodes), dieback fraction (*DF*), second shoot position (*SSP*), stem diameter at the cotyledonary node (*diam*), number of nodes of two-year old plants after subtracting dead nodes (*Tnodes*).

	Variable	Progeny effect	
		MS	<i>F</i>
1st shoot	Nodes	116.7	11.7 ***
	DF	0.22	5.8 ***
	SSP	0.07	2.8 **
2nd shoot	Nodes ₁	62.3	1.6 ns
	DF ₁	0.57	7.3 ***
	nodes ₂	121.7	3.9 **
	DF ₂	0.51	6.7 ***
Two shoots	Diam	52.5	11.2 ***
	Tnodes	348.8	6.7 ***

Subscripts 1 and 2 for the second shoot indicate that the first GU or the sum of both GUs, respectively, were compared. *** $p < 0.001$, ** $p < 0.01$, ns: $p > 0.05$.

3.2. Second-year shoots

All progenies were similar regarding the percentage of second-year shoots with two GUs (between 4 and 17%; $\chi^2 = 12.2$, $p > 0.05$), and the percentage of dead terminal buds in group I shoots (41 to 68%; $\chi^2 = 7.7$, $p > 0.05$). Almost all group II shoots had terminal bud abscission after the extension of the first GU; only one plant produced a second, though axillary, GU without terminal bud abscission. The percentage of second GUs with terminal bud abscission varied between 50 and 90% for different progenies.

Significant differences among progenies were found regarding the *DF* of the first GU but not for the total number of nodes; for both variables group I plants had higher means than group II plants (Figs. 2A and 2B). The total number of nodes and the *DF* of the second shoot after considering both GUs in case of group II plants also differed among progenies (Figs. 2A and 2B).

Second-year shoots derived from the terminal bud of the first-year shoot had, on average, four more nodes than those derived from an axillary bud of first-year shoots with terminal bud abscission and no dieback ($F = 13.4$, $p < 0.001$; including progeny and block as random factors; all progenies and groups I and II pooled). The latter difference was nullified when the number of dead nodes of the second shoot was subtracted ($F = 0.5$, $p > 0.05$). Similar proportions of second-year shoots of terminal and axillary origin consisted of two GUs ($\chi^2 = 1.8$, $p > 0.05$).

3.3. Two-year main-stem development

The basal diameter and the number of nodes (dead nodes excluded) of the main stem after two years of growth differed

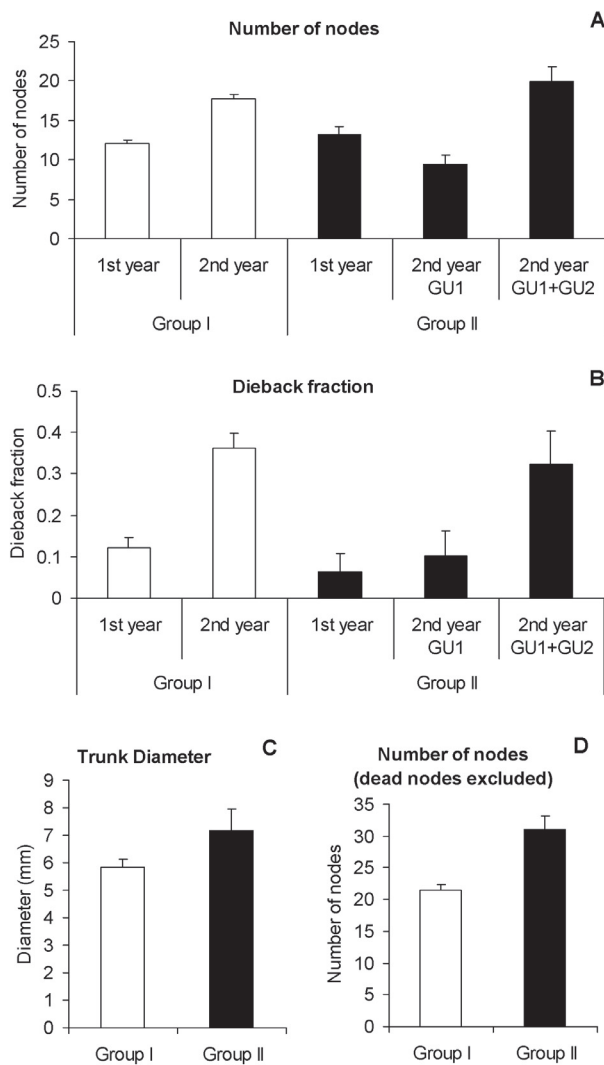


Figure 2. (A, B): Mean (+95% confidence interval) number of nodes (A) and dieback fraction (number of dead nodes expressed as a proportion of the total number of nodes; (B) of the first-year and second-year shoots of group I (white bars) and group II (black bars) plants; the means for the first growth unit (GU1) and both GUs (GU1+GU2) of the second-year shoot of group II plants are shown separately. (C, D): Mean (+95% c.i.) basal trunk diameter (C) and number of nodes after excluding the dead nodes (D) for group I and group II plants after two growing seasons.

significantly among progenies; group II plants had, on average, a 20% thicker stem at the cotyledon level and a 50% higher number of nodes than group I plants (Figs. 2C and 2D).

4. DISCUSSION

4.1. Shoot size and dieback

Nothofagus obliqua seedlings derived from different mother trees of the same population differ, when growing under similar conditions, in the number of nodes and the fate of

the distal end of first-year and second-year shoots. The present study shows that, at least for *N. obliqua*, the phenomenon described synthetically as apex death involves two components: the abscission of the terminal bud and the desiccation of distal nodes and internodes (dieback). The natural abscission of a shoot's terminal bud means the death of both apical meristem and leaf primordia, usually soon after shoot extension [26]. Terminal bud abscission is a more common event in South American *Nothofagus* species [2] than in species of other "fagalean" genera such as *Quercus* and *Fagus*, at least for early growth stages [3, 15, 16, 21]. The factors determining terminal bud abscission are still unknown. Since the development of progressively shorter internodes precede terminal bud abscission [1, 2], internal and/or external restrictions to further shoot growth and terminal bud persistence may be presumed. Recent studies suggest that terminal bud abscission in *Nothofagus* is less likely at the seedling stage than at sapling or adult stages [31, 34] but is not affected by interactions among nearby buds [29]. The present study shows that, at least for *N. obliqua*, terminal bud abscission and dieback may have a genetic component. The abscission of the terminal bud of the first-year shoot without dieback in *N. obliqua* proved to impact negatively on the size of the second shoot. This result contrasts with that of a study on *N. dombeyi* saplings, in which shoots of terminal and distal axillary origin reached similar sizes [24]. This discrepancy may indicate a difference between these species regarding the allocation of resources among the distal buds of a shoot; age differences between the plants included in both studies may also be implicated.

In *N. obliqua*, dieback may occur together with terminal bud abscission. Shoot dieback in trees has been associated with stressful environmental conditions [17]. Low water availability in summer is the major stress factor throughout the distribution area of *N. obliqua*, as well as in the area where the present study was performed [4, 8]. Since water was supplied all along the experiment reported here, water shortage seems an unlikely explanation for shoot dieback in this case. Water supply could act as a growth promoter in this species, so that trunk shoots of watered plants may be still extending in early autumn and be exposed to morning frosts, which could then cause shoot dieback. This idea would agree with the results of other studies pointing at frost damage on *N. obliqua* and *N. alpina* shoots and its negative effect on the establishment of forestries with these species in northern Europe, where summer droughts are uncommon [6, 7, 33].

The development of a relay branch from an axillary bud after either terminal bud abscission or dieback is frequent in the trunk of *N. obliqua* plants. In this study, plants belonging to different progenies with a low extent of dieback in first-year shoots tended to develop a second shoot consisting of two GUs and reached a larger size than those with 1-GU second shoot (see next section). A more extensive dieback in a first-year shoot has a negative effect on the size of the plant at the end of the following growing season. These results support the idea that buds in different positions have different potentialities in terms of the size of the shoot they would eventually develop [1]. In the case of *Nothofagus* species, such potentialities vary following a distal-to-proximal decreasing trend in the number

of organs per bud and the number of leaves of fully-extended shoots [26, 27, 32]. This study suggests that the genetic constitution of trees affects the response of growing shoots to the death of distal organs. Genetic and ontogenetic factors might be related to the production of stress-tolerance promoters, as found for other plant species [19, 23, 35] and suggested by other studies on *Nothofagus* [9]. Many of the plants included in the present study have been transferred to experimental field populations. The architectural analysis of these plants in the future would allow the relationships between plant progeny and growth traits in older plants to be assessed.

4.2. Progeny selection in *N. obliqua*

A study on *N. obliqua* seedlings performed in parallel with the present one and in the same nursery revealed large variations within provenances (Quila-Quina among them) in shoot size and dieback [28]. The results of the present study indicate that such variations may be progeny related and, therefore, genetically controlled. Both within- and between-provenance variations are to be considered in the selection of trees with either conservation or timber production purposes. The selection of progenies of *N. obliqua* for forestry purposes must bear in mind not only the growth potential of each progeny but also the possible effects of stressful environmental conditions on each progeny. Severe shoot dieback after extension may significantly reduce shoot-size differences among progenies. Plants with main-stem shoots of intermediate size but with low rates of terminal bud abscission and dieback and a high frequency of shoots with two GUs would reach a larger size than those with larger main-stem shoots but higher abscission and dieback rates. Specific trees might be more suited as seed sources depending on the region of forestry establishment. The extension period of long shoots of this and other *Nothofagus* species proceeds until late summer and early autumn [24]. These shoots might be more susceptible than shorter shoots to early frost hazards. Seedlings with a higher tendency to produce large shoots may be adequate in sites where stressful environmental conditions in late summer are unlikely. In other sites, plants with shorter shoot-growth duration may be a more sensible choice.

From the timber production perspective, the absence of terminal bud abscission and dieback after GU extension may be preferable for the sake of trunk straightness [17]. In *N. obliqua* seedlings, the development of a vertical (relay) branch following terminal bud abscission affects stem straightness only in the short term. In all *Nothofagus* species so far studied, branching is predominantly pseudomonopodial and most external signs of terminal bud abscission and a low extent of dieback disappear few years after relay-shoot development due to secondary stem thickening [2]. Whether this would be so in cases of more extensive dieback still awaits evaluation. The present study shows that those plants with two GUs in the second shoot had a thicker main stem and more nodes (excluding dead nodes) than those with single-GU second shoot. This would imply a mechanically more stable trunk [22] as well as more potential sites for further growth in the former than in the

latter group of plants. Such traits might be adequate for forest establishment in windy and/or sloping sites, although experimental testing of this idea is necessary.

Acknowledgements: We are grateful to L. Oudkerk for establishing and maintaining the plants utilized in the present study, N. Baccalá for statistical advice and the Administración de Parques Nacionales for allowing seed collection from conservation areas. This study was supported by INTA, Universidad Nacional del Comahue (projects B704 and B096) and CONICET, Argentina.

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