Diameter growth: can live trees decrease?

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Summary

Growth refers to an increase in dimensions with time and is implicit in the expected continual increase in tree dimensions. Tree diameters, however, could decrease during the growing season due to water depletion. Annual negative growth measurements are usually attributed to human error and not to other physiological or physical processes. Although seasonal and diurnal fluctuations of diameter have been well documented, perennial decrement of diameter has not been the focus of physiological research. The aim of this work was to analyse the potential causes of decrease in annual diameter growth related to tree mortality due to self-thinning in *Nothofagus pumilio* forests and to quantify the variations in water depletion of the tree trunks. Some trees did present negative annual diameter increments associated with a water content decrease in the trunks (77 per cent in live trees compared with 56 per cent in recently dead individuals), which produced a contraction (more than 8 per cent of the initial diameter) in the wood and the bark. Trees could survive during 2–5 growth seasons with continual decreases in their diameters (14 per cent, standard error 5 per cent of the trees in the studied stand) until the water content reached a limit where mortality resulted. Therefore, the occurrence of data showing a diameter decrease in successive forest inventories may be due to physiological and physical processes in the natural dynamics of the stand, and not exclusively be explained away as the results of human measurement errors.

Introduction

The woody part of trees consists of a series of annual layers, which overlap one another, as a series of cones covered by the bark (Kramer and Kozlowski, 1960). The cambium is a layer of lateral meristematic tissue between the xylem and phloem in the tree stems, which produces secondary growth. Within the wood, the vessels allow the water movement from the roots to the leaves (Klepac, 1976).

Tree growth refers to the increase in dimensions of an individual over a given period of time (e.g. diameter growth in cm year^{-1}) (Vanclay, 1994). It has been implicit that tree dimensions invariably increase (Klepac, 1976). However, height growth can decrease from one year to another, due to the death or breakage of the main branch in advanced development phases, for example, as reported by Martínez Pastur *et al.* (1997) in 300-year-old *Nothofagus pumilio* (Poepp. et Endl.) Krasser trees. This has also

been observed in diameter, due to bark removal or wounds over the stem. However, tree diameter could also decrease during the growing season due to water stress (Kozlowski and Winget, 1964; Dobbs and Scott, 1971; Sall, 1988; Kozlowski *et al.*, 1991; Zücher *et al.*, 1998; Vesala *et al.*, 2000; Donoso and Ruiz, 2001; Sevanto, 2003), recovering the positive increments after the adverse climate conditions ended. Negative values of annual diameter measurements have usually been attributed to human errors and not to other physiological or physical processes related to the tree dynamics (Lesser and Kalsbeek, 1999; Martínez Pastur *et al.*, 2001, 2002a). Although seasonal and diurnal fluctuations of diameter have been well documented, perennial decrement of diameter has not been the focus of physiological research. The aim of this work was to analyse the decrease in annual diameter growth as related to tree mortality due to self-thinning and to quantify the variations in water content of the tree stems.

Methods

Data for five growing seasons (1999–2004) from permanent plots were analysed. There were eight plots each of 25 m² and a total of 603 trees, which were identified with numbered tags and aluminium nails, located 14 km from Tolhuin city in Tierra del Fuego, Argentina (54° 36′ 35″ SL, 67° 15′ 43″ WL). The studied stand was a secondary forest of *N. pumilio* of medium site quality (Martínez Pastur *et al.*, 1997), which developed following clear cutting in 1965–1967 (Cozzo *et al.*, 1967). It developed naturally without any silvicultural management or cattle grazing pressure. Stem circumference (precision 1 mm), using the same diameter tape for the same field survey, was measured once each austral winter season (May–June) for all tagged trees, also recording tree mortality. Tree circumference data were converted into diameter values with an expected precision of 0.03 mm.

For the analysis of the wood water content, two samples were taken 4 km from Ushuaia city (Tierra del Fuego, Argentina) (54° 46′ 42″ SL, 68° 12′ 55″ WL) in a secondary forest of *N. pumilio* of medium-low site quality (Martínez Pastur *et al.*, 1997), which originated by clear cutting in the 1950s (Gea *et al.*, 2004). In the first assay, 63 stem cross-sections of nine live trees were sampled (4.7–8.8 cm d.b.h., 51–59 years old and 8.5–11.2 m total height) during the austral summer season (January 2004). They were classified according to the crown class of the tree (dominant, co-dominant, intermediate and suppressed), position within the tree (lower, middle and upper stem), age (years through tree-ring analysis) and diameter. Each cross-section was measured with a digimatic calliper (Mitutoyo Corp., Japan) with a precision of 0.01 mm in the laboratory under ×10 magnification, along two diameters, differentiating the wood and the bark. The points of measurement in each cross-section were identified with waterproof ink for the subsequent measurements. The cross-sections were dried in an oven at 70°C and measured (cross-section diameters and water content) each day until constant weight was obtained. This analysis was done to study the diameter decrease in relation to wood water content, and not necessarily reflect the natural drying.

In the second assay, 15 trees (12.1–15.0 cm d.b.h., 38–41 years old, 8.5–10.9 m total height) were cut during the summer season (January 2004), and five cross-sections were obtained from each tree along the stem. Seven of the selected individuals were live trees with green healthy leaves, while the others eight trees were recently dead (the trees did not sprout after the winter or still presented dry leaves on the branches). The cross-sections were dried in an oven at 70°C until constant weight was obtained and water content was quantified as described above.

For all the experiments, comparisons of main factors were carried out by analyses of variance with the F test. Significantly different averages were separated with Tukey's honestly significant difference test ($P < 0.05$).

Results

Diameter growth and mortality by self-thinning

The studied stand had a mean d.b.h. of 3.6 cm with a standard error (SE) of 0.6 cm. Its basal area (BA) was 35.3 m² ha⁻¹ (SE 7.7 m² ha⁻¹) with 30 400 trees ha⁻¹ (SE 5559 trees ha⁻¹) and a high rate of mortality due to inter-tree competition (2850 trees ha⁻¹ year⁻¹, SE 705 trees ha⁻¹ year⁻¹). The dominant trees accounted for 27.7 per cent (SE 5.6 per cent) of the BA, with 26.5 per cent

(SE 3.7 per cent) for co-dominants, 19.1 per cent (SE 6.2 per cent) for intermediates and 26.7 per cent (SE 3.1 per cent) for suppressed individuals. Dominant trees had the highest average annual increase in diameter (0.20 cm year^{-1} average, SE 0.03 cm year^{-1}), followed by co-dominant trees (0.13 cm year^{-1} average, SE 0.02 cm year^{-1}) and intermediate trees (0.06 cm year^{-1} average, SE 0.03 cm year^{-1}). The diameter for suppressed trees decreased 0.01 cm year^{-1} on average (SE 0.02 cm year^{-1}). When the growth trend of the stand trees was considered (Figure 1), it was observed that: (1) 62.4 per cent (SE 5.6 per cent) increased their diameter in all years of the studied 5-year period; (2) 13.4 per cent (SE 2.5 per cent) did not increase their size in at least 1 year of the studied period; (3) 14.3 per cent (SE 4.9 per cent) decreased in at least 1 year of the studied period; and (4) 9.9 per cent (SE 1.8 per cent) died. These data indicated that 27.7 per cent (SE 6.4 per cent) of the trees in the stand decreased or did not increase their diameter in some of the studied years. Analysing dead trees separately, it was observed that all of them belonged to the suppressed crown class, growing under the dominant canopy stratum. Only 10.7 per cent (SE 7.9 per cent) of the dead trees increased their diameter during the years before death, while 54.7 per cent (SE 29.9 per cent) decreased, 8.6 per cent (SE 7.9 per cent) did not increase and 26.0 per cent had null or negative values in two successive periods (SE 25.5 per cent). This meant that 89.3 per cent (SE 7.9 per cent) of the trees had not presented positive diameter changes in the previous years before their death.

Loss of diameter due to changes in water content in stem cross-sections

The stem cross-sections of live trees had 75.6 per cent (SE 9.5 per cent) water content by dry weight, and when the moisture declined due to their being dried, their diameter also decreased. Expressing this decline as a percentage of the original cross-section diameter, it decreased 7.6 per cent (SE 1.2 per cent) compared with the original dimensions (Figure 2). This diameter decrease did not have a linear relationship with the loss in the humidity content, where it was greater at water contents less than 20 per cent. The bark and the wood did not decrease in the same proportion (Figure 3). Wood occupied 90.5 per cent (SE 2.7 per cent)
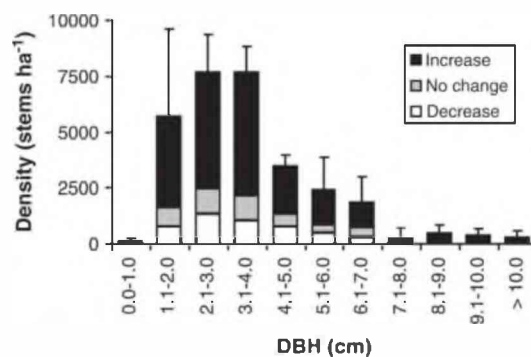

Figure 1. Diameter frequency distribution of *Nothofagus pumilio* trees in the permanent plots showing the percentages of individuals which increased their diameter in all years of the studied period, showed no change in their size in at least 1 year of the studied period, and decreased in at least 1 year of the studied period (1999–2004). Bars represent the SE of the total average density of each class.
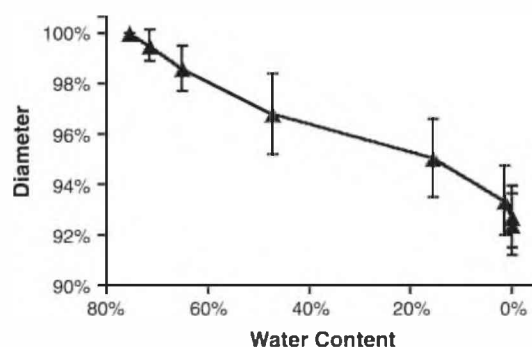

Figure 2. Percentage of diameter reduction related to the water content in cross-sections of live trees of *Nothofagus pumilio*. Bars represent the SE.

of the cross-section diameter when its water content was at its maximum, but changed to 93.5 per cent (SE 1.6 per cent) with the minimum water content. For these, the bark had a greater reduction (9.5–6.5 per cent of the cross-sections diameter) when water content was lowered.

The water contents of the cross-sections in the dominant and co-dominant crown class trees were significantly higher than those of lower crown classes (F crown class = 33.47, $P < 0.01$). The position of the cross-sections within the stem also influenced the water content (F position = 100.02,
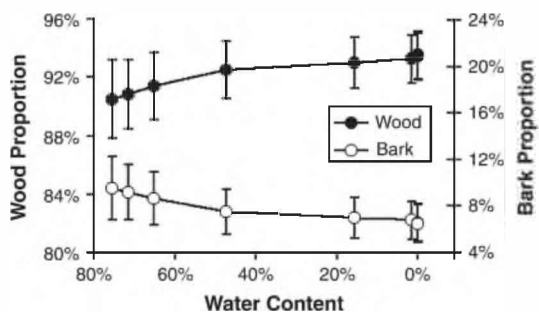
Figure 3. Wood and bark proportion into the stem diameter related to the water content in cross-sections of live trees of *Nothofagus pumilio.* Bars represent the SE.

$P < 0.01$) with significantly higher values in the upper third than the middle third and the lower third. Age also had a significant influence on water content (F age = 76.41, $P < 0.01$), being lower in older cross-sections (>30 years), than in cross-sections between 15–30 years and in younger cross-sections (<15 years). Finally, diameter also influenced the water content of the cross-sections (F diameter = 18.11, $P < 0.01$) with significantly higher water values in smaller cross-sections (<40 mm) than in the bigger cross-sections (>40 mm).

Loss of diameter was significantly less in the trees of the dominant class, compared with the other crown classes (F crown class = 67.81, $P < 0.01$). The position of the cross-sections within the stem also influenced significantly the reduction in diameter (F position = 70.36, $P < 0.01$). Diameter loss was highest in the cross-sections of the lower third, compared with the middle and upper thirds. Age also had a significant influence in diameter reduction (F age = 92.61, $P < 0.01$). Younger cross-sections (<15 years) had greater loss than cross-sections between 15 and 30 years or older cross-sections (>30 years). Finally, the cross-section diameter also had an influence in the loss of diameter (F diameter = 142.08, $P < 0.01$) with significantly greater reduction in the smaller cross-sections (<40 mm), than in cross-sections of middle size (40–55 mm), than in the biggest cross-sections (>55 mm).

Water content in live and dead trees

Significant differences (F = 10.11, P = 0.01) in the water content of the live trees were found compared with the recently dead trees. Live trees had greater moisture (76.6 per cent) than dead ones (55.9 per cent). On the other hand, the trees that did not sprout after the winter had less water content (41.5 per cent, SE 7.7 per cent) compared with those that sprouted and then died during the spring (66.8 per cent, SE 12.6 per cent).

Discussion

The forest structure and dynamics in these surveyed stands are in agreement with other pure *N. pumilio* stands without forest management in southern Patagonia (Cozzo *et al.,* 1967; Martínez Pastur *et al.,* 2001). Early development phase stands have high mortality rates due to inter-specific competition (self-thinning), which declines in more mature phases (Martínez Pastur *et al.,* 2002b). Usually, it is thought that this mortality is due to the lack of light in the lower canopy stratum, because *N. pumilio* is a shade intolerant species (Donoso, 1990). However, suppressed trees can survive many decades, waiting for the canopy to open (Gea *et al.,* 2004). Another possible reason for the observed mortality could be another limiting resource, such as water or nutrients. Regardless of the limiting factor, mortality in *Nothofagus* mainly occurs in suppressed trees (Martínez Pastur *et al.,* 2001, 2002a; Peri *et al.,* 2002), which was accompanied with yearly changes in the crown classes between the trees of the stand. The gradient in diameter increase among crown classes described here agrees with other reports for *N. pumilio* (Peri and Martínez Pastur, 1996; Martínez Pastur *et al.,* 1997). Negative growth values of the suppressed individuals are expected as well, since it could be related to the trees' die back.

Wood shrinking is mainly associated with the contraction produced by loss of moisture (Skaar, 1988; Hunter, 1995; Baronasa *et al.,* 2001) and could be related to the water content of living and dead trees. The water content and shrinking rate varied with age, diameter, crown class and position inside the stem. The youngest and thinnest trees of the lower crown class had a greater tendency to loss diameter due to dry out, and could be related to lower wood and bark density. However, more research is needed to clarify if the loss of diameter due to different water content in natural and artificial drying is comparable.

Portions of the *N. pumilio* trees can survive for a long time with no functional roots or a dead radical system. Peri *et al.* (2002) carried out a study in a 67-year-old secondary forest on Tierra del Fuego Island (Argentina). Several trees were girdled at breast height to kill them. Bark, cambium and two to three tree rings where cut, removing the connectivity between roots and branches. These trees continued living during 2–4 years after the interventions (G.M. Martínez Pastur, unpublished data), maintaining the trunk alive above the cut, but dead below it. Furthermore, in a thinned permanent study plot within a 35-year-old secondary forest, half of the trees were cut down during the summer and left on the forest floor (Martínez Pastur *et al.*, 2001). After the winter, many of these felled trees sprouted in the spring and grew for one more season (data not shown). This phenomenon suggests that *N. pumilio* trees can survive during one or more growth seasons using nutrients and/or water that are available within the stem.

According to our results, most of the dead trees showed a decrease in diameter growth during the previous years. This could indicate that the stem contracted due to loss of moisture because the tree could not absorb the necessary water through the roots, which is the main reason that might explain the tree die back. This mortality must occur mainly because of root competition rather than competition for light, since suppressed trees of *N. pumilio* are known to live more than 200 years under the canopy of old-growth forests (Martínez Pastur *et al.*, 1994; Gea *et al.*, 2004). These findings indicate that the survival of the suppressed trees could extend until they reach a minimum limit of trunk moisture, which is between 67 and 77 per cent, thereafter resulting in mortality at lower water contents.

During the reduction of water content in the suppressed trees, the shrinking of the wood and bark stem caused a decrease in diameter from one year to the next. This shrinking might be due to the contraction of wood or bark, which occurs at different rates (Perämaki *et al.*, 2001; Sevanto, 2003). The absence of positive increments is an excellent tool to predict stand mortality through self-thinning. The shrinking and swelling of stem diameters were widely described for short periods of time (days or weeks) (Kozlowski and Winget, 1964; Dobbs and Scott, 1971; Sall, 1988; Kozlowski *et al.*, 1991;

Zücher *et al.*, 1998; Vesala *et al.*, 2000; Donoso and Ruiz, 2001; Sevanto, 2003; Sheil, 2003). These diameter changes are thought to reflect the water balance inside the stem (Donoso and Ruiz, 2001; Mäkinen *et al.*, 2002; Sevanto, 2003). In this work, extended periods of time (more than one growing season) are analysed, not just daily values. On the other hand, negative measurement values during successive forest inventories usually are related to human error (Lesser and Kalsbeek, 1999). However, it has been shown here that a decrease in tree diameters found in suppressed individuals could also be due to competition for water.

Conclusions

Trees can present negative annual diameter values due to a decrease of the water content in the stem, which produces a contraction in the trunk's wood and bark. *N. pumilio* trees furthermore can survive during several growing seasons with a continuous decrease of their diameters, but a threshold limit exists after which they finally die. Thus, the occurrence of decreasing values in successive forest inventories could be due to natural physiological and physical processes, and not exclusively related to human measurement errors. As a result, we advice caution in the interpretation of negative diameter results in forest inventories and suggest that these data can be used to explain forest growth in succession dynamics.

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