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Long-term trends in radial growth associated with *Nothofagus pumilio* forest decline in Patagonia: Integrating local- into regional-scale patterns

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ABSTRACT

Forest decline, or the premature loss of forest health, is a complex process not yet fully understood. Although reductions of radial growth have previously been recorded for individuals affected by decline, studies describing the whole range of growth patterns from decline-affected stands are rare. We used principal component analysis to identify dominant patterns of radial growth in eleven *Nothofagus pumilio* stands in northern Patagonia that show external manifestations of forest dieback. At most sites, dominant growth patterns significantly different from the stand mean growth chronology were identified using either ring widths or basal area increments (BAIs). Due to the pervasive trend of decreasing ring width with increasing tree diameter, patterns of tree growth related to forest decline are better captured using BAIs. Three dominant patterns of growth were identified at most sites: (1) trees with the highest rates of growth during the first decades of the 20th century started a sustained reduction in radial growth in early 1940s reaching the lowest increments in the late 20th century; (2) trees with low growth over most of the 20th century substantially increased their growth rates in the 1960s concurrent with the growth decline in the previous group, and (3) trees with intermediate growth rates until mid-20th century showed a subsequent 20–30 year period with high rates of growth followed by a gradual reduction from the late 1980s to present. The onset of negative trends in radial growth associated with forest decline (patterns 1 and 3) occurs simultaneously at most stands. Contrary to expectations, large-dominant trees with the highest rates of growth seem to be the most severely affected by reductions in radial growth. These results are consistent with the concept of "decline disease stabilizing selection" where healthy dominant fast-growing trees in the forest are selectively affected by a combination of specifically detrimental factors. Dominant patterns at stand scale exhibit similar trends in radial growth between sites separated by more than 400 km in northern Patagonia suggesting that meso- to macro-scale environmental forcings modulate regional forest decline. Our results challenge traditional sampling designs used in dendroecological and dendroclimatological studies. Traditional sampling strategies, mostly targeted to dominant, climate-sensitive trees, will over emphasize the 20th century negative trends in *Nothofagus* stand growth associated with the largest stand trees. Only by including all individuals within a plot, will sampling provide consistent tree-growth estimates that represent the entire population. Additionally, as endogenous stand dynamics are not clearly reflected in mean growth estimates, dominant growth patterns within a stand should be identified to correctly assess dynamic processes such as forest decline.

1. Introduction

Forest decline or forest dieback is a global phenomenon associated with the premature loss of tree vigor leading, in many cases, to forest health decay and subsequently to massive tree mortality (Hennon et al., 1990; Mueller-Dombois, 1992). Depending on species, forest characteristics and site conditions, forest decline can extend over large regions altering diverse forest ecosystems (Huettl and Mueller-Dombois, 1993; Koepke et al., 2010). Factors influencing forest decline are not easily identified since multiple interactions occur between trees and environmental conditions (Franklin et al., 1987; Hogg et al., 2008). Pioneer studies in Europe and eastern North America during the 1980s, attributed forest

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decline to large-scale air pollution and acid rain (Haemmerli and Schlaepfer, 1993). At the same time, forest decline was associated with forest dynamics and climate stress in areas not severely affected by human activities such as the Pacific Islands (Mueller-Dombois, 1993).

Changes in tree-ring patterns can be used to characterize the trends in tree growth in healthy and affected trees and determine the onset of the decline. Persistent low rates of growth were observed in individuals prior to death or in trees exhibiting partial crown mortality (LeBlanc and Raynal, 1990; Ryan et al., 1994; Bigler and Bugmann, 2003; Amoroso and Larson, 2010). The reduction in radial growth substantially slows the water transport through the stem creating a physiological imbalance between the water-demanding foliage in the canopy and the water-provider root and water-transport stem systems (Manion, 2003). This physiological imbalance increases the susceptibility of trees to pests, diseases or other factors contributing to mortality, initiating a cascade of unfavorable events (Manion, 1981, 2003). Consequently, the assessment of growth variations over time can provide useful information on the temporal evolution of dieback processes and the identification of radial growth patterns in trees more prone to decline. Recent studies postulate a relationship between growth rates and lifespan within species. They indicate that early dominant, fast-growing trees are more vulnerable to decline or mortality than those that experience slower growth rates (Manion, 2003; Black et al., 2008; Bigler and Veblen, 2009).

Forest decline studies differ in their approaches including differences in sampling strategies and type of data used. Most studies on dieback have previously categorized individuals into healthy versus affected trees and differences in radial growth between these two groups have been attributed to forest decline (Hogg et al., 2002; Duchesne et al., 2003; Mundo et al., 2010; Amoroso et al., 2012). In most cases, individuals unequivocally classified into clearly defined cases were selected, avoiding trees in intermediate situations that were difficult to classify. Analysis of all trees in the stand, independently of their external appearance, has rarely been considered as a sampling strategy. However, analyses based on the complete range of health conditions can identify the range of tree-growth patterns present within these stands and provide a more comprehensive view of the temporal variations in growth and interactions between trees during dieback processes. Additionally, recent studies quantifying the influences of sampling design on tree growth estimates indicate that tree-ring measurements from all trees within a given area provide the most realistic representation of forest growth (Nehrbass-Ahles et al., 2014).

Most assessments of tree dieback based on tree growth have traditionally used standardization techniques to remove biological trends from ring-width data associated with tree age and endogenous disturbances (Cook et al., 1987; Johnson et al., 1988). Duchesne et al. (2003) suggested that basal area increment data (BAIs) provide better indications of tree health and vitality than ring-width data since the negative trends in BAIs are more consistently related to poor health or tree senescence than those in ring-width series. Mean chronologies reflecting growth variations of the whole stand are also frequently used to study growth decline (Johnson et al., 1988; Piovesan et al., 2008; Silva et al., 2010). However, since most stands showing dieback include different proportions of healthy and affected trees, the use of a single chronology to represent stand growth can mask significantly different growth patterns in individual trees (LeBlanc, 1990).

Studies in the *Nothofagus* forests of New Zealand have proposed that permanent saturation of soils during very wet years (Ogden et al., 1993), severe droughts (Grant, 1984) and the combination of extreme climatic events (Ogden et al., 1993) are triggers of forest decline. Forest decline and massive mortality of *Austrocedrus chilensis* and *Nothofagus dombeyi* in the Patagonian Andes have been related to extreme drought events during the 20th century (Villalba and Veblen, 1998; Suarez et al., 2004; Amoroso and Larson, 2010; Mundo et al., 2010). Although dieback affects large areas along the dry limit of *Nothofagus pumilio* distribution, study of forest dieback in this species has received comparatively little attention. Veblen et al. (1996) indicated that the *N. pumilio* stands located at the forest-steppe ecotone or at exposed windy sites with reduced water availability are the most vulnerable to decline. On a regional scale, the partial crown mortality in *N. pumilio* is mainly localized in the eastern, relatively dry, margin of the species distribution (Veblen et al., 1996). However, in the same stand trees with advanced crown mortality and reduced foliage coexist with healthy trees. This indicates that the dieback process can show different expressions between trees or groups of trees within the same stand and therefore the individual characteristics of each tree may differentially contribute to decline (Bossel, 1986).

In this study, we use dendrochronological methods to determine the dominant patterns of *N. pumilio* tree growth related to forest dieback in northern Patagonia, Argentina. In contrast to most studies of forest decline based on a comparative approach of symptomatic and asymptomatic trees, we sampled all trees at the stand level to identify all major patterns of growth and their interactions. Since meso- to macro-scale environmental variations have also been related to forest dieback, we looked for common regional expressions of forest decline by sampling eleven stands of *N. pumilio* along a latitudinal gradient from 38° 01′S to 43° 01′S. Several authors have already pointed out the benefits of using BAI in dieback studies but few have compared ring-width and BAI measures of dieback (Johnson and Abrams, 2009). Therefore, we compare growth patterns derived from both ring width and BAI to evaluate their application in forest dieback studies of *N. pumilio.* Since endogenous stand dynamics may not be recorded in mean growth estimates, dominant growth patterns within a stand are identified to assess internal dynamical processes associated with *Nothofagus* forest dieback. In addition, our results provide the opportunity to identify potential bias in growth estimates related to traditional sampling strategies of *Nothofagus* forests in the Patagonian Andes.

2. Materials and methods

2.1. Study sites and sampling design

The study sites are distributed across north Patagonia, east of the Andes between 38° and 43° S (Table 1 and Fig. 1). Most selected plots were located in pure *N. pumilio* stands near the eastern limit of the species distribution between 1000 and 1500 m elevation. At Hualcupen and Pino Hachado, *N. pumilio* coexists with dominant, open canopy *Araucaria araucana* trees.

In northern Patagonia (37°–43° S), summers are mild and relatively dry whereas winters are cold and wet (Villalba et al., 2003). At these latitudes, there is a strong precipitation gradient from west to east due to the blocking effect of the Andes. Therefore, trees located near the eastern boundary of *N. pumilio* distribution are more frequently affected by water stress than those located to the west. Total annual precipitation at 41° S ranges from 500 mm at around 900 m near the steppe boundary to 4000 mm at 3000 m in the Andean continental divide.

Study plots were located in forest stands exhibiting external signs of dieback, including partial crown mortality, dead apical stems and branches, damaged bark, presence of hemiparasites and bores from insects and birds. In these stands, high rates of mortality were also registered. There was no evidence of recent fires, selective logging or intensive grazing at these sample stands. Sizes of study plots range from 0.08 to 0.27 ha (Table 1). Unlike