Chapter 14
Forest Decline in Northern Patagonia: The Role of Climatic Variability

Mariano M. Amoroso, Milagros Rodríguez-Catón, Ricardo Villalba, and Lori D. Daniels

Abstract Forest decline is driven by several factors interacting in complex ways, and it is often exacerbated by climate, adding complexity to the process and making it more difficult to identify the causing factors. The long-term perspective provided by tree rings has proven to be successful for disentangling the causes of forest decline worldwide. We present recent dendroecological studies developed to determine the influences of climatic variation on the radial growth patterns and death of trees in declining *Austrocedrus chilensis* and *Nothofagus pumilio* forests in northern Patagonia, Argentina. These results were used to distinguish between possible causes and interactions of abiotic and biotic stress factors versus stand dynamics processes in the development of the forest declines. For our study forests, we found complex interactions between abiotic and biotic factors acting at different spatial and temporal scales that predispose trees, then incite and contribute to the development of the symptoms leading to their subsequent death. We summarize our findings in a conceptual model presenting forest decline as a spiral of processes driven by interactions between abiotic and biotic stress factors that predispose, incite and contribute to stand-level decline in these forests. Our framework formalizes an alternate hypothesis to single causal agents of decline in Patagonian forests by emphasizing the role and importance of climatic variability as a driver of decline.

M.M. Amoroso (✉)
Instituto de Investigaciones en Recursos, Naturales, Agroecología y Desarrollo Rural, Universidad Nacional de Río Negro, El Bolsón, Río Negro, Argentina

CCT CONICET Patagonia Norte, Consejo Nacional de Investigaciones, Científicas y Técnicas, San Carlos de Bariloche, Rio Nego, Argentina
e-mail: mariano.amoroso@gmail.com

M. Rodríguez-Catón • R. Villalba
Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET, CCT-Mendoza, C.C. 330, 5500 Mendoza, Argentina
e-mail: mrodriguez@mendoza-conicet.gob.ar; ricardo@mendoza-conicet.gob.ar

L.D. Daniels
Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada
e-mail: lori.daniels@ubc.ca

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14.1 Introduction

Tree death normally involves multiple processes that can be difficult to understand and reconstruct. Death occurs as a direct result of discrete events or disturbances (White and Pickett 1985; Oliver and Larson 1996), in response to environmental stress (Condit et al. 1995; Villalba and Veblen 1998; Williamson et al. 2000; Suarez et al. 2004), due to direct competition with other trees (Waring 1987; Kobe et al. 1995; Lutz and Halpern 2006), and as a result of complex interactions of different factors (Mueller-Dombois et al. 1983; Hennon et al. 1990; Minorsky 2003). In the latter case, mortality can involve environmental stress factors interacting with different biotic agents in forests of various ages and stages of development, resulting in broad-scale forest decline (Houston 1981; Mueller-Dombois 1983; Manion 1991). Unlike discrete disturbances such as fire, landslides or avalanches, forest declines around the globe are driven by many factors that interact in complex ways making it difficult to identify or isolate specific causes (e.g. Pedersen 1998; Cherubini et al. 2002; Hartmann and Messier 2008; Camarero et al. 2015). Several conceptual models have been developed to describe the process of mortality in trees and forests based on different biotic agents and/or environmental stress (Houston 1981; Mueller-Dombois 1983; Manion 1991). It is now generally accepted that mortality usually involves complex processes and multiple interactions among disturbance agents and stress factors acting at different time scales (Franklin et al. 1987).

Dendrochronology provides a novel method to estimate the timing of tree death, to assess the patterns of tree growth prior to death, and to evaluate the role of climatic events as a driving force contributing to tree death and forest decline (Jump et al. 2006; Sánchez-Salguero et al. 2012). In declining forests, individual trees exhibiting partial crown mortality often have persistent low rates of growth prior to death (LeBlanc and Raynal 1990; Ryan et al. 1994; Bigler and Bugmann 2003; Amoroso and Larson 2010). Temporal changes in tree growth can be used to determine the onset of the decline in symptomatic trees and quantify differences in the vitality of healthy (asymptomatic) versus affected (symptomatic) trees. The substantial reduction in radial growth often exhibited by declining trees indicates reduced water transport through the stem creating a physiological imbalance between the water-demanding foliage and the water-providing roots (Manion 2003). This imbalance in the water-transport system alters the carbon balance and biochemical composition, increasing tree susceptibility to pest, diseases and other stressors (Mattson and Haack 1987; McDowell et al. 2008; Wang et al. 2012). This physiological change initiates a cascade of interconnected events contributing to the process of tree mortality (Manion 1991, 2003). In this context, the dendroecological assessment of the variations in tree growth over time provides useful information on timing and duration of decline processes and can be used to identify signature radial growth patterns indicating trees prone to decline.

In recent decades, several species in the Andean-Patagonian forests of Argentina have exhibited widespread forest decline and tree death. In this chapter, we present recent dendroecological research investigating temporal aspects of decline in *Austrocedrus chilensis* and *Nothofagus pumilio* forests, emphasizing the role of climatic variability as a major triggering factor.

14.2 The Decline of *Austrocedrus chilensis* Forests

14.2.1 Background

Austrocedrus chilensis (D.Don) Pic. Sern.et Bizarri forests exhibit stand-level decline and mortality of overstory trees on mesic sites throughout the species' distributional range in Argentina. This disturbance, locally referred as 'mal del ciprés' (cypress sickness), was first documented about 60 years ago on Victoria Island and near the town of Epuyén in northern Patagonia (Varsavsky et al. 1975; Hranilovic 1988) and has continued to expand up to the present. Because of its magnitude and the ecological and economic consequences, the decline in *A. chilensis* forests represents one of the most important disturbances in Andean-Patagonian forests.

The occurrence of *A. chilensis* decline is generally associated with particular site conditions, specifically stands on low elevation sites with poor soil water drainage (Filip and Rosso 1999, La Manna and Rajchenberg 2004, La Manna et al. 2008a, b, 2012), as well as those at moderate elevations with greater precipitation (Baccalá et al. 1998). In these forests, decline either appears as aggregations of declining and dead trees forming patches of varying sizes immersed in a matrix of asymptomatic trees (Rosso et al. 1994; La Manna and Rajchenberg 2004) or as dispersed declining and dead trees forming a disaggregated pattern within stands (La Manna and Rajchenberg 2004; La Manna et al. 2008a). The decline of the trees often begins in isolated parts of a stand, and then expands forming patches or aggregations of trees in various stages of decline (Havrylenko et al. 1989; Rosso et al. 1994). In declining forests, all individuals are prone to symptoms and eventual death, regardless of their age and size (Hranilovic 1988; Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Loguercio et al. 1998).

Trees in declining *A. chilensis* forests present diverse symptoms before dying. Tree-level symptoms are manifested below and above ground. Below-ground symptoms include brown rot that can affect the main roots or the entire root system and can spread to the root collar and base of the tree stem (Rajchenberg and Cwielong 1993; Barrotaveña and Rajchenberg 1996). The first visible symptom is the loss of tree vigor manifested as progressive discoloration and wilting of leaves, followed by gradual defoliation (Havrylenko et al. 1989). It is believed below-ground symptoms precede the loss of tree vigor and crown symptoms (Varsavsky et al. 1975; Havrylenko et al. 1989; Hennon and Rajchenberg 2000). In general, the loss of vigor of the crown leads to slow death of trees; in some cases, trees die quickly after a sudden change in foliage color (Filip and Rosso 1999). Another symptom associated with loss of vigor and subsequent death of *A. chilensis* trees is the reduction in radial growth of affected trees (Calí 1996; Mundo et al. 2010; Amoroso et al. 2012a, 2015). Recent dendroecological studies have shown the radial growth decline, an internal symptom, actually precedes external crown symptoms (Amoroso et al. 2012a, 2015).

14.2.2 Dendroecological Studies

Tree-ring research over the past decade has enhanced our understanding of the timing, causes and effects of *A. chilensis* forest decline. Investigations have addressed tree-level radial-growth decline, mortality rates, gap formation and stand dynamics, and the role of climatic variability on these processes. A reduction in radial growth is associated with vigor loss and subsequent death of *A. chilensis* trees in declining forests (Calí 1996; Mundo et al. 2010; Amoroso et al. 2012a, 2015). Mundo and collaborators (2010) reported significant differences in the radial growth patterns of trees with and without crown symptoms in declining *A. chilensis* forests. These authors found that the growth of 50 symptomatic living trees was consistently lower than paired asymptomatic trees, and the growth reductions were prolonged over four to six decades. Studying 12 declining stands in the same area, Amoroso and collaborators (2012a) reported over half of the *c.*1000 *A. chilensis* trees that they sampled presented a decline in radial growth relative to asymptomatic trees. They reconstructed the diameters of 632 *A. chilensis* to estimate relative tree size at the onset of decline, showing trees of all diameters were susceptible and radial growth decline was independent of the canopy position of trees. More than half were overstory trees at the onset of decline, 43% of which were living but had crown symptoms and 39% were dead at the time of sampling. The remaining 18% of overstory trees with radial growth decline were classified as having healthy, asymptomatic crowns in the field. This noteworthy finding was common among study sites; 22–40% of trees per stand showed a declining growth pattern but did not exhibit crown symptoms. The sequential order of these two symptoms supports the hypothesis that the reduction in radial growth precedes the loss of crown vigor of affected trees.

The temporal patterns of radial growth decline in overstory trees varied greatly among trees and stands (Amoroso et al. 2012a). At the tree level, two common patterns in the rate of decline of radial growth were found. The majority (78%) of trees exhibited gradual and constant decline in radial growth over time. The other 22% of trees exhibited an abrupt decline over 1–3 years, followed by relatively constant narrow rings over time. The length of the radial growth decline (e.g. the number of years since onset of decline) varied among trees and sites. It averaged 27 years for all trees, with a maximum of 80 years. Scaling up to the stand level, the onset of decline started as early as the 1920s in some stands and as late as the

1960s in others. Within stands, temporal patterns of the number of trees exhibiting radial growth decline also varied. In some stands, 30–50 years elapsed with a steady increase in the percentage of trees exhibiting decline, eventually exceeding 50% of trees. Alternately, the percentage increased abruptly to more than 50% of trees in less than 20 years in other stands.

Several studies have described and attempted to quantify mortality rates in declining *A. chilensis* forests (Havrylenko et al. 1989; Rosso et al. 1994; Baccalá et al. 1998; Loguercio et al. 1998; Rajchenberg et al. 1998), but only a few have estimated years of death of the trees using information obtained from tree-rings (Relva et al. 2009; Amoroso and Larson 2010). Amoroso and Larson (2010) crossdated ring width series of individual trees to determine years of death, then quantified and described long-term patterns of overstory mortality over several decades. These authors found the death of adult trees was erratic, unpredictable and highly variable over time, even in stands exhibiting forest decline. As a result, mortality patterns and growth rates of surviving trees were highly variable within and among stands.

The mortality of overstory *A. chilensis* trees created gaps in the canopy, driving stand dynamics. New trees successfully established in the understory in all stands; however, the abundance of regeneration and response of residual overstory trees was variable (Amoroso and Larson 2010). Understory establishment varied among stands, depending on the density of the overstory. In some stands, new establishment enhanced an ongoing increase in the abundance of *Nothofagus dombeyi* ((Mirb.) Oerst.) relative to *A. chilensis* regeneration, representing an important shift in composition and increase in complexity of stand structure (Amoroso et al. 2012b). Similarly, the radial growth response of the residual overstory trees varied among stands. While trees in almost all stands released in the gaps created by the mortality of overstory trees, no distinctive patterns in timing, number and magnitude were discernable. In some stands, growth releases occurred after single or multiple tree deaths suggesting a coupled relationship between these processes, while in other stands this was not the case (Amoroso and Larson 2010).

Recent dendroecological research has helped understanding another symptom associated with *A. chilensis* forest decline: the partial death of the cambium of living trees (Rajchenberg and Cwielong 1993; Calí 1996). Amoroso and Daniels (2010) reported that partial death of the cambium affected about a third of *c*. 800 living *A. chilensis* trees in declining stands, with greatest affects in subcanopy, symptomatic trees. Living trees can persist for years to decades despite partial death of their cambium (Amoroso and Daniels 2010); Calí (1996) showed partial cambial mortality can precede tree death by 75 years.

14.2.3 Climatic Influence on Radial Growth Decline and Mortality of Trees

Tree-ring studies have shed light on the role of climatic variation as a causal agent of decline and death of A. *chilensis* trees. Mundo et al. (2010) found that the onset of a persistent reduction in radial growth in trees with external symptoms of decline (e.g., chlorotic leaves or defoliated crowns) was influenced by adverse climatic conditions during the previous growing season. Amoroso and collaborators (2015) expanded on this preliminary result and examined the role of inter-annual climatic variation as a factor contributing to the radial growth decline and death of trees. More precisely, these authors examined the effects of drought (a) on the onset of radial growth decline on a large number of dead and living trees stratified by canopy position at the onset of decline, and (b) on the time of death of the trees stratified by radial growth patterns and canopy position at death. The onset of growth decline in a large proportion of trees was significantly associated with moisture deficit. Late spring and summer droughts triggered immediate radial growth decline in overstory trees (65% of the declining or dead overstory trees). Based on the frequency of trees exhibiting an onset of decline in each year, 17 high-magnitude onset-of-decline events were shown to be concurrent with major and moderate droughts in the twentieth century (Fig. 14.1). Similarly, high-magnitude overstory-tree mortality events were concurrent with significant droughts (Amoroso et al. 2015).

Dendroecological studies have shown climatic variability contributes to stand-level forest decline in *A. chilensis* forests (Mundo et al. 2010; Amoroso et al. 2015). In an alternate interpretation, *A. chilensis* tree mortality results from complex interactions among biotic and abiotic factors, including climatic variation (La Manna and Rajchenberg 2004; Greslebin et al. 2007; El Mujtar 2009; Greslebin and Hansen 2009, 2010; Amoroso and Larson 2010; Mundo et al. 2010; Amoroso et al. 2012a, b). Amoroso and collaborators (2015) present a framework for interpreting tree decline and mortality as a forest decline process driven by multiple factors (sensu Manion 1991; Manion and Lachance 1992). Several factors may simultaneously predispose trees to decline, including site condition, genetic variation and the sex of trees, as *A. chilensisis* is a dioecious species. The occurrence of decline and mortality is not random among stands, but associated with sites at low and moderate elevations with poor soil water drainage and those with abundant precipitation (Havrylenko et al. 1989; Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004; La Manna et al. 2008a, b, 2012). Within stands, genetic variation and the sex of trees appear to be important as predisposing factors. El Mujtar (2009) found genetic differences between individuals with and without symptoms and El Mujtar et al. (2011) reported that female trees were more prone to develop symptoms of decline than male trees. Inciting or triggering factors can be abiotic and biotic agents. Dendroecological studies have demonstrated that drought is associated with the onset of decline in radial growth, potentially rendering individuals more susceptible to subsequent factors, including biotic agents (El Mujtar 2009; Mundo et al. 2010; El Mujtar et al. 2011; Amoroso et al. 2015). Other research has implicated the fungus *Phytophthora austrocedrae* (Grel. & E.M. Hansen) as an important agent of forest decline as it causes necrotic lesions in the root system and conduction tissues at the base of the trunk of *A. chilensis* trees (Greslebin et al. 2007; Greslebin and Hansen 2009, 2010; Velez et al. 2012). Both climatic variation and *P. austrocedrae* can incite or ultimately contribute to tree death, and have potential to can act synergistically. Drought can incite stress making trees more susceptible to

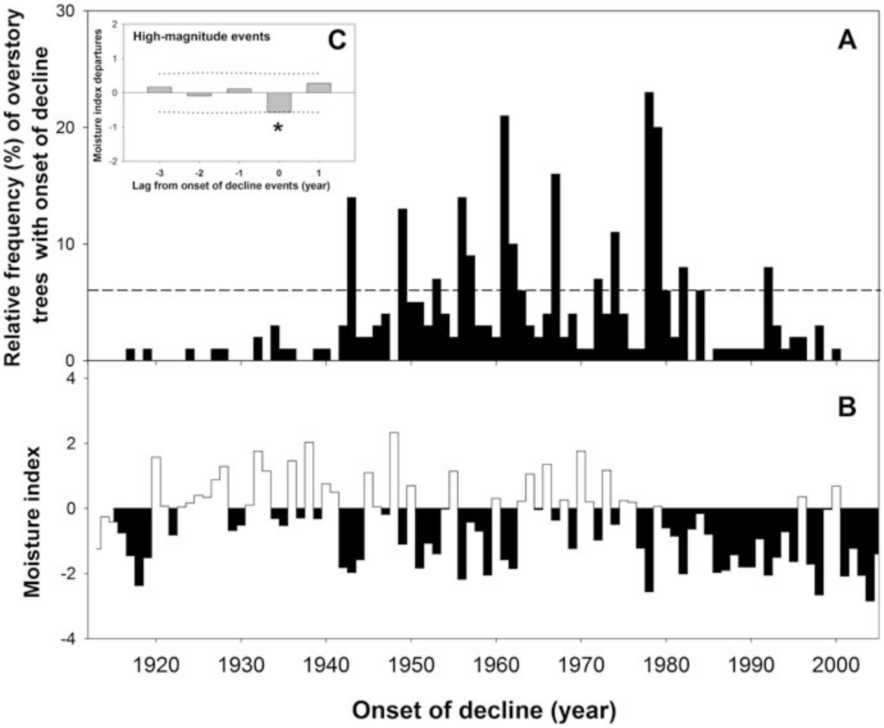

Fig. 14.1 Onset of decline of 301 overstory *Austrocedrus chilensis* trees (**a**) in comparison with the December–February moisture index (**b**) from 1914 to 2005. In the *top panel* (**a**), relative frequency is the percentage of overstory trees exhibiting onset of decline in each year relative to the number of living overstory trees that did not exhibit decline but had the potential to exhibit decline. The *horizontal dashed line* indicates the threshold value above which relative frequencies indicate high-magnitude onset of decline events. In the *bottom panel* (**b**), negative departures (*black bars*) indicate low moisture indices or drought years resulting from low precipitation and/or warm temperature; positive departures (*white bars*) indicate high moisture indices resulting from abundant precipitation and/or cool temperature. In the *upper left* inset (**c**), the association between the onset of decline of high-magnitude events and the December–February moisture is investigated. *Dashed lines* represent the 95% confidence limits based on 1000 Monte Carlo simulations. The *asterisk* indicates a statistically significant departure ($P < 0.05$) from the mean during periods of high-magnitude onset of decline

P. austrocedrae, which generates necrotic lesions that ultimately contribute to tree death (El Mujtar 2009). Alternately, drought and/or infection by *P. austrocedrae* can incite stress, causing trees to exhibit symptoms of decline and making them more susceptible to extreme droughts that ultimately contribute to their death. Amoroso et al. (2015) conclusively showed climatic variation both incites and contributes to the death of *A. chilensis* trees. Similarly, extreme droughts have resulted in widespread death of *A. chilensis* in other parts of northern Patagonia (Villalba and Veblen 1998). It remains possible that other factors predispose, incite and contribute to tree mortality; nevertheless, climatic variation and extreme drought are critical factors driving the decline of *A. chilensis* forests.

14.3 The Decline of *Nothofagus pumilio* Forests

14.3.1 Background

Large areas with partial crown mortality and abundant tree mortality have been observed in *Nothofagus* species since the beginning of the twentieth century in Patagonia (Kalela 1941). Extensive areas affected by forest decline exist along the dry limit of *N. pumilio* distribution in the Patagonian Andes; however, forest dieback in this species has received little attention. According to Veblen et al. (1996), *N. pumilio* stands located in sites with reduced water availability, such as the forest-steppe ecotone or wind-exposed sites, are the most vulnerable to decline. On the regional scale, partial crown mortality in *N. pumilio* is mainly located in the eastern margin of its distribution. The eastern margin of the species distribution mostly corresponds to Argentinean forests and it is relatively dry due to the blocking effect of the Cordillera de Los Andes, which intercepts the wet air masses originated in the Pacific and generates a strong precipitation gradient from west to east. In this area, water availability is reduced due to high temperatures together with the occurrence of low precipitation rates. Consequently, trees located near the eastern boundary of *N. pumilio* distribution are more frequently affected by water stress than those located to the west, which is translated in lower growth rates in these forests (Srur et al. 2013).

At regional to global scales, most studies have focused on the effect of climate variations on tree mortality events (Suarez et al. 2004; van Mantgem et al. 2009; McDowell et al. 2010; Michaelian et al. 2011; Anderegg et al. 2013 and references therein). Comparatively, the influence of climate as a trigger of forest decline related to partial tree mortality and growth decline has been poorly addressed (Leaphart and Stage 1971; Di Filippo et al. 2010; Liu et al. 2013). Extreme climatic events, such as temporary saturation of soils during very wet years (Ogden et al. 1993) or severe droughts (Grant 1984) have been proposed as triggers of forest decline in *Nothofagus* forests (Ogden et al. 1993). Using a combination of dendrochronological methods and instrumental data, Rodríguez-Catón and collaborators (2015, 2016) linked extreme climatic events with past changes in *N. pumilio* tree growth associated with forest decline. They showed that the onset of long-sustained periods of *N. pumilio* growth reduction was induced by adverse climate events such as droughts.

14.3.2 Integrating Stand-Level to Regional-Level Forest Decline

In *N. pumilio* stands affected by forest decline, trees with advanced crown mortality and those with reduced foliage coexist with healthy trees. As a consequence, declining *Nothofagus* forests encompass a whole range of external traits among trees or groups of trees within the same stand; therefore, the particular growth patterns of each tree may contribute differentially when characterizing decline at the stand-level (Bossel 1986). Rodríguez-Catón and collaborators (2015) described in detail the radial growth patterns of all *N. pumilio* individuals at 11 decline-affected stands in northern Patagonia. The study sites were distributed across northern Patagonia, Argentina, along a 500-km transect on the eastern boundary of *N. pumilio* distribution, between 38° and 43° S. Most selected sites were located at pure *N. pumilio* stands between 1000 and 1500 m elevation. Using principal component analysis, Rodríguez-Catón and collaborators (2015) identified the dominant growth patterns in each plot, which surprisingly diverge from the stand mean growth pattern typically calculated to represent tree growth at the stand level. At most sites, three dominant patterns of growth, expressed either as ring widths (RWs) or basal area increments (BAIs), were identified: (1) trees with a sustained reduction in radial growth starting in early 1940s; (2) trees with a gradual reduction from the late 1970s to present; and (3) trees with increasing growth rates since the 1960s. The onset of negative trends in radial growth associated with forest decline (patterns 1 and 2) occurs simultaneously at most stands and negative growth trends were present in all sampled stands. Interestingly, those trees with the highest rates of growth during the early to mid-twentieth century persistently reduced their radial growth to show the lowest rates in recent years. On the other hand, those trees with the lowest growth rates during the early to mid-twentieth century increased their radial growth in the 1960s to show the highest rates of growth at the stand-level today.

The *local growth patterns* exhibiting similar trends in radial growth were subsequently grouped to obtain *regional dominant patterns* of tree growth (Fig. 14.2a). Based on ring widths and basal area increments, two and three *regional dominant patterns* of *N. pumilio* tree growth, respectively, were identified by Rodríguez-Catón and collaborators (2015). Two BAI regional patterns show high rates of growth from early to mid-twentieth century, followed by sustained negative trends over the last 3–6 decades, respectively, whereas the third pattern is characterized by a positive trend since the 1960s (R1–R3 in Fig. 14.2a).

Since tree size or age may be related to long-term trends in radial growth, Rodríguez-Catón and collaborators (2015) calculated mean and standard deviations in the diameter at breast height (DBH) and tested the statistical differences between trees in different pattern. At most stands, trees showing negative trends in growth had significantly larger DBHs. Consistently, larger trees were more frequently associated with declining patterns at the regional scale.

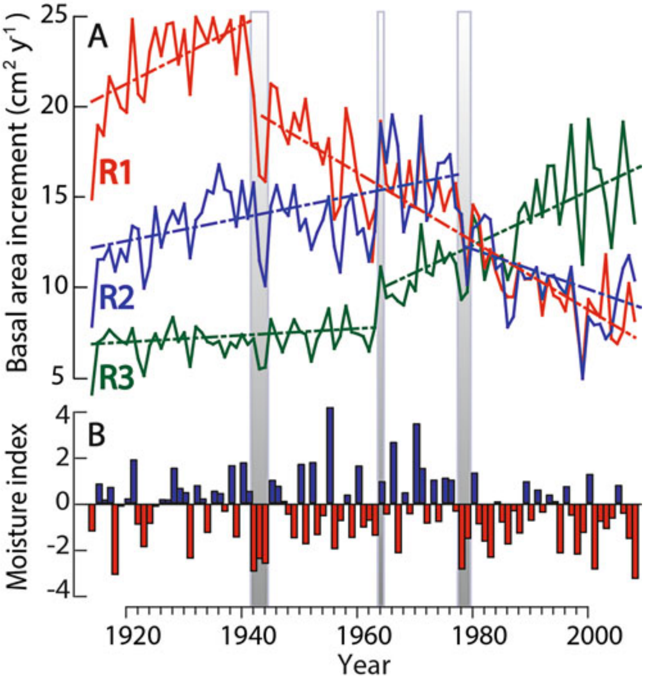

Fig. 14.2 Breakpoints recorded in regional patterns of tree growth in *Nothofagus pumilio* forests with external decline in northern Patagonia (Argentina) during the period 1914–2008. (**a**) Regional basal-area increment patterns R1, R2 and R3. Breakpoints in each growth pattern, were determined using piecewise regression models. (**b**) Barplots represent moisture index departures for December–January. Climatic conditions associated with breakpoints are highlighted with vertical bars. Adapted from Rodríguez-Catón et al. (2016)

These results illustrate several interesting features of tree response to forest decline. First, 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. The analysis based on the complete range of health conditions can identify distinctive growth patterns within declining stands and provide a more comprehensive view of the temporal variations in growth. Additionally, dominant growth patterns within a stand should be identified at the individual level to correctly assess dynamic processes such as forest decline.

Another interesting feature documented in Rodríguez-Catón and collaborators (Rodríguez-Catón et al. 2015) addresses the effect of the pervasive trend of decreasing ring width with increasing DBH. The decrease in ring width with age limits the ability to properly discriminate growth trends associated with forest decline versus those related to tree age. Due to this limitation, these authors concluded that patterns of tree growth related to forest decline are better discriminated using basal-area increments instead of tree-ring widths. As the estimation of BAIs takes into account the diameter of each tree, the age-related noise is eliminated, and the trends in growth associated with forest-decline are better captured.

14.3.3 Climate as a Regional Synchronizing Factor of Growth Decline

In a recent contribution, Rodríguez-Catón and collabortors (2016) compared the tree-growth patterns related to forest decline with climatic variations across the northern Patagonia Andes. The most significant changes in BAI trends over the past 100 years, determined using piecewise linear regression, occurred in 1942 and 1978 (Fig. 14.2a). For pattern R1, the positive trend in radial growth from the early twentieth century until 1942 contrasts sharply with the persistent negative trend from 1942 to the present. Similarly, a change in trend was observed for pattern R2 in 1978. In contrast to the declining R1 and R2 patterns during the past decades, the growth pattern R3 shows a positive trend that starts around 1964 and continues to the present with greater variability in recent years.

The breakpoint in growth trend of the first pattern, R1, was associated with three consecutive extreme dry-warm climate events in 1942–1943, 1943–1944 and 1944–1945 (Fig. 14.2b). Similarly, the abrupt change in growth trend shown in pattern R2 was concurrent with an extreme summer drought during 1978 (Fig. 14.2b). Both events corresponded to severe spring-summer droughts that were preceded by up to 10 years of wet periods (Rodríguez-Catón et al. 2016). In response to the humid environmental conditions from mid-late 1930s to early 1940s, canopy trees recorded the highest rates of growth but were the most affected by the dry-warm extreme event 1942–1944 (Fig. 14.2a, b). After the dry conditions prevailing during 1942–1944, trees in the pattern-R2 group also showed a reduction in the positive trend in BAI. On the other hand, R2 trees maintained a relatively stable rate of growth during the following two decades to reach the highest growth rates during the moist-cool environmental conditions during late 1960s to mid 1970s. These trees were the most affected by the dry conditions during spring-summer 1978, the driest year of the previous 36 years (Fig. 14.2a, b). In contrast, the change in trend to a sustained growth increase in pattern R3 around 1964 was not clearly related to an extreme weather event. A relatively wet and cold period from 1963 to 1977 had possibly favored the steady increase in growth of trees in R3. However, the positive growth trend has continued during the last decades, concurrent with dry and warm conditions in northern Patagonia. In this context, R3 trees may have been favored by the gradual release of resources, such as light and water, due to the progressive dieback of individuals with declining R1 and R2 patterns.

The documented changes in tree growth recorded by Rodriguez-Catón and collaborators (2016) show differences in growth responses of *N. pumilio* trees coexisting at the same stand to unfavorable weather events. Larger trees showing higher growth rates are the most susceptible to show decline in response to abrupt unfavorable climate events as dry spells. During severe droughts, water provided by roots fail to meet the water requirements of large crowns, resulting in the death of some branches and sectors of the cambium. In addition, large trees under warmer conditions increase their respiration rates and their vulnerabilities to adverse climatic events (Gillooly et al. 2001, McDowell et al. 2008, but see Reich et al. 2006). Consistent with our observations, other studies suggest that large, dominant trees are most at risk of suffering drought-driven growth decline (Piovesan et al. 2008; McDowell and Allen 2015). Therefore, the size and current rate of growth of *N. pumilio* trees are related to tree decline by extreme climatic events. In addition, our observations are consistent with the concept of "decline disease stabilizing selection" (Manion 2003). Manion (2003) stated that dominant trees are most likely to be affected by mortality to genetically stabilize forests. According to Manion (2003), short-term environmental disturbances, such as droughts, affecting highly competitive dominant trees, facilitate stress-tolerant trees to attain the upper canopy and, in consequence, breeding positions in the population.

Rodríguez-Catón and collaborators (2016) also noted a reduction in radial growth sensitivity to climate variations following the onset of decline. Statistically significant correlations between spring-summer moisture index and radial growth were observed before the dry event in both R1 and R2 patterns, whereas a loss of growth sensitivity to climatic variations takes place following the dry events. Johnson et al. (1988) postulated that the weaker responses of tree growth to climate after extreme climate events are another manifestation of forest decline. In consequence, stands with forest decline should be used cautiously for tree-ring based climatic reconstructions (Wilmking et al. 2004; Andreu et al. 2007; Büntgen et al. 2010).

Since similar trends in tree growth were recorded between 11 stands of *N. pumilio* along 500 km in northern Patagonia, Rodríguez-Catón and collaborators (2015) concluded that meso- to macro-scale environmental forcings modulate regional forest decline at regional scales.

14.3.4 Predisposing and Triggering Factors According to Manion's Spiral of Forest Decline

We have shown how severe droughts occurring after wet periods trigger the decline of large, dominant *N. pumilio* trees with high rates of growth. Following our results, we propose that tree size and age are factors related to the vulnerability to forest decline. Other predisposing factors in these forests are periods of high growth rates favored by wet periods followed by severe droughts (Rodríguez-Catón et al. 2016). Extreme droughts affecting *N. pumilio* forests along dry environments could be considered the triggering factors of forest decline. Following severe droughts, and in the absence of any observed or reported pathogenic activity, contributing factors in *N. pumilio* may be the repeated occurrence of dry events or other environmental changes.

Rodríguez-Catón and collaborators (2016) work provides valuable insights to assess the susceptibility of trees to climatic impacts. For instance, if the positive trend in radial growth recorded in R3 trees continues, resulting in large trees with fast rates of growth in the near future, these trees will be the most vulnerable to future drought-induced decline, following the pattern recorded in the declining R1 and R2 trees. Thus, early-warning indicators of forest decline in *N. pumilio*, such as big size and high growth rates, should be taken into account to predict future events of drought induced forest decline or mortality (Lenton 2011; Camarero et al. 2015).

14.4 Summary and Conceptual Models of Forest Decline

Forest declines worldwide are driven by many factors interacting in complex ways. Forest decline is often exacerbated by climate, adding complexity to the process and making more difficult to identify the causing factors (e.g. Pedersen 1998; Cherubini et al. 2002; Hartmann and Messier 2008; Camarero et al. 2015). In this context, the long-term perspective provided by tree rings have proved to be successful for disentangling the causes of forest decline (e.g. McClenahen 1995; Beier et al. 2008; Sánchez-Salguero et al. 2012). In this manuscript we present recent dendroecological studies that were used to determine the influences of climatic variation on the radial growth patterns and death of trees in declining *A. chilensis* and *N. pumilio* forests in northern Patagonia. Furthermore, these results were used to distinguish between possible causes and interactions of abiotic and biotic stress factors and stand development processes in the development of the forest declines. For the studied forests we found complex interactions between abiotic and biotic factors acting at different spatial and temporal scales that predispose trees, and incite and contribute to the development of the symptoms leading to the subsequent death of trees.

We summarize our findings within the framework of a the conceptual model (spiral) of forest decline (sensu Manion 1991; Manion and Lachance 1992) presenting processes driven by interactions between abiotic and biotic stress factors that predispose, incite and contribute to stand-level decline in these forests (Fig. 14.3). Site conditions, genetic variation and sex of trees are predisposing factors in the development of the *A. chilensis* decline while site location, wet periods and tree size predispose the occurrence of decline in *N. pumilio* forests. In both forest declines, extreme droughts incite or trigger immediate changes in the radial-growth patterns of trees resulting in consistent declining growth rates over time. For *A. chilensis*, particularly, drought-induced stress could become susceptible to the pathogen *P. austrocedrae*, which would act as a secondary agent of decline but could also act independently affecting healthy trees. Ultimately, adverse conditions due to

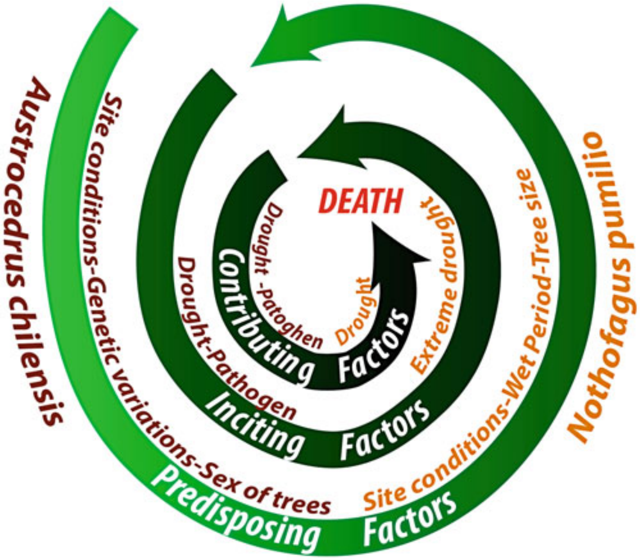

Fig. 14.3 The Manion decline Spiral depicting abiotic and biotic factors that predispose, incite and contribute to stand-level decline and tree death in *A. chilensis* and *N. pumilio* forests in northern Patagonia

climatic variability will contribute leading to tree death in both forests; alternately, the lesions caused by *P. austrocedrae* in *A. chilensis* would eventually kill the trees. Our frameworks formalize the alternate hypothesis to single causal agents of decline in these forests by emphasizing the role and importance of climatic variability as a driver of decline.

There is increasing concern about the effects of climatic variability on forest ecosystems given recently documented climatic change and forecast global warming in the twenty-first century (Dale et al. 2001; Adams et al. 2009; Allen 2009). Numerous studies have documented increased rates of tree mortality and forest decline in diverse forests worldwide seemingly due to the occurrence of droughts in recent decades (Williamson et al. 2000; Guarin and Taylor 2005; Allen et al. 2010; van Mantgem et al. 2009). Furthermore, the effects of global warming are usually exacerbated by extreme events which are difficult to predict but are expected to become more common in the future (IPCC 2013). Climatic predictions suggest an increase in the frequency and intensity of drought events not only in areas where *A. chilensis* and *N. pumilio* forests experience stand-level decline but also in unaffected areas. Based on these considerations, we predict the stand-level processes of decline above described for *A. chilensis* and *N. pumilio* Patagonian forests will exacerbate in the future.

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