Tree health influences diameter growth along site quality, crown class and age gradients in *Nothofagus* forests of southern Patagonia

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ABSTRACT: We examined the influence of tree health on annual diameter increment of trees along gradients in stand site quality, crown classes and tree age in *Nothofagus pumilio* forests of Southern Patagonia. Healthy trees had higher annual diameter increment than unhealthy trees along all gradients (site quality, crown class, tree age). We argue that tree health could be employed as a qualitative variable in models of tree growth to estimate aboveground biomass and carbon stocks in this forest system.

Keywords: *Nothofagus pumilio*; annual diameter increment

Tree growth is an important parameter used in forest management planning (García 1988) and is usually estimated using allometric models of different complexity of variables used to fit them (Vanclay 1994). Previously proposed models of tree growth were age based (e.g. Richards 1959), but recently other stand and individual tree variables have been included (e.g. tree crown class, stand site quality and silvicultural treatments) (Zeide 1993; Vanclay 1994; Trasobares et al. 2004; Adame et al. 2008; Martínez Pastur et al. 2008; Subedi, Sharma 2011). During forest inventories, several variables are measured, and they can potentially be used to increase the accuracy of the estimates of tree growth rates and the rate of accumulation of woody biomass in forests. Assessment of individual tree health can refine estimates of biomass accumulation and tree growth. Tree health is commonly estimated from the external characteristics of trees (Donoso, Caldentey 1996; Martínez Pastur 2006) and recently this assessment and monitoring of forest health have been incorporated into environmental policy and management of environmental resources (Ferretti 1997) to facilitate the access of their use in growth modelling. We define a healthy tree like a tree without external symptoms which are mostly related to fungal diseases. In fact, in southern Patagonia, *Nothofagus* forests are affected by several endemic fungal diseases (e.g. *Postia pelliculosa*, *Piptosporos portentosus* or *Phellinus andinopatagonicus*) (Rajchenberg 1997) that decay living tree trunks from the inside. Wood-decaying fungi may affect or not the diameter growth compared to other healthy issues, but there is a direct relation between the decaying fungi and other damage and diseases. The fungal decay in stems can be facilitated by (*i*) mechanical damage due to wind-exposure or insects (e.g. *Strongylaspis* sp., *Lautarus* sp., *Grammicosum* sp. or *Gnathotrupes* sp.) (CONAF-FAO 2008); (*ii*) cavities produced by woodpeckers (e.g. *Campephilus magellanicus*)

(Ojeda 2004) that facilitate fungal invasion; and (*iii*) hemiparasitic plants (*Misodendrum* sp.) on trunks and branches (Henríquez-Velásquez et al. 2012) that induce tree decay and promote diseases.

The fungal damage and the consequently rotten wood affect the timber yield of natural forests, and the products obtained by the local sawmill industry (Martínez Pastur et al. 2000). Besides this, these fungi can influence individual tree growth, and thus stand productivity along natural gradients (e.g. stand site quality, crown classes and tree age). Here we examine the influence of tree health on annual diameter increment of trees along gradients in stand site quality, crown classes and tree age in *Nothofagus pumilio* forests of Southern Patagonia. We predicted that: (*i*) healthy trees would grow faster than unhealthy trees; (*ii*) the influence of tree health is greater at lower quality sites and lower crown classes than in higher ones; and (*iii*) the influence of tree health on growth rate is greater in older than in younger trees.

MATERIAL AND METHODS

Data collection

Samples were taken in 125 homogeneous, even-aged, pure *Nothofagus pumilio* stands at densities consistent with carrying capacity estimates. Stands on San Justo Ranch, Tierra del Fuego, Argentina (54°06'S, 68°37'W), were selected for sampling across site quality classes and across available stand ages.

The mean height of two dominant individuals and age of stand were used to estimate site index as dominant height at the age of 60 years (SI_{60}) using published height-age relationships (Martínez Pastur et al. 1997) and this placed the stands in one of the three site quality classes (SI_{60} > 19.9 m, SI_{60} = 13.2–19.9 m, SI_{60} < 13.2 m).

The sampled stands had SI_{60} in the range of 9.7 to 23.2 m and stand age in the range of 30 to 450 years. Variable area plots were employed using the Bitterlich wedge sampling method (Bitterlich 1984). The plots were selected based on the following criteria proposed by Martínez Pastur et al. (2008): (a) homogeneous and even-aged stands, (b) dense individual packing without canopy gaps, (c) no dead trees in the plots, and (d) including between 18 to 20 trees in each sampling plot. These conditions are representative of forests under natural dynamics in Southern Patagonia. Forest structure of the sampled stands was described previously in Martínez Pastur et al. (2009).

Tree measurements

In each plot, all trees were sampled with an increment borer, their diameter at breast height (DBH) and total height (TH) were measured, and each individual was categorised by crown class and tree age according to the development phase (Schmidt, Urzúa 1982). Crown classes were classified as: (*i*) dominant, when crowns extend above the general level of the canopy with full partial lighting above and laterally, and therefore they are larger than the average of the mass, with well developed crowns; (*ii*) co-dominant, when crowns are formed at the general level of the canopy, receiving little lighting above and laterally, then the crowns are of medium size and tight development on the sides; (*iii*) intermediate, when trees are lower than the preceding height of crowns included within the overall housing, and received light is little and hardly any from the laterals, with small and tight crowns; and (*iv*) suppressed, when trees are submerged with their tops at a lower level than the general cover, getting no sunlight either above or laterally.

One core was taken from each tree, all of which were oriented towards the centre of the plot. Cores were mounted on wood supports and mechanically polished using gradually finer grades of sandpaper. Each tree-ring width was measured under a microscope (×10) with a digital calliper Mahr MarCal (Mitutoyo, Aurora, USA) to the nearest ± 0.01 mm. We used an estimate of tree growth during the last 20 years (5 periods of 4-year growth in each tree). We assumed no mortality during these 20 years, since no dead trees were included in the plots, and stand growth conditions were not significantly different across a stand (Martínez Pastur et al. 2008). Finally, tree health was categorised by the external characteristics of the tree trunk and crown that indicated decay (Donoso, Caldentey 1996; Martínez Pastur et al. 2001; Martínez Pastur 2006), and included two classes (good quality – trees without external decay, and bad quality – trees with both localised and generalised external decay). Defects included the presence on the trunk and major branches of: (*i*) anomalous growths, presence of galls and mushroom fructifications; (*ii*) cracks, splits, cavities and evident tree decay; (*iii*) dead branches and fallen bark; (*iv*) insect damage to wood and woodpecker activity; or (*v*) general crown dieback (Hellgren, Stenlid 1995; Donoso, Caldentey 1996; Ferretti 1997; Rajchenberg 1997; Martínez Pastur et al. 2000, 2009; CONAF-FAO 2008; Henríquez-Velásquez et al. 2012).

Statistical analyses

Multiple ANOVA was used to analyse total tree height (TH) (m) and annual diameter increment (ADI) (cm·yr^{-1}). Four main factors were used: (*i*) stand site quality (3 levels), (*ii*) tree crown class (3 levels), (*iii*) tree age (2 levels), and (*iv*) tree health (2 levels). Differences in the means of the main effects were examined using Tukey's multiple comparison test at $P \leq 0.05$. Ordination by Principal Component Analysis (PCA) was conducted using a non-centred matrix of stand and tree variables, and a randomisation test (Monte Carlo, with 999 randomisation runs). After the PCA, plots were grouped by stand site quality, tree crown class, age and health.

RESULTS

Our data base included 13,704 growth ring estimates of DBH from 2,456 trees for all the studied gradients (Table 1). The data were not normally distributed and there was an unbalanced distribution of the data among the forest structure classes defining the gradients: (*i*) crown class gradient was 23% for dominants, 41% for co-dominants and 36% for subdominant classes, (*ii*) age gradient was 47% for young trees (< 90–100 years) and 53% for old trees (> 100 to 120 years), and (*iii*) the health gradient was 33% for good and 67% for bad qualities. Additionally, along the stand site quality gradient, less data were obtained in high and medium quality (20% and 25%, respectively) compared to lower quality site stands (55%).

As was expected, total height of the trees varied significantly along site quality (13.2 to 20.6 m), crown class (13.8 to 20.4 m) and tree age (15.0 to 18.9 m) gradients, being higher in older trees. Furthermore, tree height did not significantly change with tree health (16.9 m for good and 17.0 m for bad health) (Table 2). However, annual diameter increment (ADI) differed significantly along all the studied gradients. For example, ADI increased with stand site quality from 0.11 to 0.16 cm·yr^{-1}, with crown classes from 0.10 to 0.17 cm·yr^{-1}, and with tree age from 0.12 to 0.15 cm·yr^{-1}. Finally, the mean ADI was significantly different (F = 5.62, P = 0.018) between tree health classes, being higher in good (0.14 cm·yr^{-1}) than in bad health (0.13 cm·yr^{-1}) trees.

Few interactions were detected in both analyses (Table 2 and Fig. 1). Tree height interacted with: (*i*) site quality × crown class, and (*ii*) site quality × tree age. Both interactions occurred due to changes in the slope among the levels of each factor. Differences between factors in stands with lower site quality were smaller compared to stands at higher quality sites (Fig. 1a). ADI presented significant interactions with: (*i*) site quality x crown class, (*ii*) site quality × tree age, and (*iii*) crown class × tree age, and also at the third and fourth interaction levels (Table 2). Most of these interactions also occurred due to changes in the slope of the curves in each interaction graph among the levels of each factor, where differences in lower site quality stands were minor than in those of higher site qualities. The only exception was observed in site quality × tree

Table 1. Number of samples (data pairs of growth ring estimates) classified by stand site quality, tree crown class, tree age and tree health

Factor	Level	Stand site quality			Total
		high (SI_{60} > 19.9 m)	medium (SI_{60} = 13.2–19.9 m)	lower (SI_{60} < 13.2 m)	
Crown class	DOM	600	798	1,770	3,168
	COD	1,242	1,236	3,144	5,622
	INF	948	1,434	2,532	4,914
Age	young (< 120 yr)	1,716	1,716	2,976	6,408
	old (> 120 yr)	1,074	1,752	4,470	7,296
Health	good	1,116	1,200	2,214	4,530
	bad	1,674	2,268	5,232	9,174
Total		2,790	3,468	7,446	13,704

SI_{60} – site index at the age of 60 years, DOM – dominant, COD – co-dominant, INF – intermediate and suppressed trees

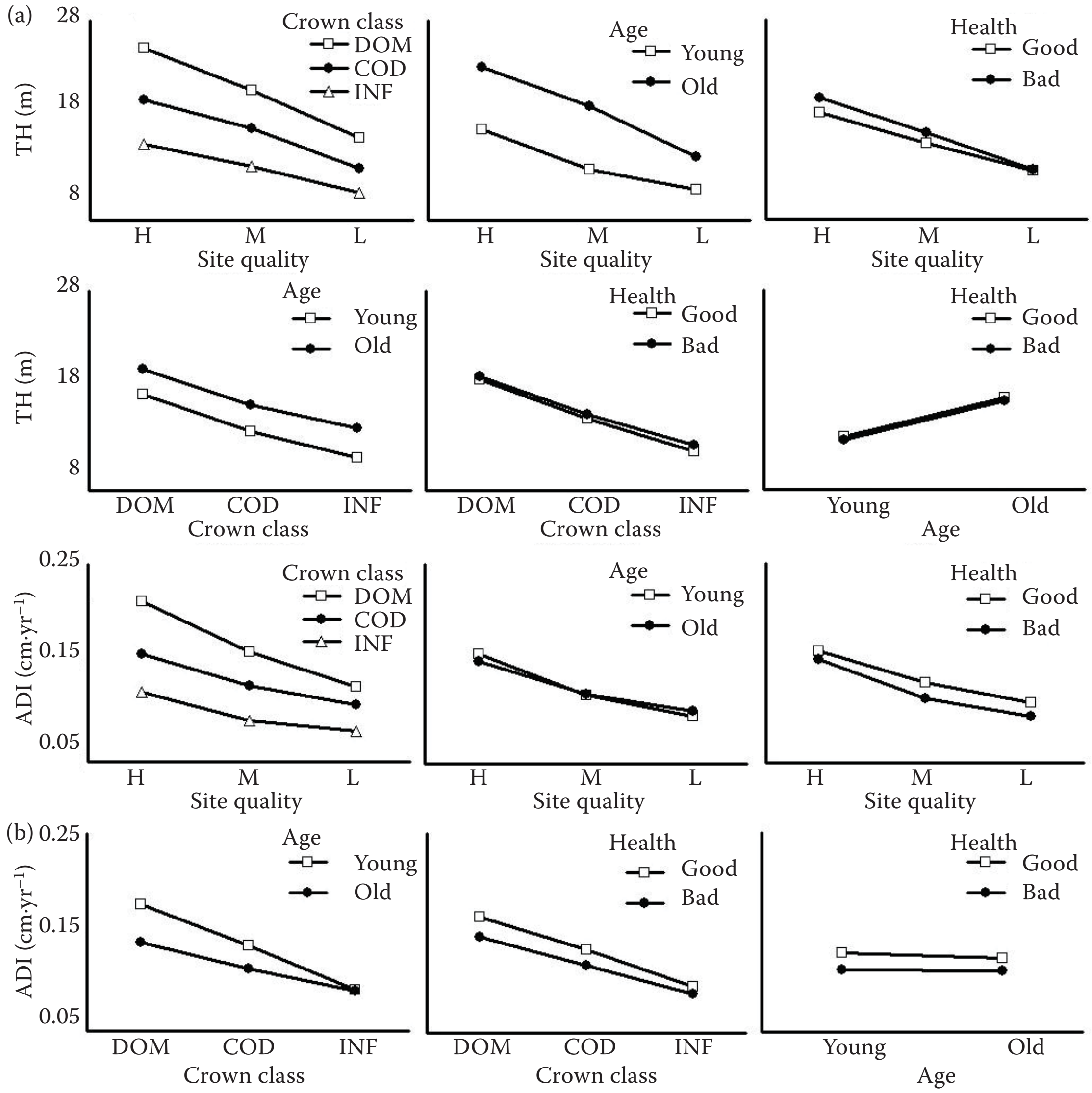

Fig. 1. Simple interactions of multiple-way ANOVA

TH – total tree height, ADI – annual diameter increment, H – SI_{60} > 19.9 m, M – SI_{60} = 13.2–19.9 m, L – SI_{60} < 13.2 m; DOM – dominant, COD – co-dominant, INF – intermediate and suppressed trees; tree age: young indicates < 120 years, old indicates > 120 years

age (Fig. 1b), where ADI was higher in young trees in high site quality stands, and lower in young trees in low site quality stands.

In the PCA only the first two axes were significant ($P < 0.002$). Axis 1 explained 92.3% of the variance, axis 2 explained 3.7%, while the other axes (3 to 5) explained 4% (Table 3). In axis 1, variables presented the following order of importance: site quality > tree age > crown class > tree health > ADI, while in axis 2 the order of importance was: crown class > tree age > site quality > tree health > ADI. Grouping the plots using forest structure variables showed graphically the described differences in the studied gradients and detected by the ANOVA (Table 2). Site quality and crown class gradients clearly separated homogeneous groups (Fig. 2a and b), where site quality was better explained by axis 1 and crown class by axis 2. Tree age and health gradients generated overlapping groups (Fig. 2c and d), equally explained by both axes (1 and 3).

DISCUSSION

Crown class, tree age, and site quality of stands are commonly included in models of individual tree growth (Klepac 1976; Payandeh, Wang 1994; Wang, Payandeh 1994; Hasenauer, Monserud 1996; López Sánchez et al. 2003).

Table 2. Multiple factor ANOVA performed on total tree height and annual diameter increment, considering stand site quality, tree crown class, tree age and tree health as main factors

Factor	Level	TH (m)	ADI (cm·year^{-1})
Site quality (A)	high	20.64^{a}	0.163^{a}
	medium	16.94^{b}	0.132^{b}
	low	13.23^{c}	0.108^{c}
	F	364.60 (< 0.001)	61.14 (< 0.001)
Crown class (B)	DOM	20.43^{a}	0.172^{a}
	COD	16.48^{b}	0.134^{b}
	INF	13.83^{c}	0.098^{c}
	F	238.77 (< 0.001)	97.55 (< 0.001)
Age (C)	young	14.99^{a}	0.145^{a}
	old	18.88^{b}	0.124^{b}
	F	266.28 (< 0.001)	24.41 (< 0.001)
Health (D)	good	16.90^{a}	0.140^{a}
	bad	16.96^{a}	0.130^{b}
	F	0.07 (0.796)	5.62 (0.018)
A × B	*F*	5.73 (< 0.001)	5.39 (< 0.001)
A × C		16.73 (< 0.001)	7.54 (< 0.001)
A × D		0.80 (0.450)	0.06 (0.944)
B × C		0.50 (0.608)	9.39 (< 0.001)
B × D		0.55 (0.576)	0.47 (0.623)
C × D		0.00 (0.984)	1.75 (0.185)
A × B × C		0.08 (0.988)	2.94 (0.020)
A × B × D		0.69 (0.597)	0.72 (0.579)
A × C × D		0.28 (0.755)	4.17 (0.016)
B × C × D		0.38 (0.686)	2.39 (0.092)
A × B × C × D		0.20 (0.939)	2.81 (0.024)

TH – total tree height, ADI – annual diameter increment, high – SI_{60} >19.9 m, medium – SI_{60} = 13.2–19.9 m, lower – SI_{60} < 13.2 m, DOM – dominant, COD – co-dominant, INF – intermediate and suppressed trees, young indicates < 120 years, old indicates >120 years, *F* – Fisher's test, different letters – significant Tukey's test at α = 0.05

As was expected, in our study, ADI increased with stand site quality and crown class of the trees, and decreased with tree age, as was previously described for *Nothofagus pumilio* forests (Peri, Martínez Pastur 1996; Martínez Pastur et al. 1997, 2001, 2005, 2008; Lencinas et al. 2002; Cellini et al. 2012). There is a direct effect of damage and disease on the forest yield, either by reduced tree vigour or a reduction in growth rate and/or mortality (Baurele et al. 1997). Several authors have identified tree health as an important factor affecting the tree growth (Kozlowski et al. 1991; Manion 1991; Dobbertin 2005), but it has not been included in models of tree growth. This could be due to the fact that tree growth modelling is mainly developed for plantation forests under intensive silvicultural management (Porte, Bartelink 2002), where tree health issues are less frequent or important. Tree health is relevant in native unmanaged forests, such as Patagonian *Nothofagus* forests, where 50–60% of the individuals present localised or generalised defects due to massive fungal attacks (Martínez Pastur et al. 2001; Rosenfeld et al. 2006; Paillet et al. 2010).

The tree health trends in the literature are consistent with our own findings. Tree health greatly influenced timber growth along site quality gradients in *N. pumilio* forests (Martínez Pastur et al. 2000, 2009), and the representation of trees in poor health increased from 60% in the high to 70% in low quality sites in stands. In addition, mean

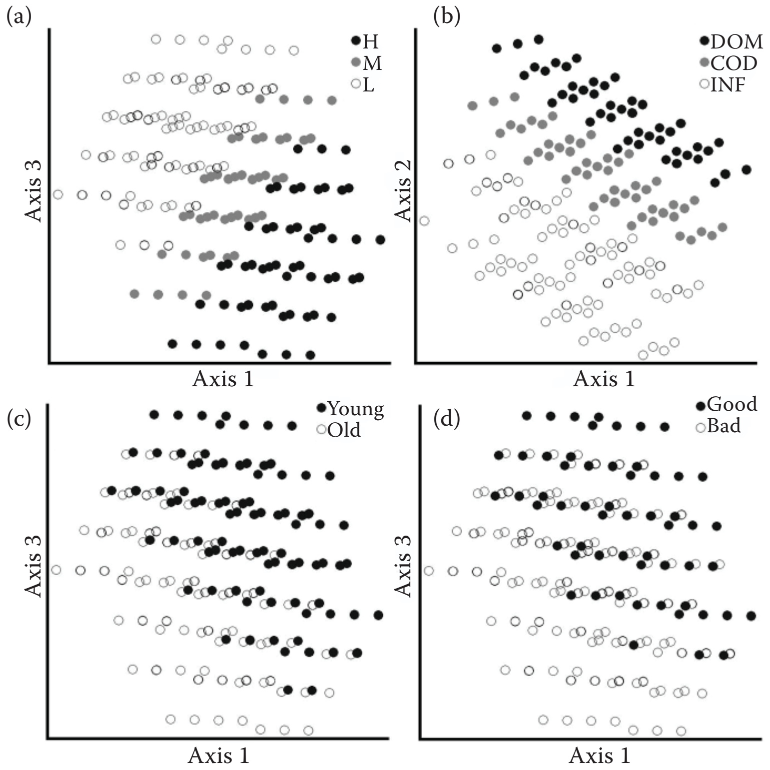

Fig. 2. Principal component analysis (PCA) ordination

A – site quality of the stands, high – SI_{60} > 19.9 m, medium – SI_{60} = 13.2–19.9 m, lower – SI_{60} < 13.2 m; B – crown class of the trees, DOM – dominant, COD – co-dominant, INF – intermediate and suppressed trees; C – tree age, young indicates < 120 years, old indicates > 120 years; D – tree health

ADI was significantly higher in healthy trees, and along the studied gradients (site quality, crown and tree age).

Responding to our predictions: (*i*) healthy trees will grow faster than diseased trees, (*ii*) the influence of the health of the tree is greater at sites of lower quality and lower crown classes than in the upper, and (*iii*) the influence of the health of the trees on the growth rate is higher in older than younger trees. Tree health is mainly related to sapwood health, but the presence of microorganisms responsible for fungal attacks also influences physiological processes at the whole tree level. Amoroso et al. (2012) stated that bad health in trees reduced diameter growth due to decreases in photosynthesis and carbon balance as a result of a generalised stress (Dobbertin 2005). The lower ADI might be an indirect result of the increased

Table 3. Variance and eigenvectors for five axes in the principal component analysis (PCA), using stand site quality, age, crown class, health and annual diameter increment (ADI) of the trees as explanatory variables

Axis	Eigenvalue	Variance (%)	Cumulative variance (%)
1	2,7155.9	92.3	92.3
2	1,080.8	3.7	96.0
3	752.3	2.6	98.6
4	410.4	1.4	99.9
5	4.7	0.01	100

Variable	Axis				
	1	2	3	4	5
Site quality	–0.6686	0.2843	0.6712	–0.1473	0.0062
Age	–0.4869	0.4094	–0.5372	0.5535	0.0207
Crown class	–0.4222	–0.8643	0.0055	0.2732	0.0013
Health	–0.3706	–0.0665	–0.5107	–0.7729	0.013
ADI	–0.00196	0.0082	–0.0136	0.0008	–0.9997

ADI – annual diameter increment

consumption of nutrients and energy associated with the production of defence compounds and repair of tissues in the zone of advanced decay of the tree (Hellgren, Stenlid 1995). Besides this, the decline in ADI at the individual level should not be interpreted as a decrease in growth at the stand level (e.g. growth of healthy trees may be positively affected by disease-induced decreases in growth and vitality of their neighbours) (Froelich et al. 1977). This is called compensatory growth and contributes to the total stand growth (Oren et al. 1985), where at low levels of herbivore damage, growth reactions of individual trees range from immediate decline to overcompensation (Rötzer et al. 2012).

Koricheva (2002) classified the costs of herbivore damage into three major groups, which are also applicable to other pathogens and stress situations: allocation costs, ecological costs and opportunity costs. Allocation costs define the internal trade-offs between growth, defence and reproduction within the individual plant. Under these conditions of limited resources, the tree has a choice either to invest in growth to stay competitive against its neighbours, or to adapt to biotic and abiotic stress to keep the gained resources (Rötzer et al. 2012)

In our study, these statistical differences between healthy and unhealthy trees reflected in differential ADI did not change along the studied gradients, where the magnitude of the difference was similar among classes.

However, the presence of defects and pathogens can influence tree dynamics (e.g. under natural dynamics some dominant trees may be reduced to lower crown classes) (Schmidt, Urzua 1982; Martínez Pastur 2006). Besides this, we expected a higher percentage of unhealthy trees in stands in the advanced stages of regeneration (Donoso, Caldentey 1996), which can be explained by self-thinning in the early development stages, and thus mortality is observed mainly in unhealthy trees in the advanced stages (Martínez Pastur 2006). Nevertheless, differences in the percentage of healthy and unhealthy trees also remained constant when it was compared between young and old stands.

Modelling and forest planning

Forest planning requires accurate models to achieve management objectives (Gregoire 1993). Volume and yield estimations are crucial for short-term planning in forest management plans and during harvesting (Martínez Pastur et al. 2000, 2009), where tree health greatly influences estimates of timber volume (Martínez Pastur et al. 2001). In this context, growth models are crucial for long-term planning at the landscape level and for the silvicultural management to be applied (Wang, Huang 2000; Kjell, Stein 2003; Martínez Pastur et al. 2008). Usually, these models include a few variables related to age and tree density rather than health or tree characteristics (Martínez Pastur 2006).

However, native forests have natural variability, which is very difficult to explain or model at the landscape scale, but it can be easily quantified by stand-scale forest inventories (Martínez Pastur et al. 1994). Tree health can be described using the external characteristics of the tree stem and crown based on proportions of rotten wood (Donoso, Caldentey 1996; Martínez Pastur et al. 2001; Martínez Pastur 2006) and can be potentially employed in growth models. We characterised trees as healthy and unhealthy, where damage and diseases were conflated into a single measure. For this reason, potential correlations between damage and disease classes and their effect on ADI should be studied in future research. Different intensities of damage and disease should also be evaluated to increase the accuracy of the growth modelling.

CONCLUSIONS

Designing accurate growth models is one of the biggest challenges facing sustainable forestry, without introducing higher costs associated with data acquisition. Incorporating a visual measure of health in the tree list used in forest estate modelling can increase accuracy. We found out that healthy trees had higher annual diameter growth than unhealthy trees along environmental and stand-condition gradients (stand site quality, crown class and tree age).

Acknowledgments

The authors gratefully thank the Centro Austral de Investigaciones Científicas, R. Vukasovic of Servicios Forestales Consultancy, San Justo Ranch and Los Castores Sawmill for their support during the realization of this work. Finally, we also thank Ch. Anderson for his comments.

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Received for publication June 4, 2013
Accepted after corrections August 27, 2013

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