

# Influence of fire severity on stand development of *Araucaria araucana*–*Nothofagus pumilio* stands in the Andean cordillera of south-central Chile

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**Abstract** Fire is the prevalent disturbance in the *Araucaria*–*Nothofagus* forested landscape in south-central Chile. Although both surface and stand-replacing fires are known to characterize these ecosystems, the variability of fire severity in shaping forest structure has not previously been investigated in *Araucaria*–*Nothofagus* forests. Age structures of 16 stands, in which the ages of approximately 650 trees were determined, indicate that variability in fire severity and frequency is key to explaining the mosaic of forest patches across the *Araucaria*–*Nothofagus* landscape. High levels of tree mortality in moderate- to high-severity fires followed by new establishment of *Nothofagus pumilio* typically result in stands characterized by one or two cohorts of this species. Large *Araucaria* trees are highly resistant to fire, and this species typically survives moderate- to high-severity fires either as dispersed individuals or as small groups of multi-aged trees. Small post-fire cohorts of *Araucaria* may establish, depending on seed availability and the effects of subsequent fires. *Araucaria*'s great longevity (often >700 years) and resistance to fire allow some individuals to survive fires that kill and then trigger new *Nothofagus* cohorts. Even in relatively mesic habitats, where fires are less frequent, the oldest *Araucaria*–*Nothofagus pumilio* stands originated after high-severity fires. Overall, stand development patterns of subalpine *Araucaria*–*N. pumilio* forests are largely controlled by moderate- to high-severity fires, and therefore tree regeneration dynamics is strongly dominated by a catastrophic regeneration mode.

**Key words:** *Araucaria araucana*, mixed-severity fire, *Nothofagus*, stand development model, Villarrica National Park.

## INTRODUCTION

An important research focus in vegetation dynamics is on how natural disturbances affect forest structures and species composition at different spatial and temporal scales (Oliver 1981; Pitcher 1987; Turner *et al.* 1994, 1997; Spies 1997; Spies & Turner 1999). Important attributes of ecological disturbances that influence their impact on vegetation and post-disturbance opportunities include the type, frequency, magnitude (intensity and severity) and spatial distribution of disturbance events (White & Pickett 1985; Glenn-Lewin *et al.* 1992). In the absence of direct observation of fire intensity (i.e. heat released) or of fire severity (i.e. lethality), the effects of past fires have become the focus of substantial controversy in retrospective studies of forest dynamics where fire potentially may occur at low severities killing mainly understorey plants and juvenile trees or at high severity killing most or all canopy trees (Covington *et al.* 1997; Covington

2000; Allen *et al.* 2002; Baker *et al.* 2007; Hessburg *et al.* 2007; Sherriff & Veblen 2007). The current paper examines the roles of past fires of varying severity in shaping the mosaic of *Araucaria*–*Nothofagus* forests in south-central Chile.

Fire effects and vegetation responses are spatially heterogeneous (Agee 1993, 1998; Fulé *et al.* 2003). Spatial patterns of forest structure may reflect spatial variability in both fire severity and in the underlying abiotic environment (Romme 1982; Agee 1993; Hessburg *et al.* 2007). Fire severity includes a continuum from almost no effect on forest structures to nearly complete mortality of the canopy and undergrowth (Kaufmann *et al.* 2006). High-severity fires that kill most canopy trees are often followed by new establishment of trees of the same or a different species creating a distinct post-fire cohort (Oliver 1981; Romme 1982; Hessburg *et al.* 2007). In contrast, low-severity fires result in no or little mortality of canopy trees, and typically do not result in a large post-fire cohort (Baker *et al.* 2007). Some forests have been shown to have had a variable severity (also termed 'mixed and variable') fire regime in which both low- and high-severity fires

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Accepted for publication August 2009.

occurred historically (Kaufmann *et al.* 2000; Ehle & Baker 2003; Sherriff & Veblen 2006). In a variable-severity fire regime, fire intervals tend to be longer than in an exclusively low-severity fire regime, and more importantly there are some high-severity fires (i.e. lethal to a large fraction of canopy trees in a stand) that strongly influence forest structure (Fulé *et al.* 2003; Hessburg *et al.* 2007). Fires that were of variable severity over relatively short distances are likely to create fine-scale patchiness in the forest age structure (Fulé *et al.* 2003; Kaufmann *et al.* 2006).

Coarse-scale disturbances play dominant roles in structuring the *Nothofagus* forests in the mid-latitudes of the Andean Range. Nearly all forest types – including *Araucaria–Nothofagus* forests – in the Andean cordillera of south-central Chile are exposed to coarse-scale disturbances such as blowdowns caused by wind, earthquake-triggered landslides, volcanic activity, snow avalanches and snow-related damage, and wild-fire (Veblen & Ashton 1978; Veblen 1979; Veblen *et al.* 1981; Veblen 1982; Veblen 1985; Veblen *et al.* 1992; Donoso 1996; Lara *et al.* 2003; Pollmann & Veblen 2004; Fajardo & Alaback 2005). Specifically in the case of *Araucaria–Nothofagus* forests, fire is the most pervasive disturbance (Heusser *et al.* 1988) and has been shown to be the key disturbance factor controlling the dynamics of these forests (Burns 1991, 1993; González 2002; González *et al.* 2005). Both the *Araucaria–N. pumilio* and the *Araucaria–N. antarctica* forest types appear to be strongly influenced by a mixed-severity fire regime – a gradient from low- and moderate-severity surface fires to high-severity crown fires (Burns 1993; González *et al.* 2005). At relatively mesic sites, *Nothofagus pumilio* colonizes gaps and open areas created by fire more successfully than *Araucaria*; it forms dense thickets and grows faster than young *Araucaria* trees. Similarly, at moderately xeric sites, *N. antarctica* dominates recently burned areas because of its vigorous resprouting, while seedlings of *Araucaria* establish slowly under the canopy of *N. antarctica*. Because of the limited dispersal range of its large seed and slow initial growth, the more shade-tolerant *Araucaria* seedlings tend to establish beneath parent trees left by fires that did not kill all canopy trees (González & Veblen 2007). At mesic sites, vigorous resprouting by large bamboos (*Chusquea culeou*) creates dense understoreys of tall culms that tend to exclude establishment of *Araucaria* (Finckh & Paulsch 1995; González 2002). Nevertheless, across the range from xeric to mesic sites, *Araucaria* trees can regenerate if they establish immediately after mortality events, including fire, that kill one or more canopy trees (Veblen 1982; Burns 1991; Finckh & Paulsch 1995; Finckh 1996).

Despite the recent advances in the study of *Araucaria–Nothofagus* forest dynamics in the Andean region of mid-latitude Chile and Argentina, and analogous progress in the ecology of subtropical

forests of *Araucaria angustifolia* in south-east of Brazil (Backes 2001; Duarte *et al.* 2006; Souza 2007), there is little understanding of how variability in the severity of past fires has shaped the structure of individual stands of the *Araucaria–Nothofagus* landscape. In this study, we use data on tree population age and size structures to interpret the occurrence of past fires of different severities and to develop a simple model of *Araucaria–Nothofagus* stand development that explicitly incorporates variable fire severity.

## METHODS

### Study sites

Two study sites in *Araucaria–Nothofagus pumilio* subalpine forests in Villarrica National Park (Fig. 1) were selected for study: Quillehue (39°35'S and 71°31'W) and Palguín (39°47'S and 71°84'W). Both sites are located in the Andes range between approximately 1250 and 1400 m a.s.l. and are bordered at lower elevation by predominantly *Nothofagus*-dominated deciduous-evergreen communities (i.e. *N. dombeyi* and *N. nervosa*). In the Quillehue area, most stands are situated on gentle slopes of the foothills adjacent to Lanin Volcano with a generally northern topographic aspect (dry in the Southern Hemisphere). In Palguín, stands are located on gentle slopes within a more dissected topography. Although some *Araucaria* stands within the Park were logged in the 1940s, stands of unlogged forests were selected as study sites.

The study area is dominated by a west-coast maritime climate with a mild Mediterranean influence, reflected by a winter-maximum in precipitation and relatively dry summers (Miller 1976). According to a nearby climate station (Pucón located at 230 m a.s.l., time period 1985–2006), annual precipitation varies between 1300 and 3000 mm with nearly two-thirds occurring in winter (between May and September). In the study areas, located at higher altitude, precipitation could reach more than 4000 mm, the majority falling as snow in the winter months (June–August). Mean annual temperature is 9.3°C, with a minimum of 4.6°C (July) and a maximum of 13.9°C (February). Snow cover persistence is highly variable, but in most years the *Araucaria* forest understorey is covered by snow from late April through October. Throughout the region, most of the soils are derived from ash deposited by relatively recent volcanic activity (Casertano 1963). In general, in the study area soils vary from poorly developed, sandy textured soils, with relatively shallow organic horizons to deep, medium textured and well drained soils inhabited preferentially by mesic *Nothofagus*-dominated forests.

### Field sampling and data analyses

In the *Araucaria–Nothofagus pumilio* forests, stands selected for sampling were chosen to represent: (i) different stand development stages from relatively recent post-fire through old (>300 years) post-fire stands; and (ii) a range of forested habitats as judged by topographic position, understorey veg-

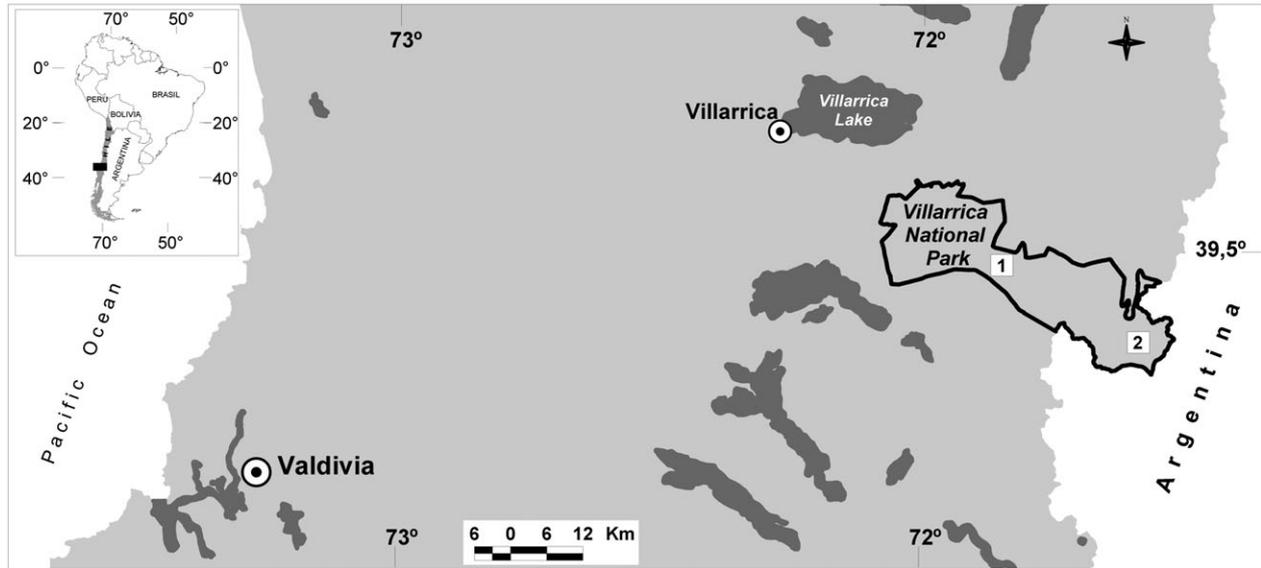


Fig. 1. Map of study sites in Villarrica National Park (1 = Palguin; 2 = Quillehue).

Table 1. Summary of stand characteristics arranged by development stages

Stands	Plot size <sup>†</sup> (m <sup>2</sup> )	Elevation (m)	Aspect	Slope (°)	Basal area (m <sup>2</sup> ha <sup>-1</sup> ) <sup>‡</sup>					
					<i>Araucaria araucana</i>		<i>Nothofagus pumilio</i>		Total	
					Live	Dead	Live	Dead	Live	Dead
<i>Recent post-fire stands</i>										
Q-3	200 (400)	1275	–	2	59.5 (80.2)	13	8 (11.8)	0.2	67.5	13.2
Q-5	1000	1400	–	2	43 (67.7)	0	20.5 (32.3)	3	63.5	3
Q-8	225	1265	N	20	13.5 (14.6)	0	79 (85.4)	0	92.5	0
Q-9	100	1260	–	1	70 (73.3)	0	25.5 (26.7)	0	95.5	0
Q-12	100	1260	N	3	80.5 (70.6)	0	33.5 (29.4)	0	114	0
P-4	100	1291	SSE	3	70 (72.2)	0	27 (27.8)	0.5	97	0.5
<i>Mid-development post-fire stands</i>										
Q-1	400	1270	–	Undulating	43.5 (60)	2	29 (40)	1.5	72.5	3.5
Q-4	800	1320	N	8	46 (64.8)	0.5	25 (35.2)	4	71	4.5
Q-11	400	1270	–	0	0.5 (0.6)	0	79 (99.4)	0	79.5	0
P-3	600	1280	SSE	3	34 (39.3)	0	52.5 (60.7)	3.5	86.5	3.5
Q-7	600	1330	SSW	20	40 (57.2)	0	30 (42.8)	0	70	0
Q-10	600	1250	NNE	2	44 (64.3)	0	24.5 (35.7)	0	68.5	0
P-1	200 (800)	1390	S	8	12 (14.2)	0	72.5 (85.8)	6.5	84.5	6.5
<i>Old post-fire stands</i>										
Q-2	1000	1280	–	1	43 (50.6)	0	42 (49.4)	0	85	0
P-2	600	1388	SW	3	13 (16.7)	0	65 (83.3)	2	78	2
Q-6	1000	1260	–	1	79.5 (88.3)	0.5	10.5 (11.7)	0.5	90	1

Dead basal areas include just dead-standing trees. <sup>†</sup>Between parentheses plot sizes for *A. araucana* trees. <sup>‡</sup>Between parentheses basal areas in percentage.

etation and elevation (Table 1). Identification of stand development stages was based primarily on the population structure of *N. pumilio* which establishes abundantly after fire and forms conspicuous post-fire cohorts (González *et al.* 2005). The following stages of stand development were recognized (Table 1): (i) recent post-fire stands; (ii) mid-development post-fire stands; and (iii) old post-fire stands.

The basic stand characteristics used to distinguish each stage were diameter and age frequency distributions of both species, which were supplemented by the physiognomic appearance of each *Araucaria*–*N. pumilio* stand. During the last 300 years fire has strongly shaped the patch structure of this landscape resulting in an abundance of relatively young post-fire stands and fewer old stands.

Within selected stands, we located and sampled 16 plots of 100–1000 m<sup>2</sup>, recording the site characteristics (i.e. aspect, slope and elevation) along with other topographic information and location. Plot size was adjusted to accommodate the wide range in stand densities so that a sufficient number of trees were included to allow a reliable interpretation of the tree population structure of each patch sampled. Thus, young dense post-fire patches were sampled with relatively small plots whereas open stands of large old trees required plots of approximately 1000 m<sup>2</sup> to capture at least 25 trees to allow interpretation of the development of that patch. In each plot, all live and dead trees (>5 cm diameter at breast height, d.b.h.) were measured for d.b.h. and cored (one core per tree) at a height of approximately 0.3 m above the ground for age determination. Trees were cored to the pith. For each increment core, the following information was recorded: core height, species, d.b.h. and canopy position (i.e. overtopped, intermediate, codominant, dominant, emergent). To estimate seedling ages and the number of years required for a tree to grow to coring height, 11 *Araucaria araucana* seedlings and 10 *Nothofagus pumilio* seedlings were harvested at two sites that are similar to current canopy conditions in sampled stands (Veblen 1992). At 30-cm height, seedlings of *Araucaria* harvested from relatively open sites had a mean of 13.8 years ( $n = 11$ ; range = 4–31 years). *Nothofagus pumilio* seedlings, at the same height and harvested from similar site conditions, were younger than *Araucaria* seedlings with a mean of 8.3 years ( $n = 10$ ; range = 3–23 years). However, these differences were not statistically significant ( $t$ -test;  $t = -1.59$ ; d.f. = 19;  $P < 0.1267$ ). Because of the limited seedling age data, in the age-class figures, age is given as age at coring height rather than correcting for time required to reach coring height.

Each forest patch (ranging from approx. 9–300 ha) that contained a sampled plot was intensively searched for fire-scarred trees. To determine the exact fire dates for individual stands we cut partial cross sections from fire-scarred trees (McBride 1983). Information collected for each fire-scarred tree included: species, d.b.h., number of visible fire scars and the azimuth of the scar face. Location (UTM coordinates) of each fire-scarred tree sampled was recorded using a handheld global positioning unit. Processing of tree cores and fire scars followed standard procedures (McBride 1983; Stokes & Smiley 1996). Fire dates were cross-dated by measuring ring widths and using the computer program COFECHA (Holmes 1983). Tree-core samples were counted and dated to determine the earliest ring date. To determine tree ages in cases where the pith was not intercepted, Duncan (1989) geometric method was used to estimate the number of missing rings near the centre, for up to a maximum of 20 and 30 years for *Nothofagus* and *Araucaria*, respectively.

## RESULTS

### Stand development of *Araucaria*–*Nothofagus pumilio* forests

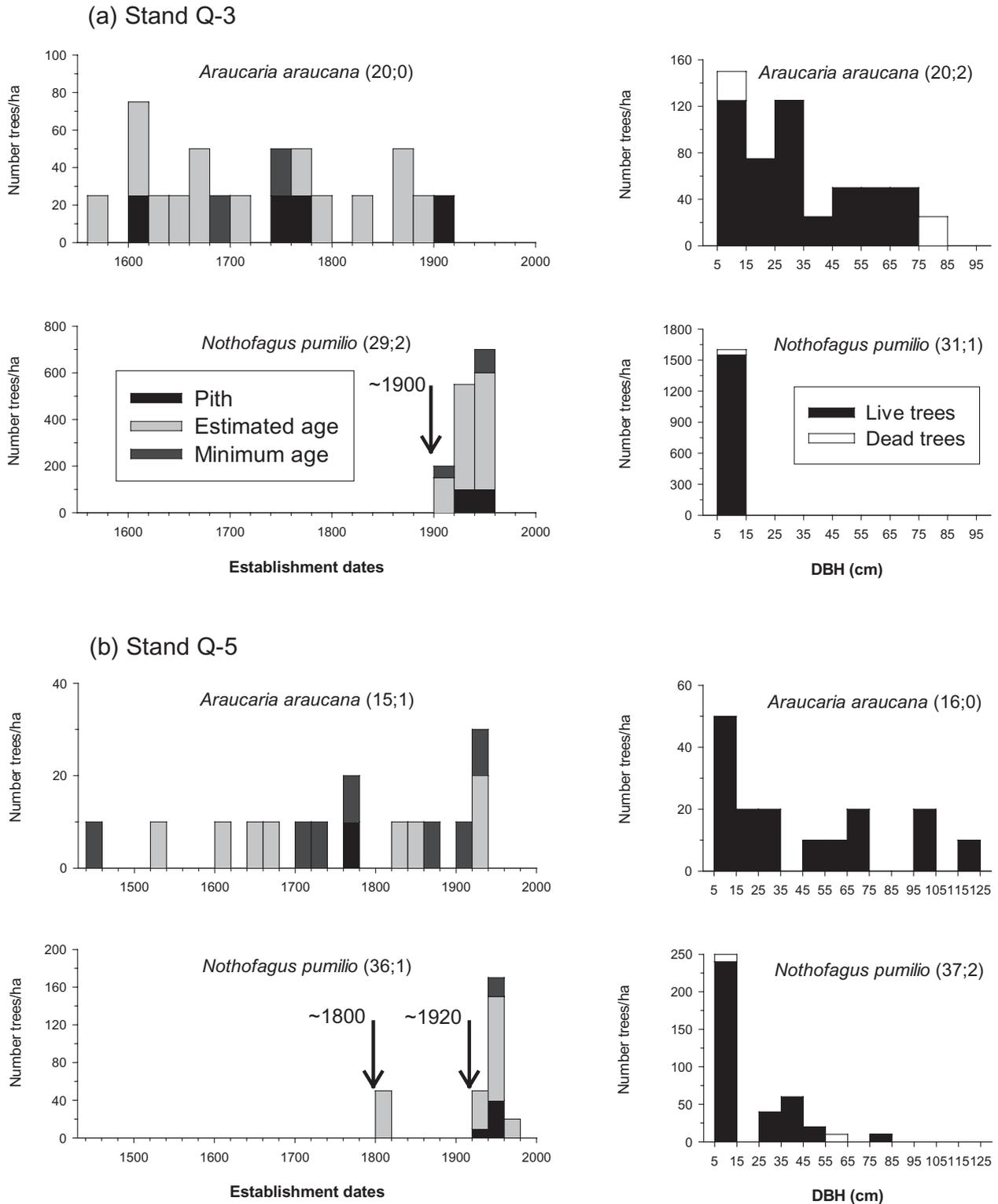
All sampled stands were exclusively dominated by *Araucaria* and *Nothofagus pumilio* tree species. The

post-fire stand age and size structures identified in the study area represent the full range of stand development patterns (*sensu* Oliver 1981) for which there was any observational support in our study area.

### Recent post-fire stands

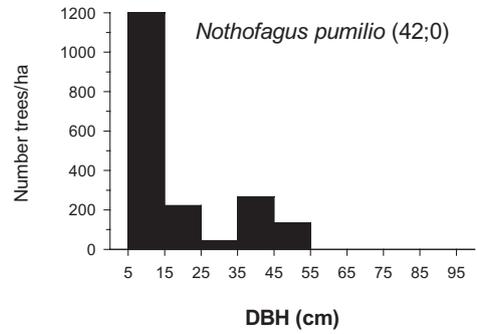
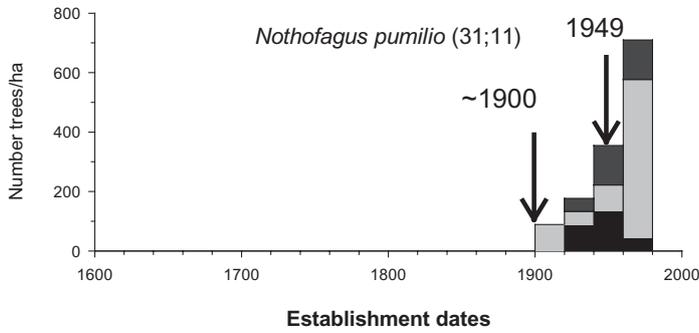
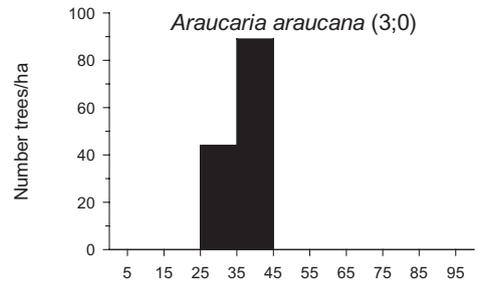
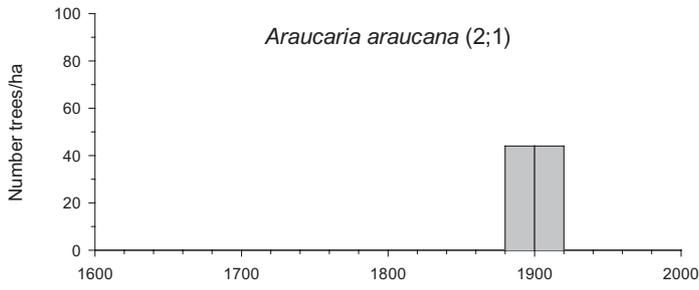
Recent and dense post-fire cohorts (<100 years old) of *Nothofagus pumilio* are the dominant feature of this stand development phase (Fig. 2). An older *Nothofagus* cohort represented by the survival of remnant trees was also a common property of several stands in this stage. For example, stands Q-8, Q-9 and Q-12 all located in the same area and affected by the same fire events (approx. 1900 and 1949), had two relatively distinct *Nothofagus* cohorts that established under a relatively open canopy of remnant *Araucaria* trees (Fig. 2c–e). Similarly, stand Q-5 exhibited two clear cohorts, one that established around 1800 and a younger cohort that began establishing in the 1920s (Fig. 2b). Although stands Q-3 and P-4 apparently show just a single *Nothofagus* cohort (approx. 1900), several *Nothofagus* remnants, which were not within the sampled plot, were scattered throughout the stand along with other *Araucaria* individuals (Fig. 2a,f). For the younger *Nothofagus* cohort, greater than 80% of its regeneration occurred over a time period of 40 years. Thus, in most stands tree frequency distributions are narrow bell-shaped age distributions, except stand Q-8, where the *Nothofagus* cohorts appear to be overlapping (Fig. 2c). In this stand, *Nothofagus* established after fires in approximately 1900 and 1949, and the two cohorts overlap in their size distributions. Many of the trees that established after the 1949 fire (and some trees established between 1927 and 1940 likely as a result of fire) were suppressed by older trees already present and consequently remained in the smallest size-class. Trees in the >40 cm d.b.h. size-class included both trees that established after the 1900 fire as well as a few fast-growing trees that established after the 1949 fire but outside the suppressing influence of canopy trees.

The *Araucaria* component in each stand varied from a few large old remnant trees to populations spanning a wide age range and forming a relatively open canopy. Even though post-fire *Araucaria* establishment is typically less dense than *Nothofagus* establishment, some stands showed a distinct pulse of establishment associated with the most recent fire disturbances. For instance, stand Q-12 had two relatively conspicuous pulses of tree establishment that match a fire event in approximately 1900 and another fire-scar-based fire in 1949 (Fig. 2e). Also, stand Q-5 showed a marked increase in *Araucaria* establishment associated with a fire event estimated to have burned in the 1920s (Fig. 2b).



**Fig. 2.** Stand structure of recent post-fire stands. Age bins are 20 years, and d.b.h. bins are 10 cm. For age distributions, the numbers in parentheses indicate the number of cored trees and number of excluded trees. For size distributions, the number of live and dead trees is given in parentheses. Minimum ages refer to trees incomplete cores that represented >70% of the tree radius and to trees for which the number of missing years to centre exceeded 20 years according to Duncan's (1989) method. Arrows indicate dated fire scars in or near the plot; '~' indicates approximate fire dates derived from maximum ages of post-fire cohorts.

(c) Stand Q-8



(d) Stand Q-9

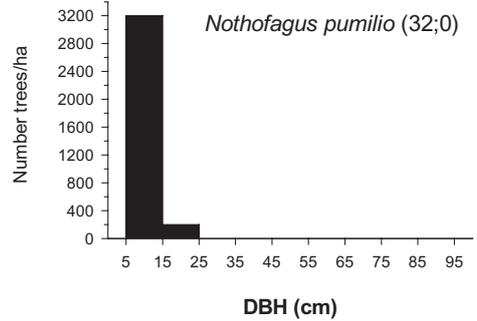
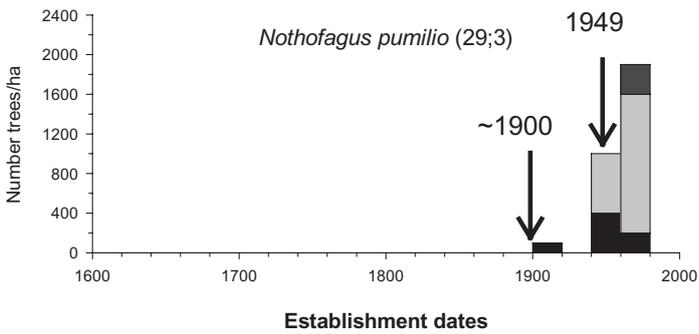
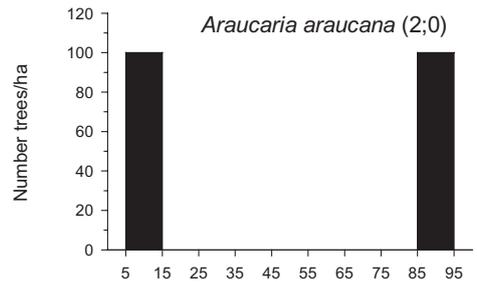
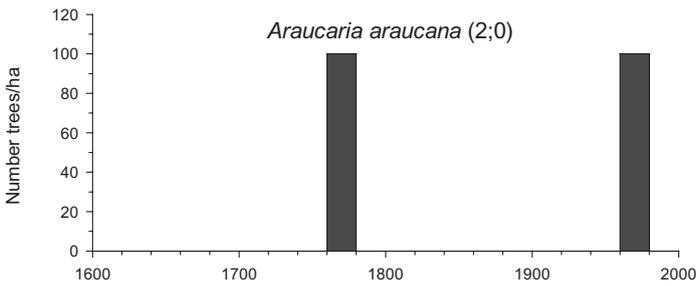
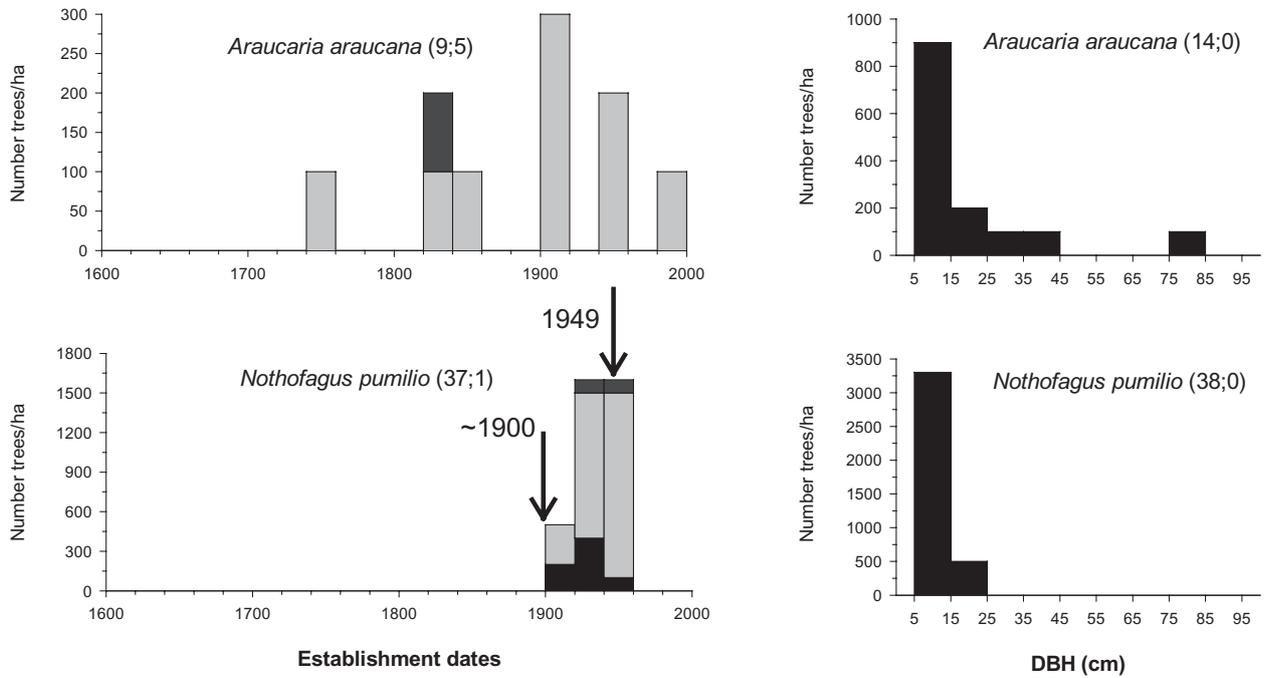


Fig. 2. Continued

(e) Stand Q-12



(f) Stand P-4

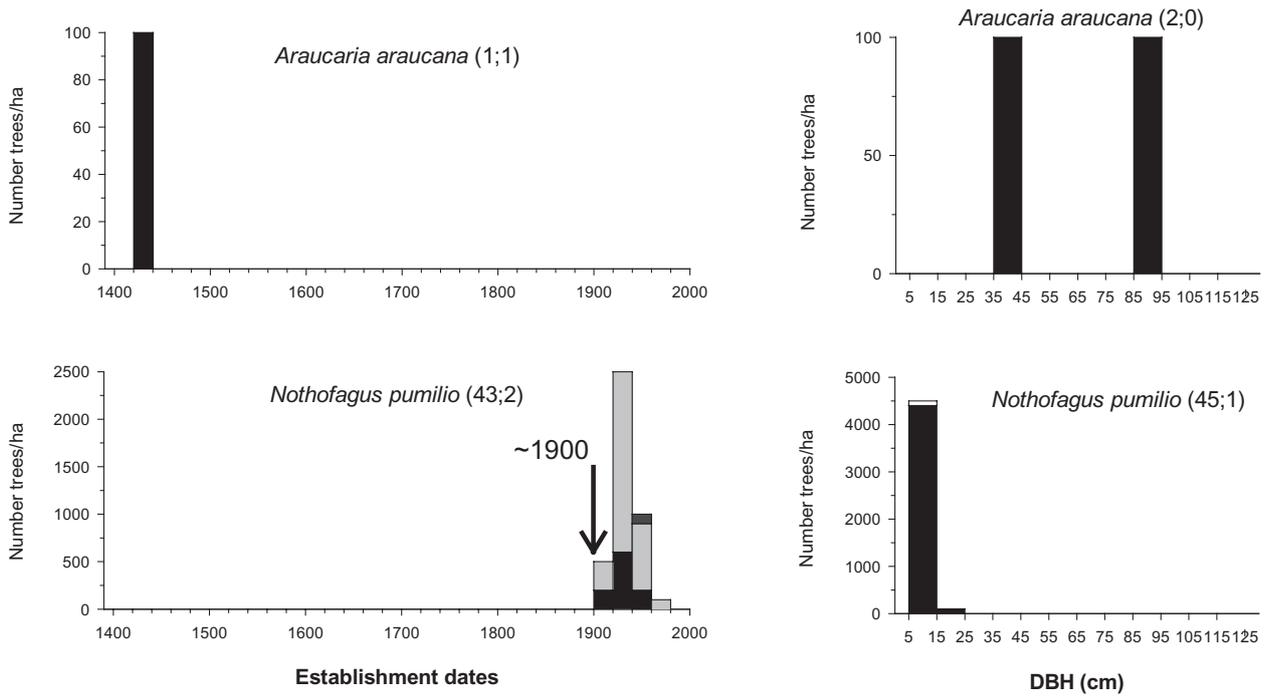


Fig. 2. Continued

**Table 2.** Frequencies of trees in crown classes in each stand sampled

Stand	Species	Overtopped	Intermediate	Main canopy		Emergent
				Codominant	Dominant	
<i>Recent post-fire stands</i>						
Q-3	Aa	6 (1)	6	1	8 (1)	
	Np	24 (1)	8			
Q-5	Aa	6	3	1	6	
	Np	24 (1)	2	5	6 (1)	
Q-8	Aa			2	1	
	Np	10	13	1	18	
Q-9	Aa		1			1
	Np	7	26			
Q-12	Aa	8	2	1	3	
	Np	4	19	10	5	
P-4	Aa				1	1
	Np	37 (1)	8			
<i>Mid-development post-fire stands</i>						
Q-1	Aa	6 (1)	2	1 (1)	5	1
	Np	29 (11)	33	3	1	
Q-4	Aa	12 (4)	3	1	4	1
	Np	0 (1)	6 (6)	5 (2)	15	
Q-11	Aa	1				
	Np				33	
P-3	Aa	3	9		2	
	Np		5 (5)	7 (4)	32	
Q-7	Aa	1	3		10	
	Np	5	7	1	10	
Q-10	Aa		3	1	5	2
	Np	2	3	2	12	
P-1	Aa	1	2		3	
	Np		1 (1)	9 (4)	12	
<i>Old post-fire stands</i>						
Q-2	Aa	1	1	3	5	
	Np	1		7	11	
P-2	Aa		1		2	
	Np			5 (1)	19	
Q-6	Aa	9 (3)	16 (2)	4	14	1
	Np		4	1 (2)	2	

In parentheses, number of dead individuals.

Although identification of post-fire cohorts was based primarily on tree ages, in a few cases the size distributions of trees were helpful in describing and interpreting stand structures. Precise age determination of the oldest trees was sometimes impeded by rotten stems. Consequently, the size distribution of trees in some stands is necessary for fully describing the structure of stands of recent post-fire cohorts mixed with remnant trees that are old and decayed (e.g. Q-5, Fig. 2b).

Total live basal area (BA) in the stands ranged from approximately 64–114 m<sup>2</sup> ha<sup>-1</sup> (Table 1). Typically *N. pumilio* constituted less than approximately 30% of the live BA. In terms of BA, only stand Q-8 was dominated by *Nothofagus* with 79 m<sup>2</sup> ha<sup>-1</sup> (85%). However, the high BA obtained for *Araucaria* in some stands could be due to the effect of large trees in relatively small plots (e.g. Q-9, Q-12 and P-4) and may not be representative of the broader landscape.

Basal area from dead *Nothofagus* trees was typically present in the lower size-classes for the stands Q-3, Q-5 and P-4 (Fig. 2a,b,f). Nearly all of these trees were suppressed individuals classified as over-topped in the context of canopy position (Table 2).

The general physiognomic appearance of younger stands is that of a main canopy (codominant and dominant crown classes) with few emergent *Araucaria* trees over a subordinate stratum of *Nothofagus*. For example, in stands Q-3, Q-5 and P-4, most individual trees are classified in the overtopped crown class, which is underneath the main canopy and emergent *Araucaria* trees in the stand (Table 2). Young trees in the over-topped crown class form a homogeneous and dense stratum where competition to gain a dominant position is intense. In stands with two cohorts, individuals are more evenly distributed throughout most crown classes (Table 2).

### Mid-development post-fire stands

The mid-development stage was characterized by the presence of one or more *Nothofagus* cohorts in the stands. Single even-aged stands varied in maximum age between 120 and 160 years (Fig. 3a–d). The absence of older *Nothofagus* cohorts suggests the occurrence of high-severity fires affecting these stands during the mid to late 1800s. The frequency distribution of *Nothofagus* establishment is distinctly bell-shaped with a period of tree establishment commonly lasting approximately 80 years. However, a high percentage of trees (between 73% and 93%) establish in short time periods of 40 years. In stands Q-1, Q-4 and P-3, *Araucaria* trees exhibited relatively irregular establishment over broad time periods that includes many pre-fire establishment dates, which implies that many of these trees survived the catastrophic fire (Fig. 3a,b,d). Conversely, stand Q-11 located in a more mesic site was primarily dominated by *Nothofagus* species, with few large *Araucaria* individuals interspersed throughout the stand (Fig. 3c). In addition to massive *Nothofagus* establishment after fire events, in these stands *Araucaria* show a slight pulse of tree establishment that is synchronous with the *Nothofagus* establishment (Fig. 3a,b,d).

The diameter distribution of the single *Nothofagus* cohorts exhibits a positively skewed distribution reflecting the competitive abilities of some individuals to grow faster and gain a dominant canopy position (Fig. 3a–d). For example, stands Q-1 and P-3 show a stage of development in which a slight size differentiation has occurred, resulting in high tree density in the lower size-classes (i.e. 5–15 and 15–25; Fig. 3a,d). In contrast, more developed or older stands such as Q-4 and Q-11 reveal individuals that were more broadly distributed in several size-classes (Fig. 3b,c). Stand Q-11, located in a more mesic site, had substantially faster tree growth resulting in some very large individuals (>55 cm d.b.h.) and a broad size distribution ranging from 15 to 65 cm d.b.h. In cases of more advanced stand development, smaller individuals (mostly <15 cm d.b.h.) are strongly suppressed. Similarly, it is in these small-diameter classes that most trees are dead.

Three mid-development post-fire stands were characterized by the presence of at least two relatively distinct post-fire *N. pumilio* cohorts that established after 1800 (Fig. 3e–g). In these stands, the recruitment periods of different cohorts appear to be overlapping, which increases the difficulty of clearly distinguishing among cohorts. Based on fire-scar data, for example, stand Q-7 was affected over the last 200 years by a series of fire events (i.e. 1827, 1861, 1909 and 1944) that are not clearly reflected by pulses of establishment (Fig. 3e). The same situation occurred in stand Q-10, which was affected by fires in approximately 1900 and 1949 (Fig. 3f). As a result, these events generated a pattern of recruitment that equivocally can be inter-

preted as one broad and extended pulse of establishment. An apparently simpler situation was revealed by the age distribution in stand P-1, which has two clear *Nothofagus* cohorts (Fig. 3g). However, based on its d.b.h. distribution and apparent homogeneous structural characteristics, this stand looks similar to a single even-aged cohort. Thus, this case exemplifies the importance of determining the complete age data as a more precise way to determine the true stand structure, especially for older cohorts.

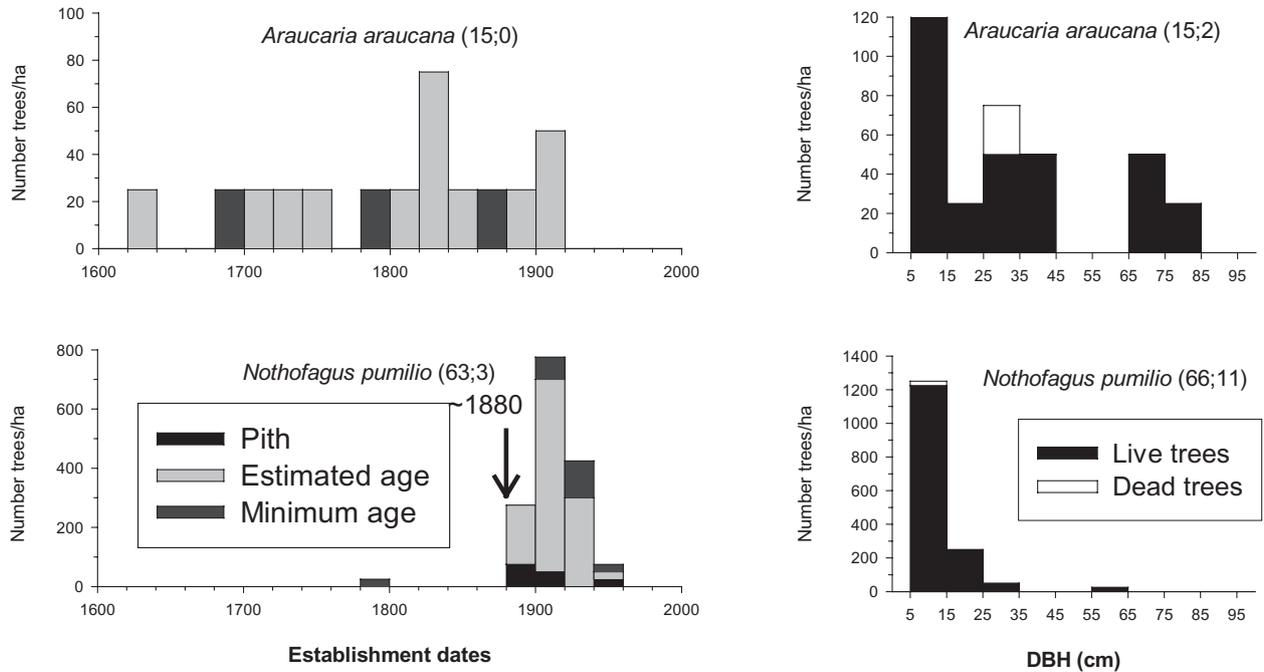
Similarly, *Araucaria* establishment distribution was mostly irregular and/or sporadic (Fig. 3e–g). Stands Q-7 and Q-10 had individuals that established throughout the late 1600–1900 period. Also, in the stands Q-7 and P-1, pulses of *Araucaria* establishment tend to coincide with periods of *Nothofagus* recruitment following fire events in 1827 (for stand Q-7), and approximately 1800 (for stand P-1).

Total live BA in this development stage ranged from 69 to 87 m<sup>2</sup> ha<sup>-1</sup> (Table 1). In contrast to young post-fire stands, *Nothofagus* species constitute >35% of the total live BA. In stand Q-11 and P-1, particularly, *Nothofagus* trees almost completely dominated the stand reaching the greatest percentage of BA (85% and 99%, respectively) among stands. Less than 7% of the BA in each stand (based on a total that includes live and dead trees) corresponded to dead standing trees. *Nothofagus* trees were the primary contributor to dead BA, especially individuals in the lower size-classes and overtopped or intermediate crown classes (Fig. 3; Table 2). Stand Q-11 did not have dead standing trees at this stage of stand development. It seems that the faster growth of *Nothofagus* accelerated the stem exclusion phase as indicated by the absence of individuals <15 cm. In addition, fire scars on several *Nothofagus* trees in the stand suggest that a surface fire dated to approximately 1950 could have thinned the stand and eliminated most of the already dead material. As a result, *Nothofagus* and *Araucaria* trees were mainly concentrated in the main canopy classes (i.e. codominant and dominant classes; Table 2).

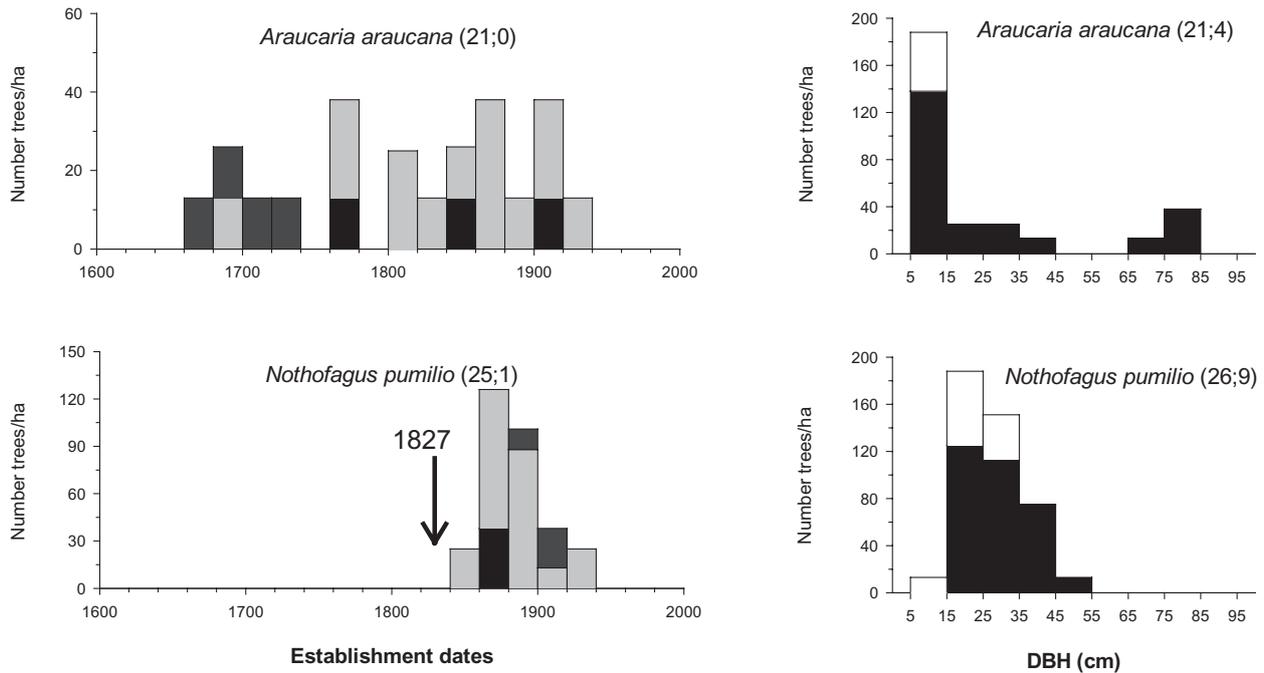
### Old post-fire stands

The most advanced stage of forest development found in the landscape, old post-fire stands, is characterized by the presence of relatively older *N. pumilio* cohorts established since approximately 1700 (Fig. 4a). The oldest *Araucaria* trees exist in this development stage and exceed 500 years in age (Fig. 4a). These old-stands were not common in the landscape and were generally located in more mesic habitats. In some cases, stands were heavily dominated by *Araucaria* with individuals establishing in nearly all time periods (e.g. stand Q-6). In other cases, *Nothofagus* individuals were the main component of the stand (e.g. stand P-2)

(a) Stand Q-1

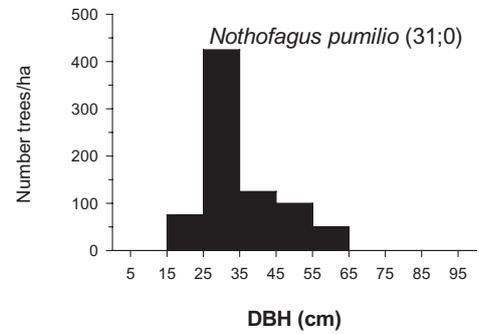
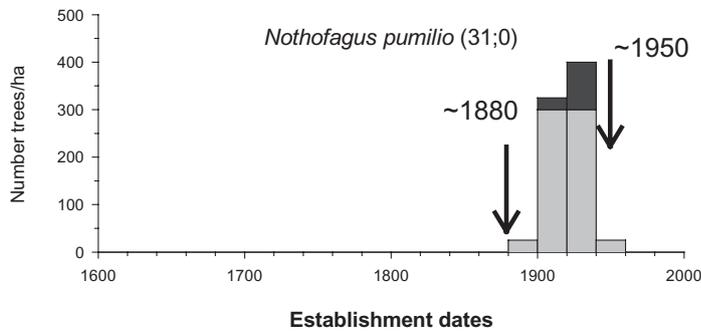
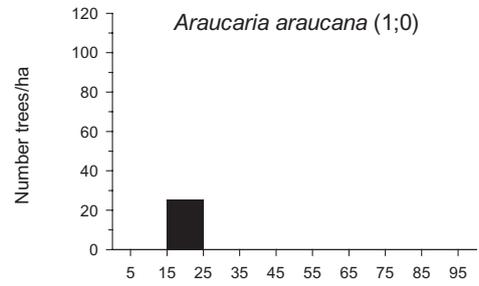
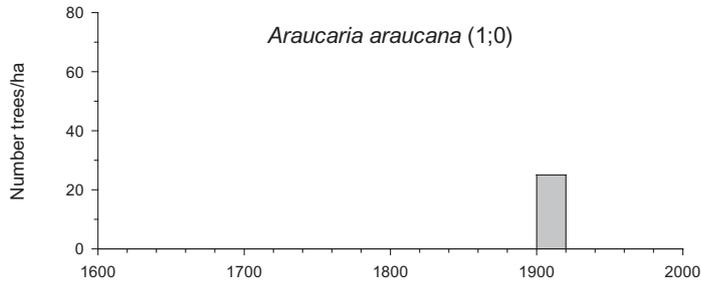


(b) Stand Q-4



**Fig. 3.** Stand structure mid-development post-fire stands. Age bins are 20 years, and d.b.h. bins are 10 cm. For age distributions, the numbers in parentheses indicate the number of cored trees and number of excluded trees. For size distributions, the number of live and dead trees is given in parentheses. Minimum ages refer to trees incomplete cores that represented >70% of the tree radius and to trees for which the number of missing years to centre exceeded 20 years according to Duncan's (1989) method. Arrows indicate dated fire scars in or near the plot; '~' indicates approximate fire dates derived from maximum ages of post-fire cohorts.

(c) Stand Q-11



(d) Stand P-3

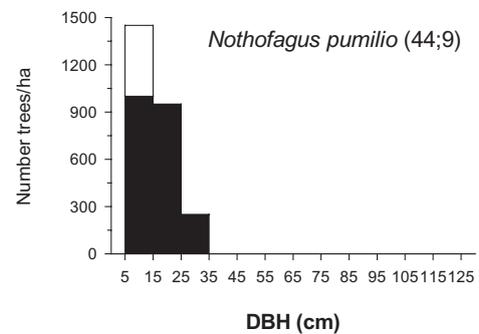
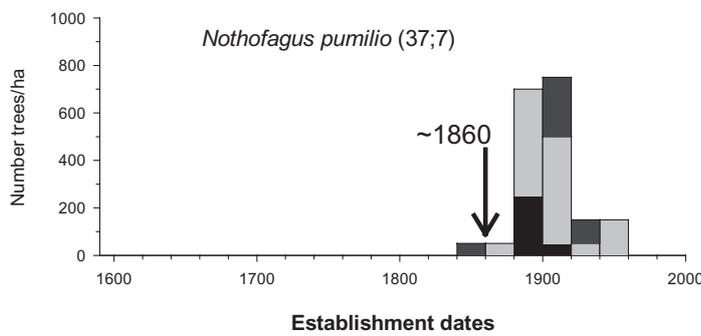
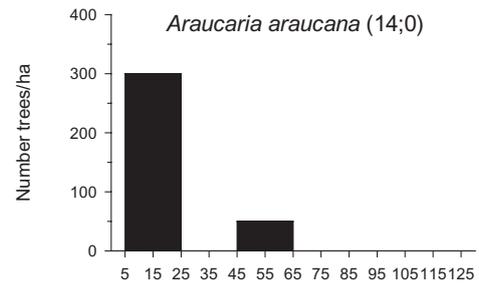
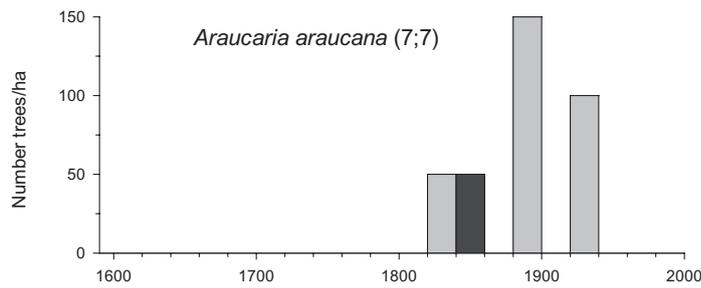
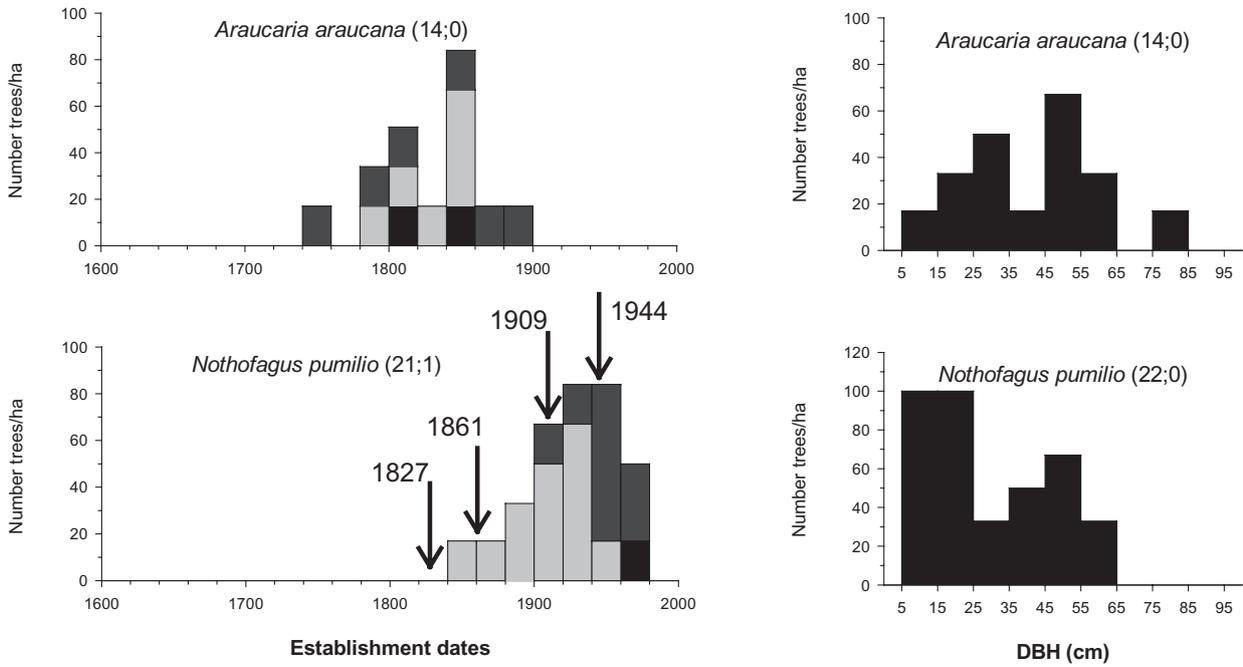


Fig. 3. Continued

(e) Stand Q-7



(f) Stand Q-10

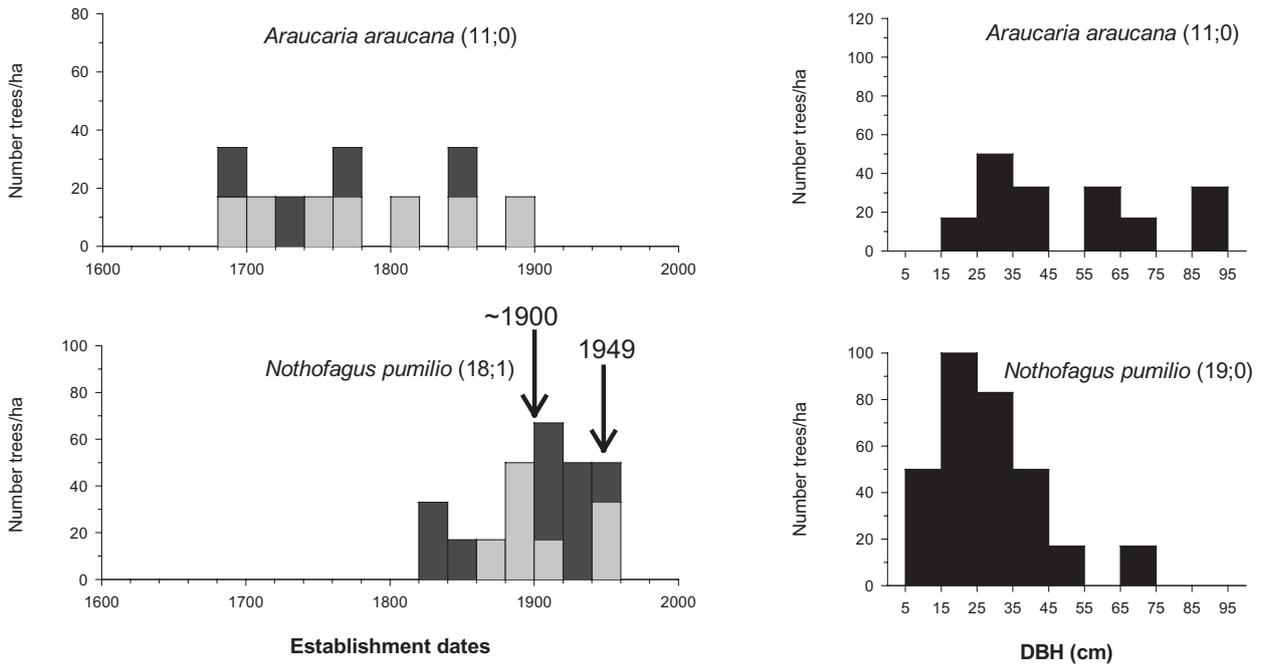


Fig. 3. Continued

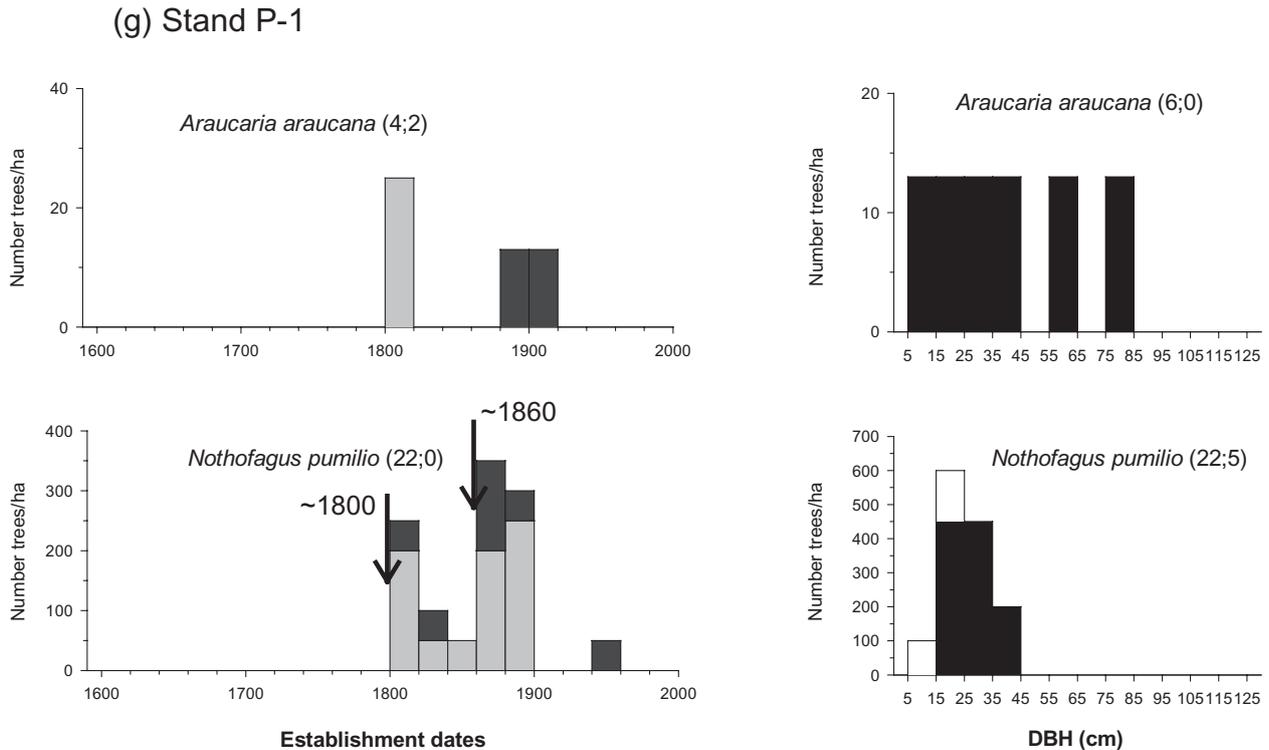


Fig. 3. Continued

along with few old *Araucaria*. Although the size structure of *N. pumilio* in these stands suggested they were generally composed of single even-aged cohorts, the age distribution showed the occurrence of at least one other post-fire cohort. Few remnant *N. pumilio* trees (approx. >400 year old), usually rotten, were also scattered throughout the patches.

Total live BA in these old post-fire stands ranged from 78 to 90 m<sup>2</sup> ha<sup>-1</sup> (Table 1). In stand Q-2, the BA was equally distributed between the *Araucaria* and *Nothofagus* populations. In stands P-2 and Q-6, >80% of the BA corresponded to *Nothofagus* and *Araucaria*, respectively. In stands P-2 and Q-6, dead individuals were mainly aggregated in the low-middle size-classes and accounted for less than 2.5% of the total BA (based on dead and live BA). In these stands, *Nothofagus* trees occurred predominantly in the main canopy crown class, with few individuals in the overtopped and intermediate classes. *Araucaria* trees occurred in all diameter classes, including one very large and old individual in the emergent class (Table 2).

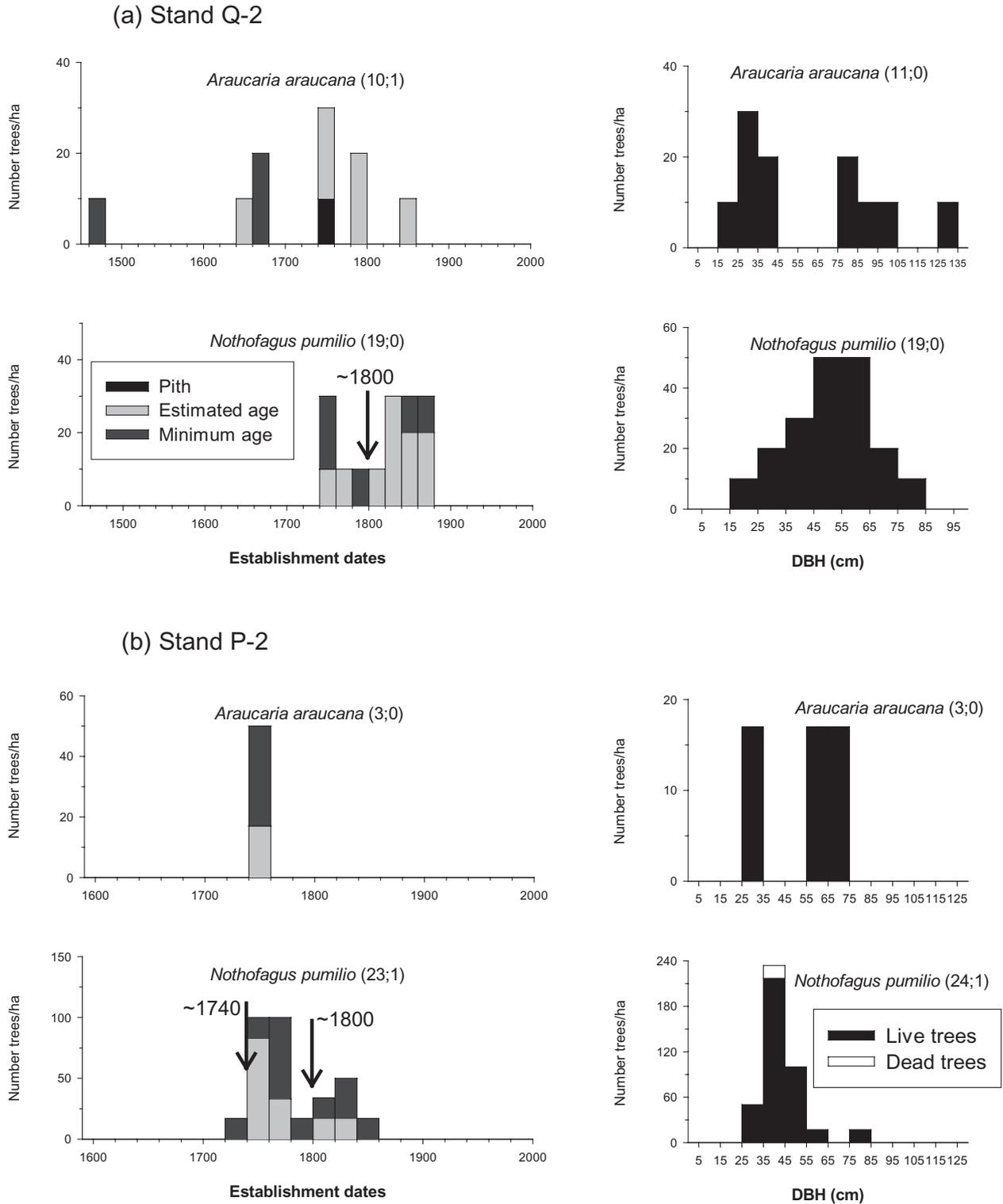
**DISCUSSION**

**Stand development of *Araucaria*–*Nothofagus pumilio* forests: a general model**

Studies of forest dynamics from many different parts of the world describe broadly similar patterns of

stand development following severe, coarse-scale disturbances that are consistent with Oliver (1981) general model of whole stand replacement. Following a coarse-scale severe disturbance, pioneer species invade and dominate the area growing together, altering the environment, and allowing still other species to invade and eventually predominate. These patterns and changes in stand physiognomy and species dominance are mostly the result of life history traits of each species expressed as their differential competitive advantages following disturbances. Patterns and changes of stand structure and species dominance of single or even-aged cohorts have been well described by the model proposed by Oliver (1981), where he distinguishes four discrete developmental stages: stand initiation, stem exclusion, understory reinitiation and old-growth.

In *Araucaria*–*N. pumilio* forests, fire disturbances frequently result in the development patterns, stand structure and physiognomic stages described by Oliver (1981) for whole-stand replacement following a severe disturbance. However, the current study also shows how a complex forest structure characterizing a larger landscape reflects repeated disturbances of variable severity. In the *Araucaria*–*N. pumilio* forests studied here, stand structure sometimes could be related to a single severe fire event, but in most cases current structures had been determined by two or several fires of differing severities. In this landscape, multicohort stands are common and their development patterns are more complex than those that follow single distur-



**Fig. 4.** Stand structure of old post-fire stands. Age bins are 20 years, and d.b.h. bins are 10 cm. For age distributions, the numbers in parentheses indicate the number of cored trees and number of excluded trees. For size distributions, the number of live and dead trees is given in parentheses. Minimum ages refer to trees incomplete cores that represented >70% of the tree radius and to trees for which the number of missing years to centre exceeded 20 years according to Duncan’s (1989) method. Arrows indicate dated fire scars in or near the plot; ‘~’ indicates approximate fire dates derived from maximum ages of post-fire cohorts.

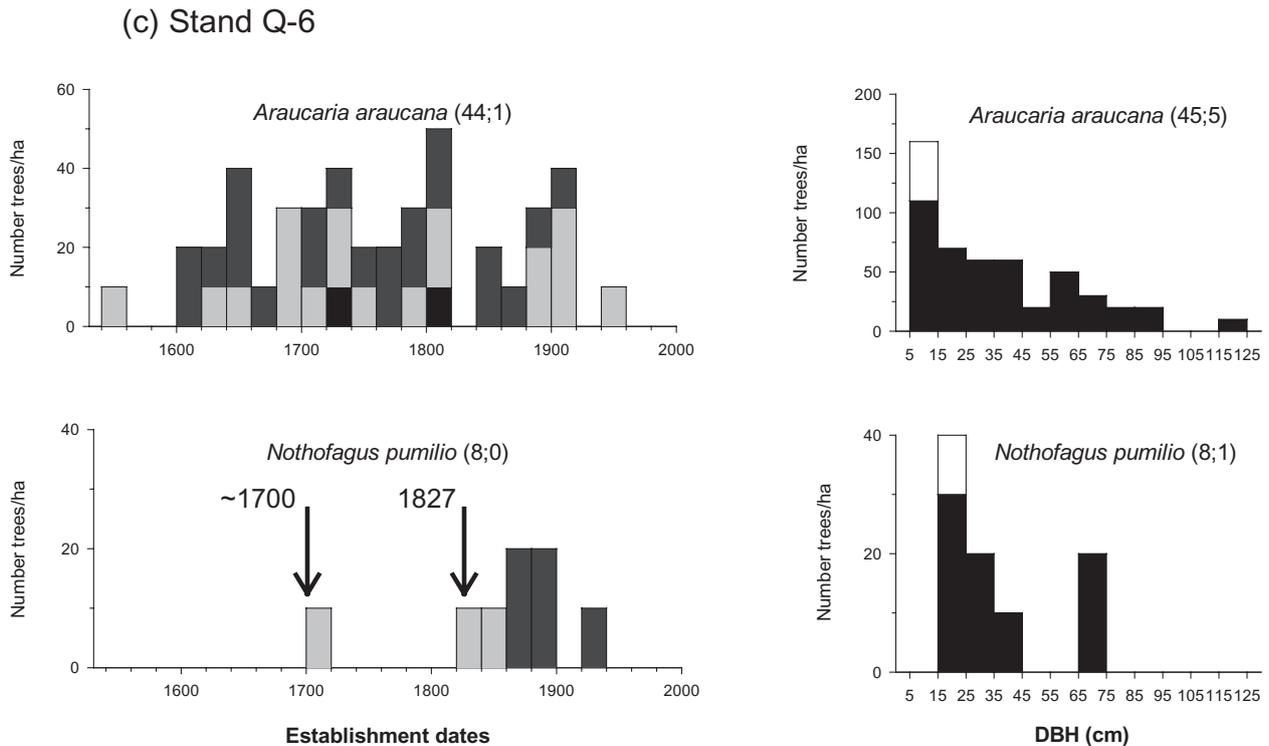


Fig. 4. Continued

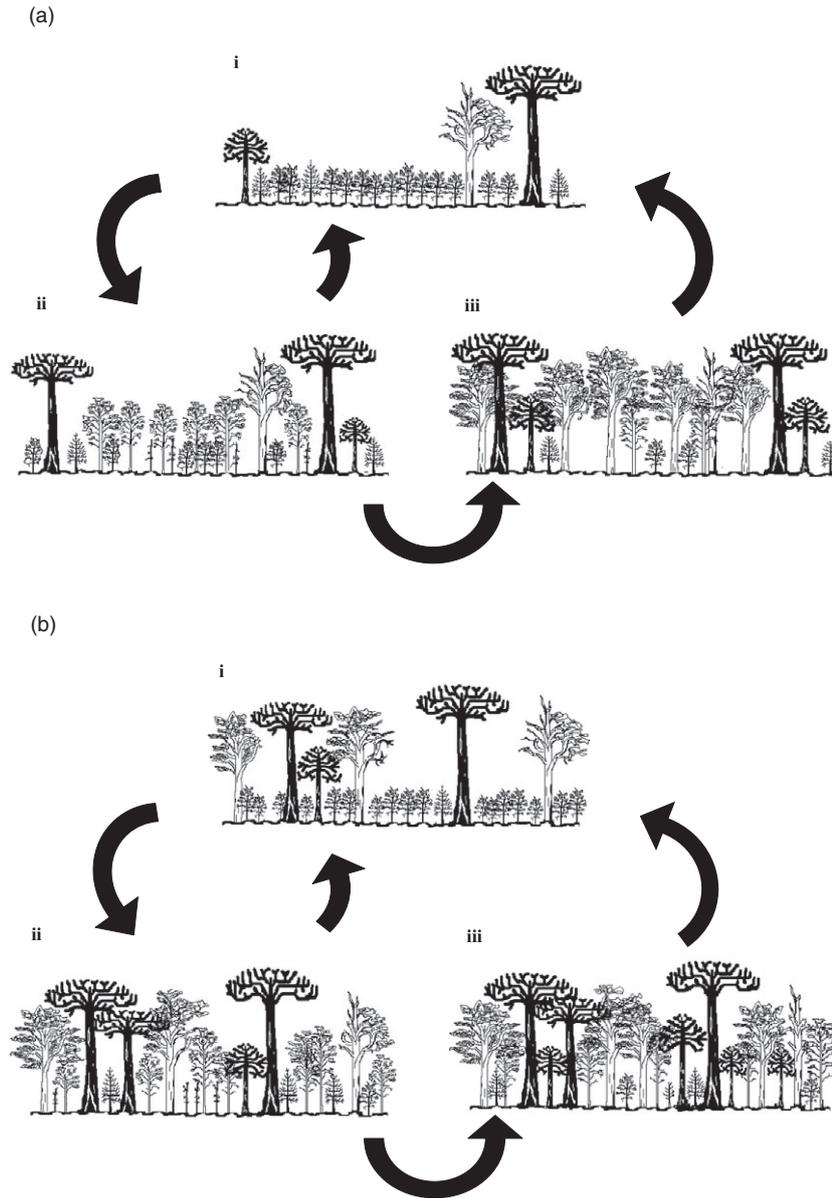
bances of a uniformly high severity. The development patterns of the multi-cohort stands studied here are related to timing and severity of past fires, differences among species in their ability to resist or recover from disturbance, and stand structural attributes related to the prior history of disturbance. In particular, the current study shows how variability in past fire severity creates more complex structures at a stand and landscape scale.

Although both surface and stand-replacing fires occur in the *Araucaria–Nothofagus* forested landscape, stand development patterns of *Araucaria* and *N. pumilio* are largely controlled by moderate- to high-severity fires. Surface fires can occur at relatively short fire intervals at particular sites such as more xeric woodlands of *Araucaria* mixed with *N. antarctica* which result in relative short composite fire intervals when fire dates are aggregated over 1000 s of hectares (González *et al.* 2005). However, in the *Araucaria* and *N. pumilio* forests examined in the current study, there was no evidence that surface fires killed canopy trees or created significant opportunities for new tree establishment. In the forests of *Araucaria* and *N. pumilio* in the current study, fires of sufficient intensity to kill large numbers of trees and trigger post-fire tree establishment occur relatively infrequently. The moderate- to high-severity fires that have shaped stand structures in the *Araucaria–N. pumilio* forests generally occur at intervals of many decades to a century or

more. Fire can burn with a variety of severities leaving a broad range of forest conditions. Characteristic stand development patterns and changes in stand physiognomy and species dominance result from various combinations of fire frequencies and severities. The pattern and rate of stand development of *Araucaria–Nothofagus* forests are highly variable depending on seed source availability, site quality and subsequent fire disturbances. Although a surface fire soon after a stand-initiating moderate- to high-severity fire would be expected to kill post-fire juveniles, in the stands studied here we did not find evidence of subsequent fire for at least several decades implying that post-fire juveniles would be large enough to survive a low-severity surface fire. For the purposes of this discussion, we present two idealized models of *Araucaria–Nothofagus pumilio* forest development following two types of initial fires (high-severity *vs.* moderate-severity initial fire event), which may include subsequent low-severity fires (i.e. surface fires).

Recent post-fire stands

Following a high-severity crown fire, most of the overstorey is removed along with the understorey vegetation (Fig. 5a; stage *i*). However, after a moderate-severity fire higher proportion of the canopy survives resulting in two or more cohorts in the stand (Fig. 5b;



**Fig. 5.** Two simplified models of *Araucaria–Nothofagus pumilio* forest development following fire of different severity. In (a) high-severity fire kills most or nearly all of the overstoreys promoting a massive and spatially continuous recruitment of an even-aged *Nothofagus* cohort (i). Synchronous post-fire recruitment of *Araucaria* occurs in small numbers. In the next stage (ii), there is a decrease in the number of *N. pumilio* stems as a result of self-thinning. The semi-shade tolerant *Araucaria* continues to slowly establish under the canopy. Remnant trees of the initial *Nothofagus* cohort continues to grow toward a final old-growth forest stand (iii). In the second model (b), moderate-severity fire leaves numerous canopy trees of both species that serve as seed sources (i). This typically results in patchy establishment of both species (ii) and a more complex stand structure (iii). For both models, subsequent moderate or high-severity fire events affecting in mid- or final stages will set back the forest development to an initial stage (i), perpetuating in this manner the patchy forest mosaic in the landscape. Solid arrows represent advances of stand development in the absence of moderate- or high-severity fires, or in the case of reversal from a later towards an earlier stage they represent the effects of moderate- to high-severity fire events.

stage *i*). A moderate-severity fire spreads along the surface and torches into the crown in some patches of trees, leaving other patches unburned. The fire-resistant *Araucaria* commonly survive fires, especially larger individuals (i.e. >30 cm d.b.h.; Fig. 5a,b, stage *i*). This species has thick bark, which insulates and

protects the cambium from fires, and a fire resistant crown that is several meters above the ground (generally >10 m). Remnant *Nothofagus pumilio* trees, which represent individuals from previous post-fire cohorts, often have tall (i.e. extending several meters above the ground) fire scars and partially dead crowns reflecting

the occurrence of severe fires. Remnant large *Araucaria* trees often present fire scars located at the base of the tree trunk.

Following either moderate or high-severity fire, which open different size patches in the main canopy, *Nothofagus pumilio* responds with vigorous and abundant regeneration from wind-dispersed seeds (Fig. 5a,b; stage *i*). Generally, the tree establishment period varies between 40 and 80 years, depending on the environmental conditions and biological legacies. However, >80% of post-fire tree regeneration occurs in a period of 40 years. As the initial colonists form a dense canopy, conditions become unfavourable for further recruitment. More mesic habitats appear to result in a relatively shorter colonization period, because of favourable site conditions for tree growth (i.e. Q-11, Fig. 3c). Moreover, dead standing trees, down logs and survivor trees play an important function by ameliorating harsh environmental conditions at post-fire sites as well as supplying a seed source (Harmon *et al.* 1986; Foster *et al.* 1998; Spies & Turner 1999). Along with the massive *Nothofagus* recruitment, post-fire *Araucaria* establishment is apparent but much less abundant. Density of post-fire *Araucaria* establishment appears to be dependent upon the abundance of overstorey *Araucaria* individuals, including fecund mother trees (e.g. P-4, Q-6; Figs 2f,4c; Finckh & Paulsch 1995). *Araucaria*'s large wingless seeds are predominantly dispersed short distances from the mother tree (Muñoz 1984). Thus, when adult trees are more abundant in the stand more abundant seedling establishment occurs. Although *Araucaria* individuals may establish synchronously with *Nothofagus*, they initially grow more slowly and therefore are commonly displaced to the overtopped and/or intermediate crown classes (e.g. Q-12, Q-5; Table 2).

#### Mid-development post-fire stands

In this more advanced stage of development, patterns of species dominance and changes in stand structure are expressed mainly as crown differentiation, where some trees become larger (i.e. in height and d.b.h.) at the expense of others (Fig. 5a,b; stage *ii*). Here, larger *N. pumilio* trees associated with faster growth rates are able to expand their crowns, taking growing space away from their neighbours. In this stage, the few *Araucaria* that established synchronously with *Nothofagus* typically take a subordinate canopy position. Also, *Nothofagus* trees start dying as a result of the intense competition, especially those suppressed individuals distributed in the lower diameter classes and canopy positions. In mesic habitats, the stem exclusion period of stand development may start earlier, because of more favourable conditions to tree growth. Furthermore, after a canopy fire some stands show evidence

of subsequent surface fires. For instance, fire scars on *Nothofagus* species indicate that stand Q-11 was affected by a surface fire in approximately 1950, 50–60 years after the stand-initiating fire. Although subsequent surface fires may kill some small trees, there is no evidence that the surface fires kill enough trees to trigger new recruitment opportunities.

A more complex stand age structure develops when stands are affected by moderate-severity fires (Fig. 5b; stage *ii*). In these cases, consecutive fires that partially killed the former *Nothofagus* cohort and provided new opportunities for tree establishment resulted in at least two different post-fire cohorts (Fig. 3e–g). Here, the fire interval between successive events of just a few decades (approx. 30–80 years) results in the coexistence of distinct cohorts that tended to overlap in ages (Drury & Veblen 2008). Compared with young stands developing after a single, high-severity fire, these stands tend to be less dense because of the effects of consecutive fires and self-thinning if the time since last fire has been longer (González *et al.* 2005). Thus, the combination of a range of fire severities and time intervals between fire event results in a complex forest landscape composed of diverse patch sizes, ages and development stages that are constantly shifting in space and time (i.e. the shifting mosaic concept; Bormann & Likens 1979).

#### Old post-fire stands

Post-fire stands representing old *Araucaria*–*Nothofagus pumilio* forests are relatively uncommon in the landscape (Fig. 5a,b; stage *iii*). Generally, more advanced stands are located in sheltered and more mesic habitats associated with less frequent but more intense fires (Johnson *et al.* 1995; Spies & Franklin 1996). In the study areas, the lack of old stands is due to the pervasive occurrence of fire disturbances which intervene before a later stage can be achieved (González *et al.* 2005). The oldest post-fire *Nothofagus* cohorts found reached slightly <300 years old. Apparently, this is the oldest these stands can be in a fire-dominated landscape, except for rare large *Nothofagus* trees located on mesic sites that exceed 400 years in age and 100 cm d.b.h. When stands start to be heavily dominated by *Araucaria*, species of *Nothofagus* tend to obviously decrease in density. For example, stand Q-6 was strongly dominated by *Araucaria*, while *Nothofagus* trees were represented by few individuals placed in the intermediate and codominant crown classes (Table 2). As seen for the younger stands, old-stands of *Nothofagus pumilio* were represented by at least two post-fire cohorts (Fig. 5a,b; stage *iii*). Although previous cohorts are more conspicuously seen in younger stands, older post-fire stands still reflect the pervasive influence of successive fires in shaping the current forest structure. Thus, multiple fire episodes likely

account for the sporadic frequency distribution of individuals in the oldest age-classes.

As fire disturbances occur more frequently than the life span of *Nothofagus* trees, treefall dynamics may be relatively unimportant in influencing forest dynamics. Instead, *Araucaria* and *Nothofagus* tree demography is strongly dominated by a catastrophic regeneration mode (*sensu* Veblen 1992). Stand-killing fires promote abundant recruitment of *Nothofagus* that usually takes place over a 40- to 80-year period. The uneven-aged distribution of *Araucaria* in many stands indicates the pervasive influence of fire in determining the mostly irregular all-aged *Araucaria* populations in contrast to self-replacing, stable populations. Fire not only plays a role in promoting the initial establishment, but also subsequent fires (i.e. surface or moderate-severity fires) that create canopy openings, seem to be crucial for *Araucaria* to reach the main canopy (Burns 1991).

Mixed or variable-severity fires, occurring within the typical life span of *Nothofagus* species, may result in stands dominated by one or two cohorts reflecting the spatial and temporal patterns and percentage of the overstorey killed by fire. Moreover, these findings represented cases in which post-fire tree recruitment was successful. However, it is important to note that large patches lacking seed sources for *N. pumilio* can result from either large, high-severity fire events, or two fire events in a relatively short period of time (shorter than the time required for *N. pumilio* to reach maturity). In these scenarios it is likely that post-fire tree establishment can fail, and instead bamboo (i.e. *Chusquea culeou*) may dominate the site for decades. In the context of recent large, high-severity fires (e.g. 2002) these scenarios of bamboo-dominated stands are increasingly likely. Understanding effects of fire on the structure of the *Araucaria*–*Nothofagus* forest landscape requires consideration of spatial and temporal variability in fire severity, environmental site characteristics and differences among the dominant species in their ability to withstand or recover from fire.

## ACKNOWLEDGEMENTS

Research support was provided by International Foundation for Science (D/3124-2), National Geographic Society (68-00) and Fundación Andes (C-13860, Chile). For permission given and facilitating access to the study areas we thank Corporación Nacional Forestal. We also thank P. Szejner, E. Cuq, E. Aguayo, J. Silva, J. Baricovich, A. Fajardo and A. Holz for their field and laboratory assistance. M. E. G. thanks the Graduate School of the Faculty of Forest Science, Universidad Austral de Chile.

doi:10.1111/j.1442-9993.2009.02064.x

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