NOTHOFAGUS BETULOIDES (MIRB.) OERST 1871 (FAGALES: NOTHOFAGACEAE) FORESTS IN SOUTHERN PATAGONIA AND TIERRA DEL FUEGO

BOSQUES DE *NOTHOFAGUS BETULOIDES* (MIRB.) OERST 1871 (FAGALES: NOTHOFAGACEAE) EN LA PATAGONIA AUSTRAL Y TIERRA DEL FUEGO

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"… for in these still solitudes, Death, instead of Life, seemed the predominant spirit (Darwin 1839)"

1. THE GENUS *Nothofagus*

Southern Patagonia and Tierra del Fuego have always been of great interest for botanists because of their evergreen plant formations and biogeographical perspectives. Antarctic families like the Winteraceae and genera like *Gunnera* and *Gaultheria* represent the ancient Gondwana flora. The biogeography of *Nothofagus*, the southern beech, has been the classical study that supports the sequence of Gondwana break-up and the linkage of the Austral biota between South America and Australasia (Swenson *et al.* 2001).

In the past the genus *Nothofagus* was included in the Fagaceae family (Rodríguez & Quezada 2003), and seemed to be closely related to *Fagus* (Hill & Dettmann 1996). More recent genetic studies have shown that the genus of *Nothofagus* belongs to a new monogeneric family, the Nothofagaceae (Hill & Jordan 1993; Hill & Dettmann 1996; Manos 1997; Jordan & Hill 1999).

There are currently 36 recognised *Nothofagus* species (Table 1), 26 of which occur in Australasia and the remaining 10 in South America. Of the total number, 78 % are evergreen and 22 % deciduous. The evergreen *Nothofagus* species can grow equally well at tropical latitudes in the mountains of New Guinea (13 species: van Royen 1983), and in subantarctic areas. *Nothofagus betuloides* (Mirb.) Oerst is the species with the southernmost distribution. However, natural hybridisation between evergreen *Nothofagus* species has been demonstrated in South America (Donoso & Atienza 1983; Donoso *et al.* 2004) as well as in New Zealand (Wardle 1984).

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TABLE 1. Distribution and leaf characteristics of the *Nothofagus* species.

Species	Distribution	Leaves	Species	Distribution	Leaves
Brassospora			**Fuscospora**		
N. aequilateralis	New Caledonia	Evergreen	*N. alessandri*	Chile	Deciduous
N. balansae	New Caledonia	Evergreen	*N. fusca*	New Zealand	Evergreen
N. baumanniae	New Caledonia	Evergreen	*N. gunnii*	Australia	Deciduous
N. brassii	New Guinea	Evergreen	*N. solandri*	New Zealand	Evergreen
N. carrii	New Guinea	Evergreen	*N. truncata*	New Zealand	Evergreen
N. codonandra	New Caledonia	Evergreen	**Lophozonia**		
N. crenata	New Guinea	Evergreen	*N. alpina*	Chile - Argentina	Deciduous
N. discoidea	New Caledonia	Evergreen	*N. cunninghamii*	Australia	Evergreen
N. flaviramea	New Guinea	Evergreen	*N. glauca*	Chile	Deciduous
N. grandis	New Guinea	Evergreen	*N. macrocarpa*	Chile	Deciduous
N. nuda	New Guinea	Evergreen	*N. menziesii*	New Zealand	Evergreen
N. perryi	New Guinea	Evergreen	*N. moorei*	Australia	Evergreen
N. pseudoresinosa	New Guinea	Evergreen	*N. obliqua*	Chile - Argentina	Deciduous
N. pullei	New Guinea	Evergreen	**Nothofagus**		
N. resinosa	New Guinea	Evergreen	*N. antarctica*	Chile - Argentina	Deciduous
N. rubra	New Guinea	Evergreen	*N. betuloides*	Chile - Argentina	Evergreen
N. starkenborghii	New Guinea	Evergreen	*N. dombeyi*	Chile - Argentina	Evergreen
N. stylosa	New Guinea	Evergreen	*N. nitida*	Chile	Evergreen
N. womersleyi	New Guinea	Evergreen	*N. pumilio*	Chile - Argentina	Deciduous

Source: Hill & Dettmann (1996); Ogden *et al.* (1996); Read & Brown (1996); Read & Hope (1996); Rodríguez & Quezada (2003)

2. *Nothofagus betuloides* – the southernmost evergreen tree species and its forests

N. betuloides is known commonly as 'coihue de Magallanes' in Chile and 'guindo' in Argentina. It was also well known to the Indian tribes of South America who referred to it as coigüe (Mapuche name), yerkianop (Alacaluf name), ouchpaya (Ona or Shelknam name), and shushchi (Yahgan or Yamana name).

2.1 Biology

N. betuloides is one of the longest-living South American *Nothofagus* species, with specimens reaching 500-600 years of age (Veblen *et al.* 1996) or more (628 years: Gutiérrez *et al.* 1991). The trees (Fig. 1) can grow to heights of 20 m, and in a few cases up to 35 m, but can also remain as only meter low shrubs in subantarctic shrublands. The trunk can reach 2 m in diameter. The bark is grey or reddish in colour and relatively smooth. The twigs are puberulent, rarely glabrous. The leaves (12-28 x 8-18 mm) are ovate-elliptical to elliptical–suborbicular, acute to obtuse, cuneate at the base, serrate, subcoriaceous, glabrous (Fig. 2) (Moore 1983).

Fig. 1. *Nothofagus betuloides* growing in Río Bueno, Tierra del Fuego (Photo: A. Promis).

Fig. 2. Leaves and seeds of *Nothofagus betuloides* (Photo: A. Promis)

Fig. 3. Seeds of *Nothofagus betuloides* (Photo: G. Cruz)

N. betuloides is a hermaphrodite. The male flowers are solitary, with a perianth 4-4.5 cm long, 5-7 lobes, and has 10-16 stamens. Female flowers occur in groups of three (Moore 1983; Rodríguez & Quezada 2003). Depending on the location, *N. betuloides* flowers between September and December (Rodríguez & Quezada 2003). However, the South American *Nothofagus* species do not flower regularly and in some years widespread non-flowering occurs, and seed production is therefore intermittent (Báez *et al.* 2002).

The fruits of *N. betuloides* (Figs. 2 and 3) are nuts occurring in threes, 5-6 x 4-4.5 mm, triquetrous, glabrous; cupule 4-partite (Moore 1983). They mature during summer and are dispersed mainly by gravity and wind between March and May (Donoso & Donoso 2007; Ibarra *et al.* 2007). Although nut development in *Nothofagus* is often close to 100 %, the majority of the seeds produced are often not viable (Báez *et al.* 2002).

The wood of *N. betuloides* has a slight lustre, and a fine and homogeneous texture. The grain is generally straight. The growth rings are annual but not clearly visible. The sapwood has a yellowish-white colour, and the heartwood is light pink to reddish-brown. The wood density has been classified as low, with a basic density of 615 kg m^{-3}, and an air dry density of 620 kg m^{-3}. With respect to the strength properties of the species, the wood has a low modulus of rupture (708 kg cm^{-2}), a medium modulus of elasticity (103 t cm^{-2}), and also a medium maximum crushing strength parallel to the grain when dry (445 kg cm^{-2}) (Pérez 1983; Manso *et al.* 2007). The wood is long lasting, even without treatment. The durability ranges from durable to very durable when it is not exposed to conditions promoting rapid decay, e.g., ground contact (Donoso & Donoso 2007).

The timber can be used as poles, flooring, indoor panelling, roofing (joist and rafter), pillars, furniture, decorative veneers and panels (Pérez 1983; Manso *et al.* 2007).

2.2. Ecology

2.2.1. Geographical distribution

N. betuloides is an endemic tree species of the Chilean and Argentinean subantarctic forests. In Chile it occurs from the Valdivia district (40° 31' S) to the archipelago of Cape Horn (55° 31' S) (Rodríguez & Quezada 2003). In Argentina it occurs mainly between 48° S to the southernmost tip of Tierra del Fuego (Veblen *et al.* 1996) (Fig. 4).

In the northern part of its distribution, *N. betuloides* grows at high elevations in both the coastal (above 800 m a.s.l.) and the Andean Cordillera (above 900 m a.s.l.), approaching the treeline. In the south it forms forests in elevations from sea level to upper treeline on the southern and western sides of Tierra del Fuego (McQueen 1976; Tuhkanen *et al.* 1989-1990; Donoso & Donoso 2007).

Fig. 4. Map of the distribution of *Nothofagus betuloides* in Chile and Argentina (Source: Dimitri 1972; Ibarra *et al.* 2007).

2.2.2. Autecology: Germination and juvenile growth

Germination is epigeous and occurs during the spring of the year in which the seed is produced (Donoso & Donoso 2007). Most *Nothofagus* species do not develop a persistent seed bank (Veblen *et al.* 1996). Germination can occur in sunny, semi-shady or shady places (Roig *et al.* 1985). The seed dormancy of *N. betuloides* is readily broken (Martínez Pastur *et al.* 1994). Pre-germinative treatments have demonstrated that with a cold-moist stratification of the seeds for a period of up to 120 days the germination rate reaches up to 45 % (Donoso & Donoso 2007). The immersion of seeds in 100 ppm giberelic acid for 12 hours results in a germination rate of 33 %. The application of potassium nitrate has no effect (Martínez Pastur *et al.* 1994).

The natural regeneration of *N. betuloides* is through seed. Vegetative reproduction by means of sprouting at the base of the trunks of living trees has also been observed on the upper slopes of Tierra del Fuego, where the trees are stunted and crooked (Krummholz) (Gutiérrez *et al.* 1991).

For all *Nothofagus* species in South America, seedling establishment occurs best under moderately high light levels and where bare mineral soil has been exposed (Veblen *et al.* 1996). For example, *N. betuloides* is able to grow as a pioneer species on open sites with mineral soils, including moraines (Armesto *et al.* 1992), recently deglaciated areas (Pisano 1978), and forest road banks. In old-growth forests, seedlings often establish on fallen logs (Roig *et al.* 1985; Veblen *et al.* 1996).

Positive rates of net photosynthesis of up to three hours (around noon) have been reported for *N. betuloides* seedlings growing under a closed canopy in Tierra del Fuego, and up to ten hours in canopy gaps (Squeo & Cabrera 1995; Arroyo *et al.* 1996). As *N. betuloides* has a relatively low light compensation point for net positive photosynthesis, seedlings can establish under closed canopy conditions. *N. betuloides* can form an abundant stock of persistent seedlings or saplings, surviving in the understorey for many decades and even exceeding one hundred years (Rebertus & Veblen 1993a; Veblen *et al.* 1996) at high elevations or latitudes, where there is little competition from ground flora.

The relationship between foliar weight and leaf area is on average lower for seedlings growing in shade (9.3 mg cm^{-2}) than for those situated in canopy gaps (11 mg cm^{-2}). The foliar nitrogen concentration of the seedlings is similar under both light conditions (ca. 1.2 %: Squeo & Cabrera 1995).

2.2.3. Synecology: Vegetation types

N. betuloides forests have been well described phytogeographically, and given the following designations: subantarctic evergreen forest (Skottsberg 1910; Godley 1960), subantarctic evergreen rain forest (Schmithüsen 1956), *Nothofagetum betuloidis* (Oberdorfer 1960; Pisano 1977), evergreen forest (Pisano 1977; Moore 1983; Pisano 1997), *N. betuloides* forest type (Donoso 1981; Veblen *et al.* 1983), sub-region of the microphyllus evergreen forest (Gajardo 1994), and Andean and coastal temperate evergreen forest (Luebert & Pliscoff 2006).

N. betuloides forests are predominantly found where an oceanic cold temperate climate prevails, characterised by a mean temperature of around 8.9 ºC in the warmest month (between 8.5 and

10°C) and 2.7 ºC in the coldest (between 1.0 and 3.5°C). The rainfall ranges between 800-2,000 mm year^{-1}; i.e., there are no arid months (Pisano 1977, Tuhkanen 1992). The climate of the mixed evergreen – deciduous forest is less oceanic, characterised by a mean temperature between 9.0 to 9.5° C, and even 11°C, in the warmest month, and between 0.5 to 2.5°C in the coldest month (Tuhkanen 1992). *N. betuloides* can also grow as creeping shrub in transition to the tundra near the Pacific Ocean. The climate there has a mean temperature of 8.8 ºC in the warmest and 4.4 ºC in the coldest month. The rainfall exceeds 2,000 mm year^{-1}, and reaches up to 4,846 mm year^{-1} (McQueen 1976; Pisano 1977; Pisano 1981).

The climate conditions, where the pure evergreen *N. betuloides* forest and the mixed evergreen forests are found, until now are only poorly known. Nonetheless, we hypothesize that the temperature would be affecting the distribution of the tree species in these forests, with mild winters adjacent to the sea and at low elevations, and decreasing minimum temperatures further inland.

In southern Patagonia and Tierra del Fuego, four characteristic forest types dominated by *N. betuloides*, and additionally occurrences in subantarctic shrublands, can be distinguished: (1) the pure evergreen *N. betuloides* forest, (2) the mixed evergreen *N. betuloides – Drimys winteri* J.R. et Forster 1775 forest, (3) the mixed evergreen *N. betuloides – D. winteri – Pseudopanax laetevirens* (C. Gay) Seem. 1894 forest, and (4) the mixed evergreen – deciduous *N. betuloides – Nothofagus pumilio* (Poepp. et Endl.) Krasser 1896 forest (Pisano 1977). (5) Outside closed forests, *N. betuloides* is able to grow as creeping shrub in subantarctic Krummholz formations and moorland.

(1) Pure evergreen *N. betuloides* forest is mainly located in inland southern Patagonia and Tierra del Fuego, and also at the treeline in some places protected from strong winds (Fig. 5).

Two soil formation processes have been described for pure *N. betuloides* forests, podsolisation on well-drained sites and hydromorphism in areas with moderate to high waterlogging (Pisano 1977; Puigdefábregas *et al.* 1999; Gerding & Thiers 2002; Romanyà *et al.* 2005). These soils are normally shallow (<50 cm), loamy in texture, acidic (pH 3.4-

Fig. 5. Pure evergreen *Nothofagus betuloides* forest in Río Condor, Tierra del Fuego (Photo: A. Promis).

5.5) and not very fertile (Gerding & Thiers 2002; Romanyà *et al.* 2005; Thiers & Gerding 2007). Accumulation of huge layers of organic matter on the forest floor and large amounts of decaying wood have been described for this forest type in Tierra del Fuego (Gutiérrez *et al.* 1991). Most of the plant roots and nutrients are located in the bottom part of a thick raw humus layer, i.e., in a soil depth of only 4 to10 cm (Pisano 1977; Gutiérrez *et al.* 1991; Gerding & Thiers 2002; Romanyà *et al.* 2005).

The *N. betuloides* forests form a very dense forest with few vascular plant species. Few individuals of the tree species *D. winteri* and *Maytenus magellanica* (Lam.) Hooker f. 1847 occur locally. There are few species in the shrub layer, which is dominated mainly by *Berberis ilicifolia* L.f. 1781. Less frequent and lower in cover are *Empetrum rubrum* Vahl ex Willd. 1806, *Fuchsia magellanica* Lam. 1788, *Pernettya mucronata* (L.f.) Gaudich. ex G.Don 1834, and *Ribes magellanicum* Poiret 1812. Vascular plant species of the ground flora are *Adenocaulon chilense* Less. 1831, *Luzuriaga marginata* (Banks & Sol. ex Gaertner) Bentham & Hooker f. 1883, *Senecio acanthifolius* Hombron & Jacquinot 1846, *Gunnera magellanica* Lam. 1789, the ferns *Blechnum magellanicum* (Desv.) Mett. 1856, *Blechnum penna-marina* (Poiret) Kuhn 1868, *Asplenium dareoides* A.N. Desv. 1811, and filmy ferns, mostly *Hymenophyllum pectinatum* Cav. 1802, *Hymenophyllum secundum* Hooker & Grev. 1831 and *Hymenophyllum tortuosum*

Hooker & Grev. 1831 (Pisano 1977; Moore 1983; Gajardo 1994). Worth mentioning is the dense cover of lower plants, dominating the forest floor, the decaying tree trunks, and as epiphytes the stems and branches of the trees. Characteristic mosses are *Acrocladium auriculatum* (Mont.) Mitt. 1869*, Dendroligotrichum dendroides* (Brid. ex Hedw.) Broth. 1905, *Polytrichadelphus magellanicus* (Hedw.) Mitt. 1859*, Dicranoloma robustum* (Hook. f. & Wilson) Paris 1904, and *Ptychomnion cygnisetum* (Müll. Hal.) Kindb. 1888. The most common liverworts are *Marchantia berteroana* Lehm. & Lindenb. 1834, *Gakstroemia magellanica* (Lam.) Trev. 1877*, Schistochila lamellata* (Hook.) Dumort. 1835, and *Lepidozia filamentosa* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees 1845 (McQueen 1976; Pisano 1977; Moore 1983). Worth mentioning are lichens like *Cladonia* sp. on the ground, and a large number of epiphytes.

A study of forest hydrology in a pure evergreen mature *N. betuloides* forest located in Tierra del Fuego showed that the canopy intercepts around 41 % of the total rainfall (779 mm year^{-1}). The direct throughfall was 59 %, and the stemflow averaged less than 0.1 % of the total rainfall. The amount of water percolated was around 31 % of the gross precipitation, and the water yield 33 % (Frangi & Ritcher 1994). The average mass of fallen coarse woody debris in stands on the Argentinean side of Tierra del Fuego has been measured at 52 Mg ha^{-1} (dry weight), with low decay rates for small branches (k=0.17). This might be related to the lower summer temperatures and saturated water conditions, which can reduce aeration of the laid logs on the ground (Frangi *et al.* 1997).

(2) Near the coast below ca. 200 m a.s.l., *D. winteri* is becoming a more regular component of the canopy, forming a mixed evergreen *N. betuloides – D. winteri* forest (Fig. 6). The precipitation ranges between 900-2,000 mm year^{-1}, and there are low thermal amplitudes, indicating hyperoceanic climate (Pisano 1977). The soils are deep, but often poorly drained and waterlogged (Thiers & Gerding 2007).

Between 8-12% of the trees are *D. winteri*, with isolated individuals of *M. magellanica* and *Embothrium coccineum* Forster & Forster f. 1775. Floristically this association is very similar to the

Fig. 6. Coastal mixed evergreen *Nothofagus betuloides – Drimys winteri* forest (Photo: G. Cruz).

pure evergreen *N. betuloides* forest. However, due to edaphic and climatic factors, the decomposition of litter is slow. The forest floors are covered by decomposed and decomposing tree trunks. These conditions facilitate the ferns *A. dareoides*, *Cystopteris fragilis* (L.) Bernh. 1806, *Grammitis magellanica* Desv. 1811, the lower plants and the filmy ferns mentioned above with the addition of *Hymenophyllum ferrugineum* Colla 1835, *Hymenophyllum peltatum* (Poiret) Desv. 1827, and *Serpyllopsis caespitose* (Gaudich.) C.Chr. 1910.

(3) At elevations below ca. 100 m a.s.l., the tree *P. laetevirens* joins the canopy, forming the coastal mixed evergreen *N. betuloides – D. winteri – P. laetevirens* forest. The precipitation ranges from around 1,500-4,000 mm year^{-1}. The soils are often organic, with a deep accumulation of peat in the first horizon. The soil is covered by a thick litter layer of coarse woody debris in different stages of decay (Pisano 1977). Tree species such as *D. winteri* and *P. laetevirens* are very characteristic. The latter is a small tree up to 5 m tall. The ground vegetation is species poor, most dominant are mosses and liverworts on decaying wood.

(4) The mixed evergreen – deciduous *N. betuloides – N. pumilio* forest can be regarded as a transition between the evergreen and the deciduous *Nothofagus* forests (Fig. 7). *N. betuloides* dominates the more humid and poorly drained sites. With

Fig. 7. Mixed evergreen – deciduous *Nothofagus betuloides* – *Nothofagus pumilio* forest (Photo: A. Reif).

decreasing rainfall the deciduous *N. pumilio* gains dominance and the transition to the deciduous forests is gradual. The soils are more fertile than those of the pure evergreen *N. betuloides* forest or the mixed evergreen *N. betuloides – D. winteri* forest (Thiers & Gerding 2007). They are predominantly brown podsolic, with increased podsolisation in stands dominated by the deciduous *N. pumilio* (Pisano 1977). The tree species *D. winteri* and *M. magellanica* are present in low numbers. The coverage of the shrub understorey is low, dominated by *B. ilicifolia* and *P. mucronata*. There are fewer filmy ferns (*Hymenophyllaceae* spp.) and bryophyte species than in the forest types mentioned previously (Young 1972; McQueen 1976; Pisano 1977; Gajardo 1994; Luebert & Pliscoff 2006).

(5) *N. betuloides* also can grow in the Magellan Mooreland, there being a minor species in shrubland dominated by *Pilgerodendron uviferum* (D.Don) Florin 1930, or as a low creeping shrub associated with *Schoenus antarcticus* (Hooker f.) Dusén 1900 and *Carpha alpina* var. *schoenoides* (Banks & Sol. Ex Hooker f.) Kük. 1939 (Pisano 1977) and mosses including *Sphagnum magellanicum* Brid. 1798.

2.2.4. Forest texture

The structure of the forests of southern Patagonia and Tierra del Fuego is shaped principally by wind. Wind acts as an agent of both coarse and fine-scale disturbance. Storms can cause the blow-down of entire stands (Rebertus *et al.* 1997; Puigdefábregas *et al.* 1999). Wavelike patterns of gap formation have been documented for both pure *N. betuloides* and pure *N. pumilio* forests in Tierra del Fuego, and for mixed *N. betuloides - N. pumilio* forests, mostly on sites predisposed to wind disturbance (Rebertus & Veblen 1993b; Rebertus *et al.* 1993; Puigdefábregas *et al.* 1999).

In most cases, windthrow of individual trees creates canopy gaps smaller than 200 m^2 (Rebertus & Veblen 1993a; Gutiérrez 1994). In pure *N. betuloides* stands, canopy openings can occur as interwoven gap complexes where discrete gaps are not apparent (Rebertus & Veblen 1993a). Promis *et al.* (*submitted*) observed small canopy gaps (51 m^2) in a pure, uneven-aged *N. betuloides* forest in Tierra del Fuego. In a mixed, uneven-aged *N. betuloides – N. pumilio* forest larger canopy gaps were found, with an average size of 107 m^2 (Promis *et al. submitted*). In Tierra del Fuego a patch mosaic pattern has been observed in *Nothofagus* forests, with patches of younger trees neighbouring larger patches of old forest, forming multicohort stands (Gutiérrez *et al.* 1991).

2.2.5. Forest dynamics and structure

Disturbances of different frequencies and intensities on different sizes of areas are a major factor shaping the forest structures. The importance of coarse and fine-scale disturbances to the forest dynamics and structures of southern South American *Nothofagus* forests has been well summarised by Veblen *et al.* (1996) and Pollmann & Veblen (2004).

Coarse-scale disturbance

Coarse-scale disturbances are generally necessary for the regeneration of *Nothofagus* at lower elevations and under a milder climate, where a number of shade-tolerant rain forest species are dominant, and a dense understorey competes with juveniles of *Nothofagus*.

Large-scale disturbance at higher elevations or latitudes can initiate regeneration patterns forming even-aged *N. betuloides* stands (Donoso & Donoso 2007). Examples are the pure, even-aged secondary *N. betuloides* forest which established after a fire on the Argentinean side of Tierra del Fuego at the end of the 1950s (Martínez Pastur *et al.* 2002), or the pure, even-aged secondary forest of the coastal Chilean side of southern Patagonia and Tierra del Fuego, which recovered through natural succession after periods of colonisation during which the forests were selectively logged, burned and grazed.

Fine-scale disturbance

At higher elevations and at higher latitudes, where species richness is low, regeneration is less dependent on coarse-scale disturbance (Pollmann & Veblen 2004). Here canopy gaps are more important for the regeneration of the *Nothofagus* species, e.g., in southern Patagonia and Tierra del Fuego. The wind-induced snapping and uprooting of trees were the most common types of mortality observed in a pure *N. betuloides* forest and in *N. betuloides* forest mixed with *N. pumilio* (Promis *et al. submitted*). In the pure *N. betuloides* forest 52 % of the tree-falls were snap and 30 % uprooting. This appears to be characteristic of other *Nothofagus* dominated forests in South America. In the mixed *N. betuloides* – *N. pumilio* forest, however, the uprooting of trees was by far the most frequent cause of tree mortality, accounting for 70 % of the tree-falls, compared to only 24 % snapped trees. This largely corresponded with the findings from Tierra del Fuego (Rebertus & Veblen 1993a).

The lower resistance to stem breakage and the prevalence of snapped trees in the evergreen *N. betuloides* forests might be related to crown dieback (Rebertus & Veblen 1993b; Rebertus *et al.* 1993). An additional cause might be due to the abundance of the magellanic woodpecker (*Campephilus magellanicus* King. 1827). Its occurrence in forests in Tierra del Fuego has been related to the density of *N. betuloides* and the occurrence of snags (Vergara & Schlatter 2004). Magellanic woodpeckers primarily consume the larvae of wood-boring coleopteras in large and decaying trees, and also drill holes in large and healthy trees to access the phloem sap (Schlatter & Vergara 2005). Although not fatal in itself, the activity of the woodpecker may lead to secondary damage by diseases and insects. Insects and extreme climatic events may also reduce the vigour of trees, inducing partial crown mortality. This, too, facilitates fungal attacks and heart rot of the bole. The decaying standing deadwood enlarges the potential of trees suited for cavity creation by magellanic woodpeckers (Ojeda *et al.* 2007).

Both *N. betuloides* and *N. pumilio* can establish in small tree-fall canopy gaps (Veblen 1989; Rebertus & Veblen 1993a; Gutiérrez 1994; Arroyo *et al.* 1996; Cuevas 2003; Fajardo & de Graaf 2004; Cavieres & Fajardo 2005). Juvenile trees are also released by the creation of these small-scale disturbances in the canopy (Veblen *et al.*1996), although the growth strategies of the species differ. The observation by Rebertus & Veblen (1993a) that *N. betuloides* is more shade tolerant than *N. pumilio* has been proved in Tierra del Fuego by Promis *et al.* (*submitted*).

In the mixed evergreen *N. betuloides* – *D. winteri* forest at low elevations near the Tierra del Fuego coast, the *D. winteri* seedlings grow well under dense canopies and, after formation of gaps in the canopy, can respond faster than *N. betuloides*, sometimes even impeding the establishment of the latter (Rebertus *et al.* 1993a; Gutiérrez 1994; Veblen *et al.* 1996). Neither saplings nor pole stage *N. betuloides* are likely to be found where there are high numbers of *D. winteri* and *M. magellanica* in the understorey (Gutiérrez *et al.* 1991).

3. Forest use in the past, the present and the future

3.1. The past

The historical forest use has strongly influenced the present forest cover. In the Magellan Region of Chile (southern Patagonia), the history of forest use can been divided into four periods (Cruz *et al.* 2007b); (1) an indigenous period (10,000 B.C.-1843); (2) a colonisation period (1843-1953); (3) an oil and industrial period (1953-1980); and (4) a forest management and industrial expansion period (1980-2004).

(1) Five different indigenous tribes inhabited Patagoni thousands of years before the arrival of the Spaniards (16th century). The Strait of Magellan was inhabited by two nomadic tribes, the canoe aborigines (the Alacalufes or Kawéskar and the Yámanas or Yaganes) and the land aborigines (the Onas or Selk'man and the Haush or Manek'enk on the large island of Tierra del Fuego or Karukinká, and the Tehuelches or Patagones on the continent).

Fig. 8. Map of southern Patagonia and Tierra del Fuego showing the past locations of sawmills.

The indigenous people mainly used the forests to collect fungi and berries, and wood for fire, bows, arrows, domestic utensils and for constructing huts. Canoes were built with the bark of *N. betuloides*. There was also a spiritual attachment, with the Onas people believing that spirits inhabited the forests (Gusinde 1944; de Agostini, 1945, 1956; Martinic 1982, 1992; Vairo 1997).

(2) Harvesting of the *N. betuloides* forests began in 1843, when the Bulnes' Fort was built on the eastern side of the Brunswick Peninsula (Fig. 8), a consequence of the colonisation policies in southern Chile. In 1848 the city of Punta Arenas (Sandy Point) was founded. At this time wood became an important resource for construction and as fuel. The first sawmill with a hydropower system was established in Punta Arenas in 1861, and in 1875 steam power was introduced to the region in the form of locomotives. In the late 19th century there were several sawmills located on the Brunswick Peninsula (Martinic 1992; Cruz *et al.* 2007b).

From the 1880s, many forests were converted to farmland and pasture through a process of logging and burning. In southern Patagonia and Tierra del Fuego, approximately 200,000-300,000 ha were transformed to pasture (Cruz & Lara 1987; Cruz *et al.* 2007b).

In the late 19th and early 20th centuries the timber industry was centred on the Chilean side of southern Patagonia and Tierra del Fuego, but with the majority of the wood harvested destined for the Argentinean side of Patagonia and Tierra del Fuego, and the Falklands. New sawmills were established near forest dominated by *N. betuloides*, such as those situated on or near Dawson Island, the Whiteside Channel, the Almirantazgo Fjord, Navarino Island (Beagle Channel), the Otway Sound and Skyring Sound (Fig. 8). During this period *N. betuloides* provided around 80 % of the timber traded. However, restrictions on the importation of wood put in place by the Argentinean government impeded the timber industry in Chile, with the lowest exportation rates recorded between 1951 and 1952 (Martinic 1992; Cruz *et al.* 2007b).

(3) In the middle of the 20th century an intensive harvesting of the forests began on both the Chilean and the Argentinean (Gea-Izquierdo *et al.* 2004) sides of southern Patagonia. This coincided with the beginning of the oil and industrial period. At this time the forest industry concentrated on forests dominated by the deciduous *N. pumilio*, because oil exploration, and the related infrastructure, was frequently situated at locations near to these forests. The demand for wood from *N. betuloides* forests, which were located near urban areas and the coast, decreased. The harvested trees were logged selectively, with the best, largest and healthiest timber trees removed from the stands (known as 'floreo' in the region). Only the poor

quality, badly shaped and unhealthy trees remained (Martínez Pastur *et al.* 2000; Klepeis & Laris 2006; Cruz *et al.* 2007a). Many other stands were burned and converted to farmland.

The introduction of fossil fuels after the 1950s as a new energy resource replaced the use of firewood. At that time *N. betuloides* accounted for around 15 % of the total wood volume traded in the Chilean Patagonia and Tierra del Fuego (Cruz *et al.* 2007b).

(4) A new period of forest use in Chile began in the 1980s. Specific silvicultural methods for the management of the native forests were developed. It was demonstrated that *N. betuloides* forests in Chile could be managed employing either a selection or a shelterwood system (Donoso 1981). In reality, however, the stands were only rarely managed, with a small number of regeneration cuts made as part of a shelterwood system (Cruz *et al.* 2007a).

In the early 1990s a new, productive development of wood and forest management began. Wood chips were exported for a short time (1991-1997), and a furniture factory using solid wood was founded (Cruz *et al.* 2007b).

3.2. The present

At present the forest surface where *N. betuloides* participates is approximately 1,396,947 ha in the Magellan Region in Chile, accounting for 53 % of the total forest area. In terms of forest structure, 51 % are old-growth, 6 % are secondary growth, 9 % represent a transition between mature and secondary growth, and 34 % are 2 to 8 m tall shrubland (CONAF-CONAMA 1999).

A new period of forest conservation on private land began in 2004. In the 1990s the American Trillium Corporation purchased 625,000 ha on the Chilean and 185,000 ha on the Argentinean side of Tierra del Fuego. However, the firm failed in its attempts to establish a sustainable logging operation. Goldman Sachs, a global investment banking firm, acquired the loans and land, and finally donated the property to the Wildlife Conservation Society (WCS) in 2004 (Duncan 2006[1]). At present, the property on the Chilean side of Tierra del Fuego is managed by WCS as a private reserve. The principal aim of the Karukinka Reserve is to preserve the wildlife existing there, and to restore its ecosystems (Karukinka 2007[2]; WCS 2007[3]). This private reserve protects more than 20 % of the *Nothofagus betuloides* forests of southern Patagonia and Tierra del Fuego in Chile (Arroyo *et al.* 1996).

Additionally, more than 49 % of the *N. betuloides* forests of Chilean Patagonia and Tierra del Fuego are protected as State Protected Wild Areas (SNASPE) (CONAF-CONAMA 1999).

It can be estimated, that ca. 280,000 ha of pure *N. betuloides* forests and forests mixed with *N. pumilio* are suitable for timber production. Because of logistical reasons, lack of ecological and silvicultural knowledge, and problems in the wood drying process, the use of these forests at present is marginal (<1 % of wood production in 2004) (Cruz *et al.* 2007b). Sawn wood of *N. betuloides* is only produced in one big sawmill for the furniture production industry, consuming <5 % of the harvested timber (Cruz *et al.* 2007b).

3.3. The future

The *N. betuloides* forest area suitable for timber production in the Magellan Region of Chile has been estimated ca. 280,000 ha. Additionally, the forested area covered by the deciduous *N. pumilio*, the most important forest resource in southern Patagonia and Tierra del Fuego, has been estimated ca. 200,000 ha (Cruz *et al.* 2007b).

For the future development of a commercial forest industry, a system of sustainable forest management is required. This includes (1) increasing the managed forest area of stands dominated by *N. betuloides*, (2) improving current timber management (carrying out intermediate practices such as thinning), (3) incorporating the forests selectively logged in the past in silvicultural management schemes, (4) applying new silvicultural treatments in order to maintain the uneven-aged and multi-layer structure of the forest, based on an ecological understanding of the natural stand development, and including the

[1] Duncan, F. 2006. Temperate Native Forests in Chile. Management, conservation and forest practices. Report to the J. W. Gottstein Memorial Trust.

[2] Karukinka 2007. Karukinka is a new model for the conservation of biodiversity. Available from: http://www.karukinkanatural.cl/Karukinka/index-english.htm (accessed 16.12.07).

[3] WCS 2007. Wildlife Conservation Society. Available from: http://www.wcs.org/sw-our_mission/institute (accessed 16.12.07).

role of natural disturbances, providing the basis on which the forest may be managed as a renewable resource and trying to leave biological legacies in order to maintain a higher diversity and richness of species.

New studies of the ecology of the *N. betuloides* forests, their distribution, silviculture, wood properties, industrial yields, and also methods of drying have been carried out in the meantime (see Cruz & Caldentey, 2007). The application of this new knowledge in combination with a diversification of the forest industry within the framework of sustainable forest management would allow the derivation of goods and services from forest landscapes, while certain levels of biodiversity and ecosystem processes could also be maintained.

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