Measurement and modeling of the forest carbon resource in the *Nothofagus* forests of Tierra del Fuego, Chile

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Abstract

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This research quantifies the carbon stored in *Nothofagus*-dominated forests of Tierra del Fuego, Chile, and investigates a number of factors that influence the amount of carbon stored in these forest ecosystems. An intensive inventory of above-ground forest biomass, including live trees, snags, and downed coarse woody debris, was conducted in 40 forest stands. Carbon content of live and dead woody material was quantified. *Nothofagus* stands in Tierra del Fuego have a higher proportion of biomass represented by coarse woody debris (downed wood and snags) than a number of other forest types from around the world.

The relationship of forest carbon in three pools (overstory, coarse woody debris, and the O+A horizons of the soil) was related to landform variables using a regression analysis. While there was a marginally significant relationship of overstory to topographic variables, the overall relationships were weak. Further research will be necessary to elucidate the relationship between landform and forest carbon pools in Tierra del Fuego.

The impacts of anthropogenic fire on forest dynamics were assessed to inform long-term forest management policy related to carbon sequestration objectives. Forest recovery is slow following fire, but post-fire areas are more species rich than in forest interiors. If managing for carbon sequestration rather than biodiversity is an objective, than reforestation of burned areas may be necessary.

The LANDIS-II forest model was utilized to predict the impacts of timber harvest on landscape-scale carbon storage in the largely unharvested *Nothofagus* forests of Tierra del Fuego. Timber harvest reduced landscape-level carbon stores up to 35%, with reductions depending upon the type and intensity of timber harvest.

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Finally, I am grateful to the Northwest Church of Christ in Shoreline.

DEDICATION

This dissertation is dedicated to the people of the Republic of Chile, who showed me great hospitality and kindness as I worked and lived in their country. This dedication is offered in the hope that their management of the native forest may stand as a powerful example to the world.

Este tésis doctoral se dedica a la gente de la República de Chile, que me mostró mucha hospitalidad y amistad mientras que trabajaba y vivía en su país. Ésta dedicación se ofrece en la esperanza que su manejo del bosque nativo pueda constituir un ejemplo poderoso al mundo.

Chapter 1 Introduction

1.1 Rationale

The sequestration of carbon is among the most important functions of forest ecosystems (Atjay *et al.* 1977; Dixon *et al.* 1994). Carbon comprises roughly 50 percent of the dry biomass of forest ecosystems which is one of the most important terrestrial pools of this element (Lieth 1975; Atjay *et al.* 1977; Rodin *et al.* 1978). Scientific attention on carbon storage in forests, and the impacts of human activities on this function, has increased in the last 20 years due to concerns over greenhouse gas-driven climate change (Houghton *et al.* 1992; Brown *et al.* 1996; de Jong 2001; Nelson and de Jong 2003). While many forest ecosystems are relatively well-studied with respect to carbon stores and dynamics, scientific attention, including establishment of baseline inventories and analysis of system dynamics, remains to be extended to a number of ecosystems (de Jong 2001).

This dissertation addresses several aspects of forest carbon storage and management in the southern beech (*Nothofagus* Blume) forests of Tierra del Fuego, Chile. Despite their high latitude, these forests sequester significant amounts of carbon. The first research segment (Chapter 2) focuses on coarse woody debris (CWD) as a forest structural element and its importance as a carbon pool in the forests of Tierra del Fuego. The second segment (Chapter 3) examines the effects of anthropogenic fire, a disturbance type that has greatly increased in Tierra del Fuego following colonization by European peoples. The third segment (Chapter 4) explores the relationship of three separate carbon pools to topographic variables. The fourth segment (Chapter 5) examines the impacts of forest management on landscape-scale forest carbon stores by modeling the natural wind disturbance regime and then analyzing several timber harvest scenarios over a four-century simulation period.

While many of the forests of Tierra del Fuego may be considered relatively pristine (Klepeis and Laris 2005), timber harvest and other activities have past and present impacts on the region (Veblen and Schlegel 1982; Rebertus and Veblen 1993; Veblen *et al.* 1996). The goal of this dissertation is to provide information on the southern beech forests of Tierra del Fuego that will be useful in managing these forests for carbon-related purposes or for other objectives.

1.2 Study Area

1.2.1 Geography and Location

The Isla Grande de Tierra del Fuego is a large island (48,000 km^2) located at the southern end of South America (Figure 1.1) and is part of the archipelago known generally as Tierra del Fuego. The geology is dominated by the old Andean granitic basement, with protruding Cretaceous sedimentary formations and Pleistocene glacio-fluvial materials forming the surficial geology (Gerth 1955; McCulloch *et al.* 1997). Strong southeast-to-northwest faulting and subsequent glacial activity has created ridge-and-valley systems adjacent to the southern coast of Tierra del Fuego. This topography grades into the relatively low relief of glacial outwash plains that comprise the northern part of the island. Elevations range from sea level to ~2000 m, with the principal mountain ranges being the Sierra Carmen Sylva in the north and the Sierra Santa Maria in the south (Instituto Geográfico Militar 1983). The research in this dissertation focuses on the area of the island bounded by Bahia Inútil, the Straits of Magellan/ Whiteside Canal, and the Seno Almirantazgo. The study area extends from approximately 53°30' to 54°30' south latitude and 68° 34' to 70° 14' west longitude. This includes the former property of Savia Forestal, Ltda. (Klepeis and Laris 2005) which is now the ecological reserve 'Karukinka', owned and managed by the Wildlife Conservation Society (Figure 1.2).

1.2.2 Vegetation

This high-latitude (53°-54°30' S lat.) island hosts an assemblage of vegetation communities, including Patagonian shrub-steppe, Magellanic tundra, and subantarctic forest of broadleaf trees (Moore 1983). Forest vegetation is usually restricted to relatively well-drained areas below an altitudinal timberline at ~800 m elevation. The forest cover is dominated by three species of southern beech (*Nothofagus* Blume) (Pisano 1977), which is a circum-austral genus of the family Fagaceae (Veblen *et al.* 1996). Coigüe (*Nothofagus betuloides* (Mirbel) Oersted) is a sclerophyllous, evergreen southern beech that is primarily coastal in distribution, decreasing in prevalence eastward to the drier pampas, or Patagonian shrub-steppes. Lenga (*N. pumilio* (Poeppig & Endl.) Krasser) is a deciduous southern beech that inhabits the drier interior, grading into coigüe forests towards the coast. On exposed slopes 300-400 m above mean sea level, pure stands of lenga occur in an ecotype known as 'montane lenga'. Ñirre (*N. antarctica* (Forster f.) Oersted) is a deciduous species that is primarily ecotonal in distribution, forming a subalpine belt in the mountains and occupying the margins of pampas and wetlands. A few minor tree species may be found as infrequent associates of coigue in the relatively mesic environment of the immediate coast, including leña dura (*Maytenus magellanica* (Lam.) Hooker f.) and canelo (*Drimys winteri* Forster and Forster f.) (Pisano 1977; Gutiérrez *et al.* 1991). An excellent review of the silvic characteristics of these species may be found in (Donoso Zegers 2006). Understory vegetation is comprised of shrubs such as *Berberis buxifolia* Lam., *Berberis ilicifolia* L.f., and *Ribes magellanicum* Poiret, and herbs such as *Geum magellanicum* Comm ex Pers., *Gunnera magellanica* Lam., and *Senecio* L. species. Cryptogam communities may be very species-rich and well developed on the forest floor and on well-decayed woody debris (Kalin-Arroyo 1996). In low-lying areas with little topography and resultant poor drainage, Magellanic moorland (Sp. 'turba'), a *Sphagnum*-dominated community forms extensive peat deposits whose development dates to glacial recession (Moore 1983).

Forest soils are generally well-developed cryogenic spodosols (Arroyo *et al.* 1996; Gerding and Thiers 2002). The primary natural disturbance agent is wind (Armesto *et al.* 1992; Rebertus and Veblen 1993; Rebertus *et al.* 1997). Fire is primarily of anthropogenic origin (Kalin-Arroyo 1996; Veblen *et al.* 1996) and is largely limited to settled areas on the Isla Grande in recent history.

1.2.3 Climate

Climate is influenced by the high latitude (53-56° S) and influences of the Antarctic Polar Front and South Pacific Cyclone (Pittock 1980; Moore 1983). Rainfall is evenly distributed throughout the year. A precipitation gradient exists from southwest to northeast, with heavier precipitation (2000-4500 mm $year^{-1}$) on the outer coast decreasing to low levels (<400 mm $year^{-1}$) in the shrub steppe east of the intermittent mountain ranges on La Isla Grande (Tuhkanen 1992). Orographic precipitation in southwestern Tierra del Fuego is significant. The temperature regime is, on average, cooler than in counterpart latitudes in the northern hemisphere, with mean monthly sea level temperatures averaging 9.5° C and 0° C for January and July, respectively (Tuhkanen 1992; Cerveny 1998). Maritime climatic moderation does, however, prevent a prolonged freezing period, and persistent snowpacks are rare. Strong winds blow year-round, but with the strongest winds actually occurring during the growing season (Weischet 1985; Tuhkanen 1992). This has the effect of limiting growth through the inhibition of net photosynthesis (Weischet 1985).

Figure 1.1 Map of South America showing location of Tierra del Fuego.

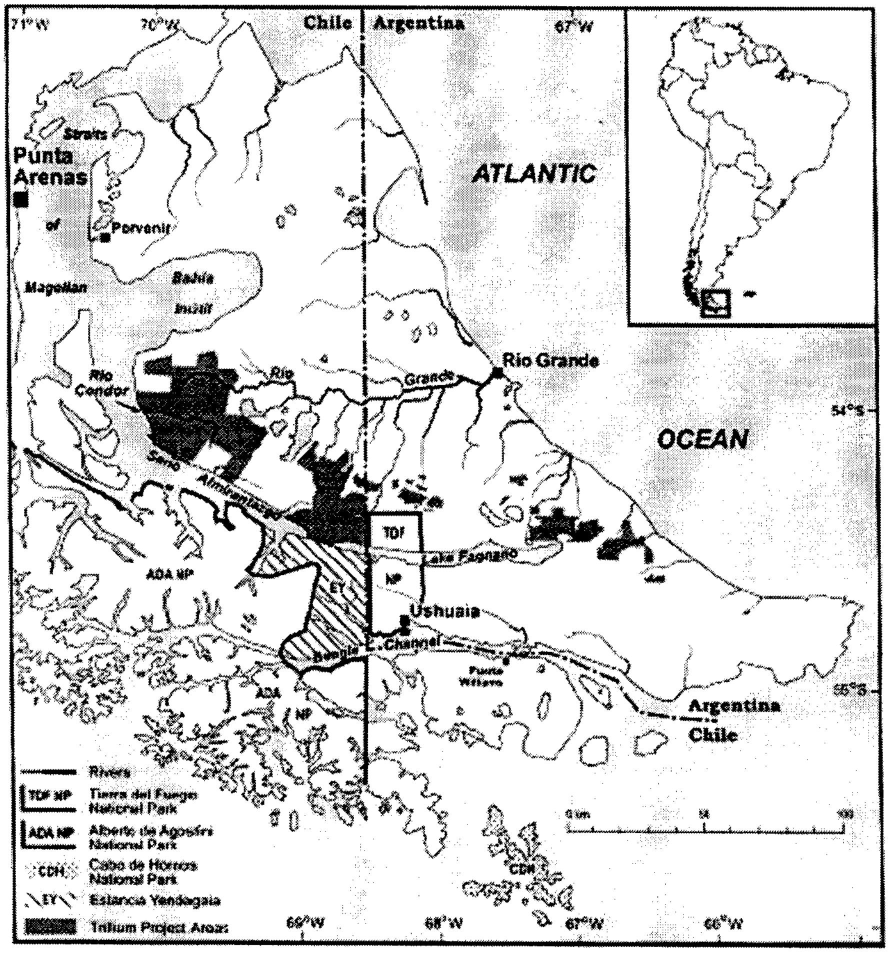

Figure 1.2 Map of Tierra del Fuego, showing extent of study area. Adapted from (Klepeis and Laris 2005).

Figure 1.3 Old-growth *Nothofagus pumilio* forest near Estancia Vicuña, Tierra del Fuego, Chile.
Photo by Dr. Jerry F. Franklin.

Chapter 2 Coarse woody debris in the southern beech forests of Tierra del Fuego, Chile

2.1 Introduction

Coarse woody debris (CWD), which includes standing dead trees and boles on the forest floor, is an important structural feature of most natural forest ecosystems (Maser *et al.* 1979; Graham 1982; Harmon *et al.* 1986). CWD has proven to be critical to many ecosystem functions, including energy and nutrient cycling and provision of habitat for wildlife and other elements of biodiversity in both terrestrial and aquatic environments (Sachs and Sollins 1986; Maser *et al.* 1988; Keenan *et al.* 1993).

Consequently, quantifying physical and chemical attributes of CWD has become an important aspect of forest mensuration (Harmon and Sexton 1996). For example, estimates of the contributions of CWD are needed in assessing fuel loadings in forest stands with regards to wildfire (Wagner 1968), carbon storage (Turner *et al.* 1995; Hart *et al.* 2003), and habitat function and capacity (Bunnell *et al.* 1999). Mass of carbon and nutrients in CWD must be calculated to fully parameterize models dealing with energy, carbon, and nutrient fluxes in forest ecosystems.

Quantification of CWD is often accomplished in a two-step process. Measurements are made in the field that allow estimates of the volume of CWD for different sizes, decay classes, and, sometimes, species of CWD. The mass of carbon and nutrients can be calculated when information is available that relates these categories (especially decay state) to wood density and carbon and nutrient concentration in the CWD.

The temperate broadleaf forests of the southern hemisphere have been fairly well studied (Donoso Zegers 1993; Veblen *et al.* 1996), but have only recently received scientific attention in terms of quantifying CWD levels (Carmona *et al.* 2002). CWD is an important structural element in stands of *Nothofagus pumilio* [Poepp. et Endl.] Krasser (Fagaceae) and *N. betuloides* (Mirb.) Oersted (Fagaceae) in Tierra del Fuego and was the subject of this study (Figure 2.1). The focus of the study was on: (1) quantification of the volume and mass of CWD in an extensive sample of *Nothofagus* forests, including stands representing different environmental conditions and composition, and (2) collection and laboratory analysis of wood samples that allow field measurements stratified by decay classes to be converted to estimates of carbon, major nutrients, and micronutrients for these forests. A broad assessment of the contribution of CWD to the carbon and nutrient budgets of these forests was my immediate goal as well as providing future workers with the data that are needed to convert structural measurements of CWD to estimates of mass of organic matter, carbon, and nutrients.

2.2 Methods

2.2.1 Study Area

Sampling plots were distributed throughout the forested areas of the study area as described in the introduction. Plots were randomly located within previously defined forest stands.

2.2.2 Measurement of CWD

CWD was defined for the purposes of this study as dead woody material ≥5 cm in diameter, whether standing (snag) or on the forest floor. The five-class decay class system (Fogel *et al.* 1973; Graham 1982; Maser *et al.* 1988; Harmon and Sexton 1996) was used to characterize the physical and chemical characteristics of *Nothofagus* woody debris through the decomposition process. Decay classes are used to index the changes in appearance, chemical composition, structural integrity, ecological function, and other attributes as CWD decomposes. The decay classes are based upon attributes as bark cover, friability, shape of cross-section, structural integrity, and color.

The decay classes employed in this research were characterized as follows:

- Class 1: A recently fallen tree. The wood is solid and its structural integrity has not been compromised by decay. Some natural heart-rot may have occurred, but the sapwood is firm. Outer bark is still intact, and fine branches may be present on crown sections. (Material is approximately 0-4 years since death for *N. pumilio* CWD 20 cm in diameter).

- Class 2: Outermost layer of sapwood wood is beginning to decay slightly, yet wood is still firm throughout. Bark is generally broken and slipping. Fine branches are usually absent. (Material is approximately 5-17 years since death for *N. pumilio* CWD 20 cm in diameter)

- Class 3: Bark is absent. The wood is beginning to lose structural integrity. Coarse branches usually sufficiently decayed that they can be broken off with modest effort. Pieces of sapwood can be removed easily. Either heartwood or sapwood are fairly firm. (Material is approximately 18-58 years of age for CWD 20 cm in diameter)

- Class 4: Debris is typically fully in contact with the ground. Sapwood is almost completely decayed and heartwood is severely structurally compromised. All large branches are gone. Debris is still at least hemispheric in cross-section. (Approximately 59-99 years of age for CWD 20 cm in diameter)

- Class 5: Debris is in an advanced state of decay. It is fully in contact with the ground, is completely composed of rotten wood, and almost indistinguishable from the forest floor. Debris in this class is elliptical in cross section. (Approximately 100+ years of age for CWD 20 cm in diameter)

In 1999 and 2001, cylindrical cross-sections of CWD from *N. pumilio* and *N. betuloides* were collected in southwestern Tierra del Fuego. All woody debris sampling was conducted in closed-canopy mature (>100 yr. old) stands broadly representative of forest conditions. Samples of *N. pumilio* were taken from Estancia Río Bueno (coastal, 53°56'S, 70°07'W) and Estancia Vicuña (interior, 54°10'S, 68°45'W). Fifteen logs representing *N. betuloides*, three from each decay class, were sampled in Puerto Arturo (coastal, 54°05'S, 70°05'W). Due to the rapid decrease in the presence of this species away from the coast, *N. betuloides* was not sampled at any interior site. At Vicuña, five logs of *N. pumilio* were sampled from each decay class, totaling twenty-five logs sampled in all. Four samples (cross-sections) were taken from each log. At Río Bueno, three logs of *N. pumilio* were sampled from each decay class, totaling fifteen logs sampled in all. Again, four samples (cross-sections) from each log were taken. In decay classes 1 through 3, the sampled cross-sections (of variable diameter) measured approximately 5 cm in thickness. These samples were removed using a chainsaw. Cross-sectional samples from decay classes 4 and 5 measured approximately 10 cm in thickness, and were removed using a sharp knifeblade and a fine-toothed saw (~5 tines per cm) where necessary. The dimensions of each sample were measured in the field for determination of sample volume. The samples were placed in plastic bags to retain all organic material and moisture during transportation from the field. The locations of Río Bueno, Estancia Vicuña, and Puerto Arturo are shown in Figure 2.1.

2.2.3 Lab methodology

Total mass at field moisture levels was determined for each sample with an Ohaus Corporation Model I-10 Series metric scale. Once total mass was measured, subsamples were taken from each sample, weighed at field moisture levels, and then dried to constant mass at 90° Celsius. In all subsamples, the initial 36-hour drying period proved sufficient to achieve constant sample mass.

Dimensions of cross-sections, taken in the field, were used to calculate volume for each of the subsamples. In decay classes 1, 2, and 3, the samples typically were sufficiently circular in cross-section to use the volume formula for a cylinder. To obtain a radius in a log cross-section that may not be precisely circular, the following equation was used: $r=0.5\sqrt{(l*s)}$ where r = calculated radius, l = long axis of the sample cross section, and s = short axis of the sample cross section. To account for variation in the width of the cross-section, the widest and narrowest parts of the cross-section were measured and averaged to obtain a mean width. In decay classes 4 and 5, the log has lost significant structural integrity due to advanced decomposition, and typically assumes a semicircular cross-section. In these decay classes, width ("diameter") of the log, thickness of the cross-section, and a vertical measurement every 5 cm across the log were taken. A close approximation of actual volume was therefore obtained calculating cross-sectional area using these measured segments as components of total cross-section.

Subsamples of woody debris were ground in a Wiley mill to a fineness of 0.2 mm, and 20 mg of each subsample were then analyzed for CHN concentration using a Leco CHN-600, similar to (Allen *et al.* 1997). Detection limits were sufficient for the expected concentrations of carbon and nitrogen, and appropriate calibration samples were used (pine wood dust). To assess the concentration of nutrients in *N. betuloides* and *N. pumilio* CWD for the respective decay classes, three to five samples per decay class were analyzed using an ICAP (Inductively coupled argon plasma) instrument (Thermo Electron Co.) for the following elements: Al, As, B, Ba, Ca, Cd, Cr, Cu, Fe, K, Mg, Mn, Mo, Na, Ni, P, Pb, S, Se, Zn, Si, and Ag. Drying and weighing of *N. pumilio* samples was conducted at the University of Magallanes in Punta Arenas, Chile, while all other laboratory analyses were conducted at the University of Washington's College of Forest Resources Analytical Laboratory.

2.2.4 Plot sampling for per-hectare woody debris volumes and sample diameter distributions

A stratified random sample of 163 temporary biomass sample plots was measured in October and November of 1999, and April of 2001, across the study area to assess CWD volume in different forest types. Overstory live tree and snag volume estimates (per hectare) were made using variable-radius plot methodology (Bitterlich 1984; Shiver and Borders 1996). The diameter at breast height (DBH), height, and height to live crown were measured on each tally tree. Downed wood was measured using the line-intercept method (Harmon and Sexton 1996; Shiver and Borders 1996). Four line-intercept transects of 25 m each were arranged in a square centered on the sample point.

2.2.5 Data Analysis

Tests of normality were conducted using the Shapiro-Wilk test for non-normality (Shapiro *et al.* 1968), and homogeneity of variance was assessed with the Fligner-Killeen statistic, which is relatively robust for departures from normality and small sample sizes (Conover *et al.* 1981). Analysis of variance (Zar 1999) was used to assess importance of factors such as species, site, and decay class to density and nutrient content. Tukey's Honest Significant Difference was used to assess significance in pairwise comparison of means between decay classes within species. A significance level of $\alpha=0.05$ was used for all tests. All data analysis was performed in the R statistical computing environment (R Development Core Team 2005).

Tissue density. Once the mass of dry biomass per sample was determined, it was divided by the volume to obtain dry biomass density. The density data for each class and site were then averaged by site and by species. Analysis of variance was used to assess the importance of site, species, and decay class in predicting tissue density. Carbon density, here defined as the mass of carbon (g) per unit volume of CWD (cm^3) (Neilson *et al.* 2006), was calculated as the concentration of carbon (percent carbon divided by 100) multiplied by the tissue density for a given decay class.

The tissue density results from this study were used, in conjunction with the time-decay equations given in (Frangi *et al.* 1997) to calculate approximate ages for the various decay classes.

Moisture Content. Dry-basis moisture content (expressed in percent) was calculated for *N. pumilio* (due to logistical constraints, moisture content data were not taken for *N. betuloides*). Samples were taken in the austral spring (December). The following formula was used to calculate moisture content:

$$MC_s = 100^* \left[(M_s - D_s) / D_s\right]$$

where MC_s is the sample moisture content (% of field mass), M_s is the sample mass at field moisture levels, D_s is the sample mass (g) after oven-drying to constant mass. Two-factor ANOVA was used to assess the significance of site (coastal vs. interior) and decay class in predicting moisture content. Tukey's Honest Significant Difference was used to assess differences between combinations of decay class and site.

Carbon and nitrogen concentration. Analysis of variance ($\alpha=0.05$) was used to assess the importance of site (coastal vs. interior) and decay class in predicting C:N ratios in *N. pumilio*.

Elemental nutrient concentrations in Nothofagus pumilio and betuloides. Averages were taken of the three samples per decay class for each species and location.

Per-hectare Woody Debris Mass and Diameter Distributions. Individual plots were separated into seven representative forest types based on geographic area and stand composition. Standing live tree biomass was calculated by first estimating total volume by using regression equations developed for *N. pumilio* (Martinez-Pastur *et al.* 1993), then multiplying volume by the tissue density estimates. Downed wood volumes were calculated using Wagner's method (Wagner 1968) for each decay class, and then multiplied by the tissue density estimates to compute biomass. Snag volumes were calculated using trunk diameter, taper and height and assuming a simple conic section, and biomass calculated by multiplying volume by the appropriate tissue density estimate. Comparisons were made with representative data from other forest types. Diameter distributions from several stand types (summed data from four plots in each stand type) were graphed as histograms. Plots (n = 159) were sorted by mean tree diameter, and correlation coefficents between mean tree diameter and CWD mass (by decay class and in total) were calculated. Diameter distributions of CWD measured in the line-intercept transects were modeled using the Weibull function, the flexibility and simplicity of which offer advantages for forest mensuration applications (Bailey and Dell 1973; Palahi *et al.* 2006). The shape and location parameters of the Weibull function were related to mean overstory DBH as determined from the variable-radius plots.

Contribution of woody debris to site nutrient stores. Five stands representing different forest types (coastal coigüe, coastal lenga, coastal coigüe/lenga, interior lenga, and montane lenga) were selected from the plot samples. Calculated volumes of live overstory, coarse woody debris, and snags were multiplied by dry tissue density to estimate per-hectare biomass of each of these pools. These were then multiplied by the measured concentration for the primary nutrients (C, N, P, K, Ca, Mg, Na, and S) to estimate per-hectare mass of the nutrients for each of the five stands. The percent of each nutrient in woody stores that is represented by woody debris was also calculated for each stand.

2.3 Results

2.3.1 Tissue density

Tissue density declined with decay class, stabilizing somewhat in decay classes four and five (Figure 2.2, Table 2.1). *N. betuloides* has a slightly higher density in decay class one than *N. pumilio* (not significant at α=0.05). The greatest decreases in density for both species were in decay classes three and four.

Decay class was the only significant factor ($p<0.0001$) in predicting the density of *Nothofagus* wood. Neither site (coastal vs. interior, $p=0.6101$) nor species (*N. pumilio* vs. *N. betuloides*, $p=0.8502$) was a significant factor in predicting density of wood samples. The ANOVA also failed to reveal any significant interaction effects among factors.

The tissue density values for *N. betuloides* display the same trends as those for *N. pumilio*, although are available only for a coastal site (Puerto Arturo) since it was absent at Vicuña. *N. betuloides* does have slightly higher (but statistically non-significant) density values than *N. pumilio*.

Carbon density strongly reflected the pattern of tissue density over the decay classes (Figure 2.3, Table 2.1) since density was more variable across decay classes than percent carbon concentration. Carbon density values for *N. betuloides* varied from 0.269 g cm^{-3} in decay class 1 to 0.061 g cm^{-3} in decay class 5. Carbon density values for *N. pumilio* ranged from 0.230 g cm^{-3} to 0.087 g cm^{-3} for decay classes 1 and 5, respectively.

Table 2.1 Density, carbon and nitrogen content, C:N ratio, and C density for the two primary *Nothofagus* species on Tierra del Fuego.

Nothofagus betuloides (Mirb.) Oersted. Coigüe de Magallanes; coihue; guindo.					
Decay Class	*Density (g cm^{-3})*	*%C*	*%N*	*C:N Ratio*	*C density (g cm^{-3})*
1	0.576 ±0.04 a	46.72 ±0.31 a, b	0.154 ±0.013 a	305.2 ±29.4 a	0.269
2	0.465 ±0.05 a, b	47.30 ±1.33 a	0.096 ±0.052 a, c	582.9 ±248.1 b	0.220
3	0.382 ±0.12 b	47.37 ±0.85 a, c	0.125 ±0.017 a, c	383. ±55.1 c	0.181
4	0.154 ±0.0.1 c	40.08 ±3.64 b	0.081 ±0.022 b, c	531. ±214.6 d	0.062
5	0.141 ±0.12 c	43.60 ±4.85 b, c	0.079 ±0.013 b, c	573.1 ±163.2 e	0.061
Nothofagus pumilio (Poeppig & Endl.) Krasser. Lenga; roble de Magallanes.					
Decay Class	*Density (g cm^{-3})*	*%C*	*%N*	*C:N Ratio*	*C density (g cm^{-3})*
1	0.491 ±0.07 a	46.82 ±0.57 a	0.174 ±0.082 a	310.6 ±192.4 a, c	0.230
2	0.453 ±0.07 a,b	46.11 ±0.56 a	0.211 ±0.060 a	316.4 ±198.5 a, c	0.209
3	0.379 ±0.09 b	46.64 ±.92 a	0.181 ±0.045 a, c	280.8 ±81.4 a, c	0.177
4	0.201 ±0.04 c	51.00 ±1.09 b	0.098 ±0.040 b, c	608.7 ±269.7 b	0.103
5	0.168 ±0.02 c	51.56 ±1.58 b	0.121 ±0.027 b, c	450.3 ±122.0 b, c	0.087

All values are means, ± one standard deviation. Letters indicate no statistical difference (95% confidence) using Tukey's honest significance difference test (comparisons made between decay classes within species). Since carbon density was calculated as a product of averages, no multiple comparisons were made.

2.3.2 Moisture content

The dry-basis moisture moisture content of downed wood, which was determined only for *N. pumilio*, did not vary by site (p>0.4), but did vary by decay class (p<0.001). Dry-basis moisture content increased with decay class (Table 2.2), resulting in percent moisture content averaging around 300% of total mass for decay classes 4 and 5. Tukey's test of honest significant differences (Zar 1999) showed that mean moisture content values for decay classes 1, 2, and 3 did not differ from each other, but were significantly different from decay classes 4 and 5. Decay classes 4 and 5 did not differ from each other in terms of mean moisture content.

Table 2.2 Dry-basis moisture content for *Nothofagus pumilio* at coastal and interior sites in the austral summer.

Site	Decay Class	n	% Moisture Mass ± one std. dev.
Río Bueno	1	3	53.1 ±22.1 *a*
	2	3	40.4 ±29.4 *a*
	3	3	77.4 ±76.5 *a*
	4	3	281.0 ±59.0 *b*
	5	3	315.2 ±44.6 *b*
Vicuña (interior)	1	5	55.6 ±24.7 *a*
	2	5	50.5 ±14.1 *a*
	3	5	95.0 ±39.9 *a*
	4	4	304.0 ±77.5 *b*
	5	5	292.9 ±34.7 *b*

2.3.3 Carbon and nitrogen concentrations

Percent carbon (by mass) ranged from 36.6 to 54.2, with a mean of 47.8. Percent nitrogen (by mass) ranged from 0.048 to 0.294, with a mean of 0.142. C:N ratios (Table

2.1, Figure 2.3) ranged from 305 to 608, averaging 410. The general trend was an increase in the average C:N ratio with increasing decay class. Carbon and nitrogen concentrations for *N. pumilio* for two sites, coastal (Río Bueno) and interior (Vicuña), are shown in Figure 2.3. Decay class was a highly significant variable in predicting C:N ratios ($p<0.001$), and differences in C:N ratios between the two sites were also significant ($p<0.01$).

Mean nitrogen concentration for *N. pumilio* differed significantly by decay class ($p>0.001$), with a two-fold decrease from decay class 1 to 5. Mean nitrogen concentration for *N. pumilio* differed significantly between Río Bueno and Vicuña ($p>0.01$), with nitrogen being higher at Vicuña.

2.3.4 Elemental nutrient concentrations of N. betuloides and N. pumilio

The dominant pattern for micronutrients was a gradual decrease from decay classes 1 and 2 to decay class 3, a subsequent increase in decay class 4, and culminating in a decrease in decay class 5. P, K, Ca, Mg, Na, and S were present in measurable amounts (Appendix A). B, Cd, Mo, Ni, Pb, Se, and Ag were detectable only in trace amounts in decay classes 4 and 5 and are not shown in Appendix A.

2.3.5 Contribution of woody debris to site nutrient stores

Woody debris accounted for 23.9-42.5% of the carbon, 23.1-37.9% of the nitrogen, 21.2-29.6% of the phosphorus, 19.5-29.7% of the calcium, 28.4-49.0% of the magnesium, 26.0-44.8% of the sodium, and 29.6-52.5% of the sulfur (Table 2.3).

2.3.6 CWD mass and diameter distributions

Biomass estimates for CWD (downed wood and snags) and live trees for the seven types of *Nothofagus* forest are presented in Table 2.4. Live tree biomass ranged from 98.4 Mg ha^{-1} to 401.9 Mg ha^{-1}. Biomass of downed wood ranges from 52.2 to 127.7 Mg ha^{-1} and snag biomass ranged from 7.5 to 38.4 Mg ha^{-1}. As a percent of total biomass, downed wood and snags had ranges of 17.2-33.0% and 2.8-11.3%, respectively.

Most downed wood biomass was in decay class 3, and most of the remaining downed wood was in decay classes 2 and 4 (Figure 2.4).

Table 2.3 Per-hectare mass of nutrient pools represented by CWD in five stands representing different forest types

		Mg ha^{-1}		Kg ha^{-1}						
Stand Type	Pool	Biomass	C	N	P	K	Ca	Mg	Na	S
Coastal Lenga	Live overstory	304.1	149.3	587.2	93.1	201.9	796.6	96.2	47.9	40.6
	Total CWD	142.3	87.1	225.9	22.5	48.2	195.9	48.0	22.3	25.2
	% in CWD	*31.9*	*36.8*	*27.8*	*19.5*	*19.3*	*19.7*	*33.3*	*31.8*	*38.3*
Coigue	Live overstory	336.3	134.3	517.7	102.9	223.3	881.0	106.4	52.9	44.8
	Total CWD	105.1	48.6	155.1	23.6	54.0	209.9	42.3	18.6	18.9
	% in CWD	*23.8*	*26.6*	*23.1*	*18.6*	*19.5*	*19.2*	*28.4*	*26.0*	*29.6*
Coastal Coigue/Lenga	Live overstory	455.0	434.7	716.1	139.3	302.1	1191.9	143.9	71.6	60.7
	Total CWD	204.1	136.6	278.8	37.8	84.8	357.1	85.4	35.6	39.6
	% in CWD	*31.0*	*23.9*	*28.0*	*21.3*	*21.9*	*23.1*	*37.2*	*33.2*	*39.5*
Interior lenga	Live overstory	259.2	127.3	500.6	79.3	172.1	679.1	82.0	40.8	34.6
	Total CWD	102.8	50.4	159.0	21.4	50.5	177.3	35.7	18.4	17.3
	% in CWD	*28.4*	*28.4*	*24.1*	*21.2*	*22.7*	*20.7*	*30.3*	*31.1*	*33.3*
Montane Lenga	Live overstory	53.4	26.2	103.2	16.4	35.5	140.0	16.9	8.4	7.1
	Total CWD	41.4	19.4	62.9	6.9	15.0	63.8	16.2	6.8	7.9
	% in CWD	*43.6*	*42.5*	*37.9*	*29.6*	*29.7*	*31.3*	*49.0*	*44.8*	*52.5*

Table 2.4 Comparison of biomass of standing live trees, downed wood, and snags for a number of forest types.

Forest type	*Stand age*	*Dominant Species*	*Downed Wood*		*Snags*		*Live Standing Trees*		*Source*
			Mass (Mg ha^{-1})	*% total mass*	*Mass (Mg ha^{-1})*	*% total mass*	*Mass (Mg ha^{-1})*	*% total mass*	
European beech, Albania	500+	*Fagus sylvatica*	21.2	3.6	10.6	1.8	551.2	94.5	(Meyer *et al.* 2003)
European beech, Germany	160	*Fagus sylvatica*	22.9	5.6	7.8	1.9	375.7	92.5	(Muller-Using and Bartsch 2003)
Scots pine, northwestern Russia	250+	*Pinus sylvestris*	11.9	15.4	8.3	10.8	56.9	73.8	(Karjalainen and Kuuluvainen 2002)
Wet tropical forest, Costa Rica	400+	*Pentaclethra macroloba*,etc.	46.3	19.4	6.5	2.7	186.1	77.9	(Clark and Clark 2000; Clark *et al.* 2002)
Sitka spruce and western hemlock forest, Washington, USA	250+	*Picea sitchensis/Tsuga heterophylla*	92.3	6.0	241.9	15.8	1199.3	78.2	(Edmonds *et al.* 1998)
Douglas-fir/western hemlock, Washington, USA	450+	*Pseudotsuga menziesii/ Tsuga heterophylla*	59.4	9.7	57.0	9.3	497.0	81.0	(Smithwick *et al.* 2002)
Coast redwood, California, USA	1200+	*Sequoia sempervirens*	242	5.6	20	0.5	4032	93.9	(Busing and Fujimori 2005)
Coastal lenga	200+	*Nothofagus pumilio*	127.7	27.6	23.1	5.0	312.1	67.4	(this research)
Coastal coigüe	150+	*N. betuloides*	90.0	19.5	28.4	6.1	344.3	74.4	
Coastal mixed lenga/coigüe	150+	*N. betuloides/ N. pumilio*	115.4	20.8	38.4	6.9	401.9	72.3	
Interior mixed lenga/coigüe	150+	*N. betuloides/ N. pumilio*	79.6	17.2	36.3	7.8	347.5	75.0	
Interior lenga	200+	*N. pumilio*	102.2	29.7	9.6	2.8	232.9	67.6	
Interior coigüe	150+	*N. betuloides*	95.5	20.7	52.0	11.3	313.3	68.0	
Subalpine lenga	200+	*N. pumilio*	52.2	33.0	7.5	4.73	98.4	62.3	

The diameter distributions of sampled downed wood pieces along the line-intercepts largely appear to conform to the negative exponential family, with a smaller mode in the upper diameter classes (Figure 2.5). Among the decay classes, CWD mass in decay class 3 ($r^2 = 0.465, p<0.0001$) and decay class 4 ($r^2 = 0.256, p<0.01$) were significantly correlated with mean diameter of the overstory.

2.4 Discussion

2.4.1 Decay class

Decay class is a useful categorical variable in field data collection and analysis of biomass and nutrient concentration data. As a further indication of the appropriateness of the decay-class system used in this research, time-decay equations for *Nothofagus* (Frangi *et al.* 1997) were used to calculate approximate ages for the five decay classes. The calculated ages corresponded to the expected distribution for a population of woody debris with most of the mass in decay class 3 (Harmon *et al.* 1986).

2.4.2 Tissue density

Tissue density values for decay classes 1, 2, and 3 followed a decreasing pattern, and then declined sharply to decay class 4 and 5 (Figure 2.2). The slight decline in density from decay class 4 to decay class 5 is indicative of the development of a relatively stable endpoint composed of recalcitrant substances (phenols, lignified compounds, etc.). The lack of difference in density for *N. pumilio* woody debris between the coastal and interior sites indicates the likelihood that there are no major gradients in wood density corresponding to increasing continentality or decreasing precipitation. The strength of decay class as a predictor of density is demonstrated by the small *p*-value (<0.0001).

Density values for *N. pumilio* and *N. betuloides* determined in this study were similar to the density values found for woody debris in the old-growth forests of Chiloé Island, Chile (Carmona *et al.* 2002), which also showed the stabilization of density values in decay classes 4 and 5. These density values were higher than for many temperate conifers such as *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg., but lower than for tropical hardwoods (Harmon and Sexton 1996).

Since carbon density is a composite of tissue density and percent carbon, it reflected the trends of both as a function of decay class. In decay classes 4 and 5, *N. betuloides* had extremely low carbon density, since both tissue density and percent carbon declined for this species in these more advanced decay classes.

2.4.2 Moisture content

Moisture content of *N. pumilio* increased dramatically in the more decayed classes (4 and 5), indicating important changes in the physical and chemical nature of the woody debris (Kraigher *et al.* 2002). The moisture content of the extremely decayed woody debris was not significantly different between the wetter coastal site and the drier interior site, despite having been sampled during the late austral summer (December). This highlights the ability of CWD to store water, a critical ecosystem function with respect to processes such as regeneration on xeric sites (Heinemann *et al.* 2000). This ability to store water, even in dry periods, is a noted function of CWD (Fraver *et al.* 2002), and can influence decay dynamics (Progar *et al.* 2000).

2.4.3 Carbon and Nitrogen Concentrations

The most likely explanation for differences in C:N ratios between Río Bueno and Vicuña resides in the differences in precipitation between the two sites. These two sites represent opposite ends of precipitation gradient on Tierra del Fuego, with Río Bueno receiving considerably higher precipitation (~2000 mm $year^{-1}$) than Vicuña (~600 mm $year^{-1}$). C:N ratios may differ in living tissues due to differences in nitrogen availability between sites, since the relative importance of nitrogen fixation by root symbionts increases with decreasing precipitation (Schulze *et al.* 1991), and ecosystems with higher soil moisture may experience elevated denitrification rates (Zak and Grigal 1991). These differences would be apparent in the least decomposed decay classes (1 and 2). There may be higher rates of nitrate leaching loss from litter materials and soil, including CWD, due to the higher precipitation at the coast than at the dry interior (Austin and Vitousek 1998; Austin and Sala 2002). This would explain differences in the most decayed woody debris, specifically classes 4 and 5. Topography may also play a role in C and N dynamics, especially as it influences soil characteristics (Zak and Grigal 1991; Luizão *et al.* 2004), but topography was similar at the tissue sample sites (all flat plateau sites).

C:N ratios in woody debris generally decrease with decomposition (Maser *et al.* 1979; Harmon *et al.* 1986; Keenan *et al.* 1993), as free-living cyanobacteria fix nitrogen and carbon is lost through respiration, but this research shows an increase in C:N ratios with increasing decay class. Nitrogen fixation within the woody debris (e.g., by free-living diazotrophs) in Tierra del Fuego may be a minimal or non-existent process in the

CWD studied. Unfortunately, identification of a cause for the atypical results of this portion of the research is beyond the scope of this work.

2.4. 4 Nutrient concentrations in Nothofagus

Nothofagus CWD on Tierra del Fuego represents an important pool of available micronutrients, since 20-50% of the per-hectare stores of many important nutrients are held in woody debris and snags. Changes in volumes of CWD due to either forest management or changed input/decomposition rates may impact nutrient cycling and site productivity. Mass loss of carbohydrates due to leaching and decomposition serves to concentrate nutrients in CWD (Ganjegunte *et al.* 2004), thus explaining the increases of a number of micronutrients from intermediate to advanced stages of decay. In decay class 5, a decrease from the previous class is typically observed, likely associated with long-term leaching of even relatively immobile substances (Hafner *et al.* 2005).

2.4.5 Woody debris mass and diameter distributions

The per-hectare CWD mass values in *Nothofagus* forests of Tierra del Fuego are higher than in many other forested regions, although not as high as in the forests in northwestern North America (Table 2.4). Furthermore, the proportion of total aboveground woody material represented by CWD in the *Nothofagus* forests of Tierra del Fuego is among the highest levels recorded in either temperate or tropical forests. CWD mass is highly variable among different forest types in Tierra del Fuego, with generally higher volumes at lower elevation and in mixed stands of *N. pumilio* and *N. betuloides*

(Table 2.4). Most of the mass of CWD is in decay classes 3 and 4, while decay class 1 represents the smallest proportion of the mass of any of the decay classes (Figure 2.4).

Downed wood diameter distributions generated from the line-intercept transects appear to be well characterized by a Weibull distribution, but do have a bimodal component (Figure 2.5). The large frequencies in the smaller diameter classes reflect both the mortality of smaller trees and also the presence of fallen branches and crowns in the line-intercept transects. The mode with the higher mean represents large fallen canopy dominants from previous partial wave disturbance (Currie and Nadelhoffer 2002).

The high levels of woody debris input, combined with low decomposition rates, may explain the high proportion of total stand volume represented by woody debris. Many authors have commented on the importance of wind as a disturbance agent in Patagonian forests (Rebertus and Veblen 1993; Veblen *et al.* 1996; Rebertus *et al.* 1997). Decomposition in the *Nothofagus* of Tierra del Fuego is relatively slow (annual decay constant, k=0.010) compared to many tree species (Frangi *et al.* 1997) due to somewhat resistant heartwood (although heart rot fungi are common in live trees), low mineralization rates, and the generally cool temperatures at this latitude, which inhibits microbial activity. In the tropics, as exemplified by the La Selva Biological Station stand (Clark and Clark 2000; Clark *et al.* 2002), high average decay rates tend to limit woody debris accumulation (Chambers *et al.* 2000). Coniferous old-growth forests of the Pacific Northwest tend to have greater mass of CWD, but not a larger proportion of total mass represented by CWD, than the *Nothofagus* stands of Tierra del Fuego. One factor contributing to the greater mass of CWD in Pacific Northwest old-growth forests is the very large size attained by trees.

The prevalence of cubical brown rots over white rots in Patagonian *Nothofagus* stands (Cwielong and Rajchenberg 1995) means that long-lasting pieces of CWD in advanced decay classes will be prevalent and a significant component of the woody debris biomass. Additionally, wildfire is not common in Tierra del Fuego, and CWD biomass is therefore not lost to combustion. The predominance of the intermediate decay classes is a result of the fact that the residence times of CWD in each decay class increases relatively geometrically (Harmon *et al.* 1986).

The diameter distributions of CWD were remarkably similar across forest types. The general characteristic of a negative exponential distribution has been observed in other forest types (Fraver *et al.* 2002; Karjalainen and Kuuluvainen 2002). The subalpine *N. pumilio* forest had fewer individuals in higher diameter classes, likely due to the climatic limits on tree growth at the higher elevations and exposed topographic positions on which this forest type exists.

The CWD mass values in plots from the two largest diameter classes demonstrate a positive departure from the monotonic trend seen over the range of other diameter classes. This is likely due to a number of processes that become more operative in older *Nothofagus* stands: the development of very large diameter trees, increasing windthrow risk due to the increasing prevalence of root and stem fungal rots, and simply an increasing likelihood of experiencing an intense windstorm (Rebertus and Veblen 1993; Rebertus *et al.* 1997).

2.5 Conclusions

The decay class categories used to characterize CWD in the *Nothofagus* forests of Tierra del Fuego, Chile were statistically significant predictors of CWD density, moisture content, and nutrient concentrations. Some physical and chemical characteristics may be influenced by variation along the precipitation gradient (and other environmental gradients) present across Tierra del Fuego, but most characteristics of CWD examined in this study were similar between the wet coastal site and the drier interior site. Stand level plots demonstrate the significance of CWD in total organic matter and nutrient pools and emphasizes the need to consider this material in forest management planning and research.

Forest management in Tierra del Fuego has the potential to reduce the amount of CWD by reducing the number of large trees available for input, and possibly also by altering decomposition rates through microclimatic modification of stands. This study focused on CWD levels in natural stands, but future research on the effects of forest management on the CWD resource in Fuegian forests is warranted.

An important aspect of woody-debris related research that was not done in this work is to utilize a chronosequence approach to demonstrate the changes in woody debris mass with changing stand age (Spies *et al.* 1988; Carmona *et al.* 2002). Future work on coarse woody debris in Tierra del Fuego should address this important need.

Figure 2.1 Locations of woody debris tissue sampling sites.

1= Rio Bueno, 2= Puerto Arturo, 3= Estancia Vicuña.

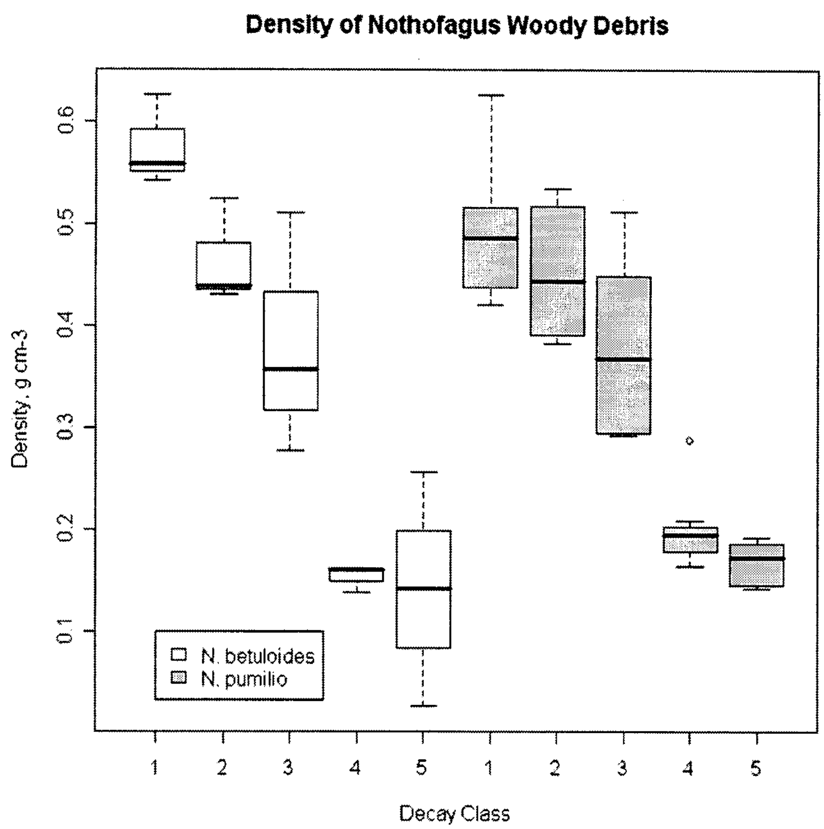

Figure 2.2 Tissue densities of *Nothofagus* woody debris.

Bold line represents the median, while the box represents upper and lower quartiles. Maxima and minima are represented by whiskers.

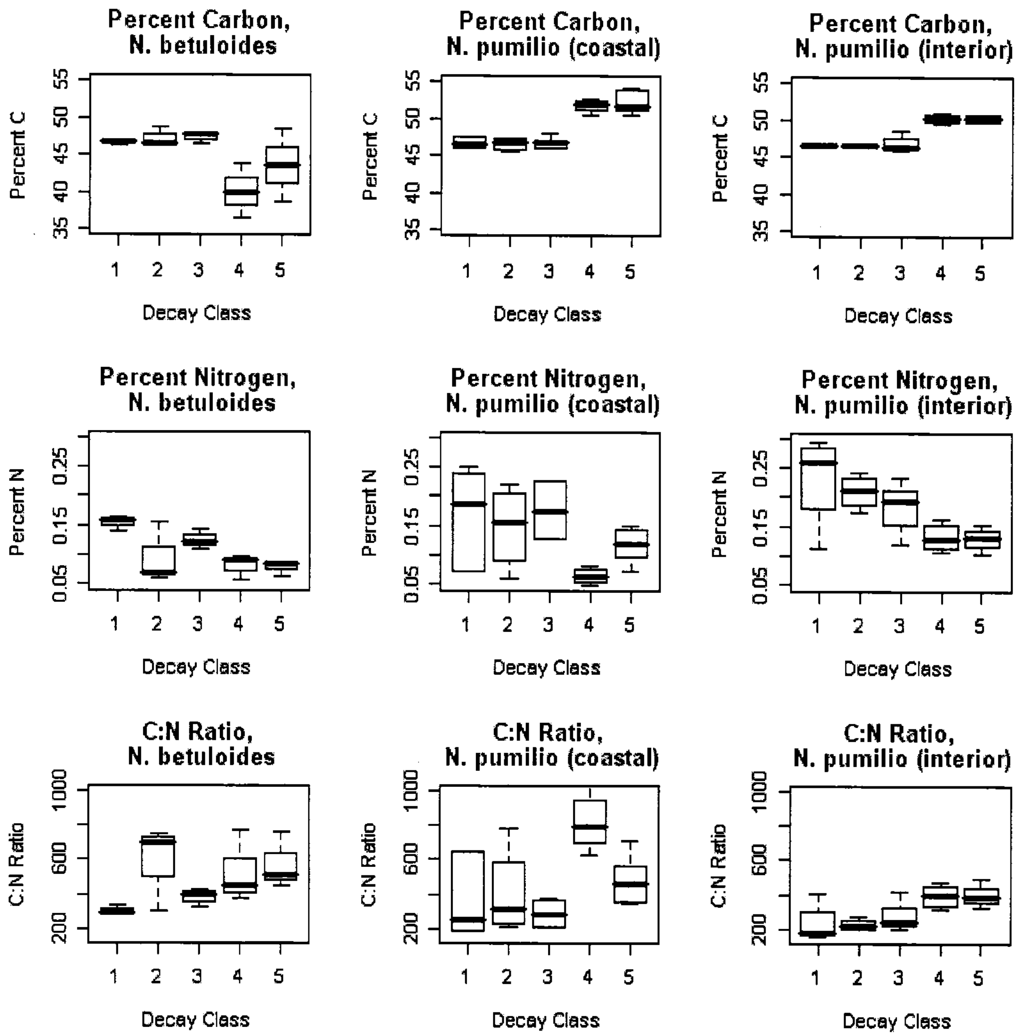

Figure 2.3 Carbon and nitrogen concentrations and C:N mass ratios for *Nothofagus pumilio* and *Nothofagus betuloides.*

Bold line represents the median, while the box represents upper and lower quartiles. Maxima and minima are represented by whiskers.

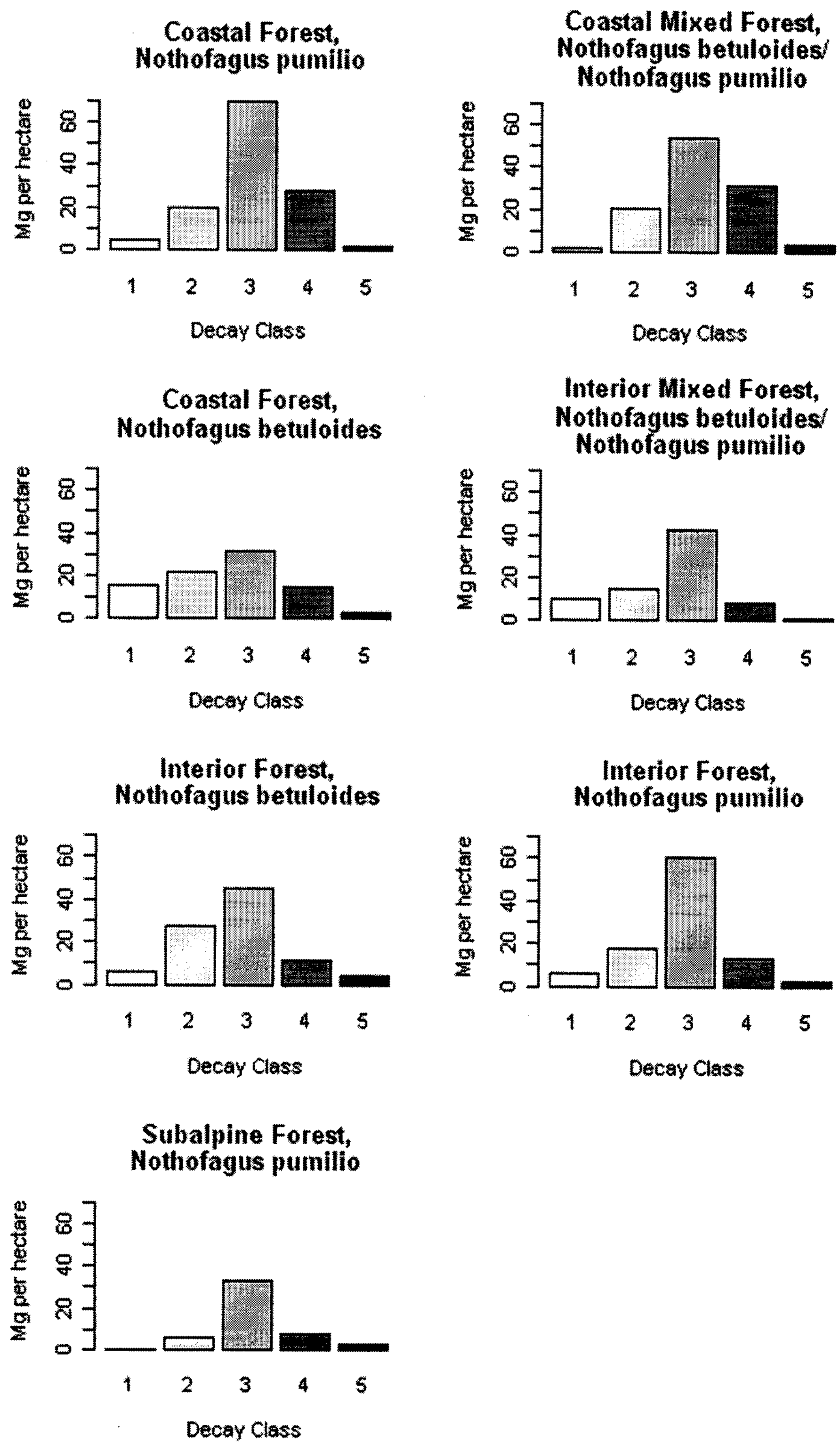

Figure 2.4 CWD biomass per hectare by designated forest types.

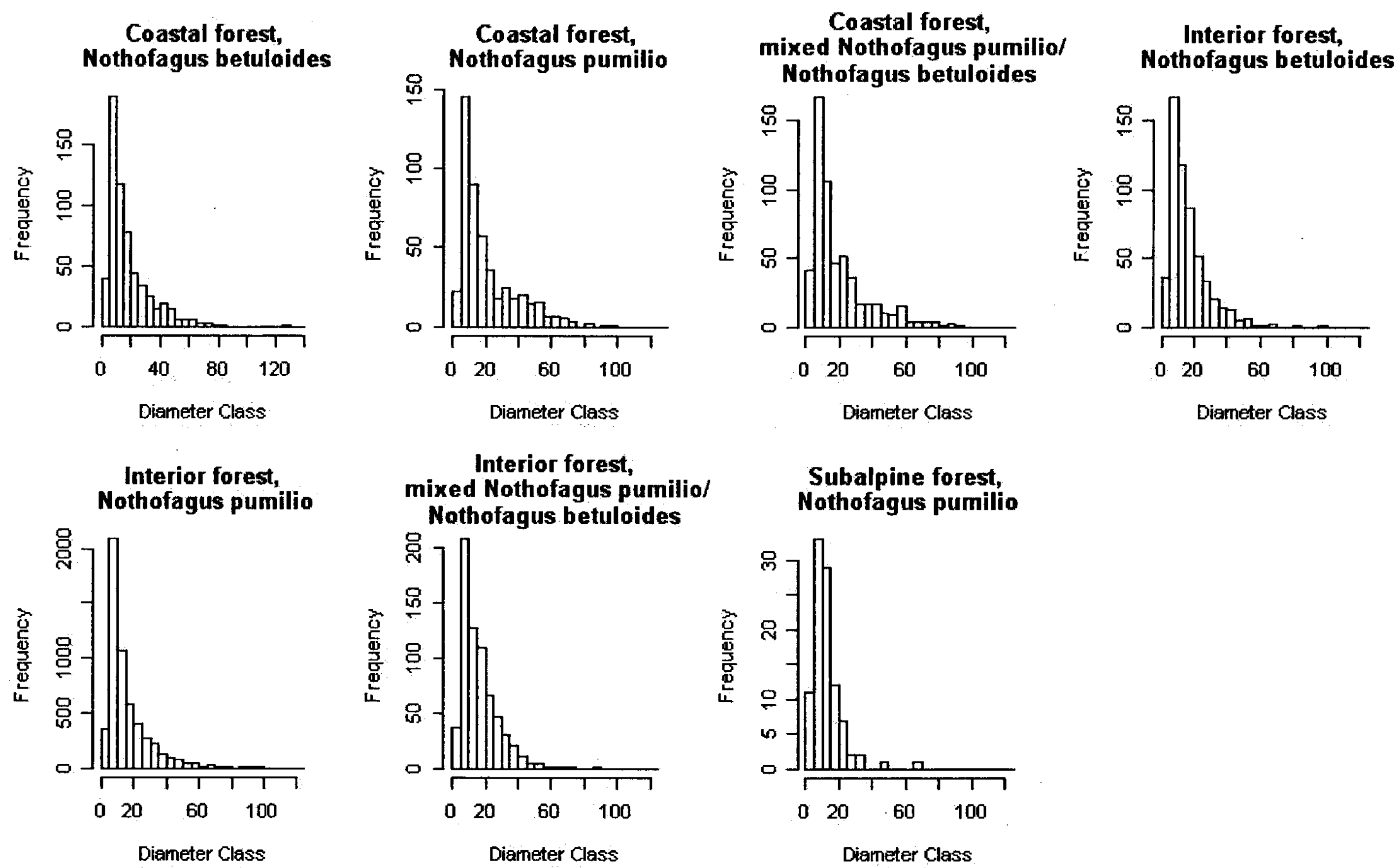

Figure 2.5 CWD diameter distributions from plots by forest type.

Chapter 3 Flora and substrates of anthropogenically burned areas in Tierra del Fuego, Chile: Composition and edge effects

3.1 Introduction

Fire is the predominant form of disturbance in many terrestrial ecosystems (Agee 1993). However, the importance of fire varies with climate, fuel characteristics, presence of ignition sources, and many other factors. Cool temperatures and the relatively heavy and year-round nature of the precipitation in southwestern Tierra del Fuego combine to make naturally occurring fire an infrequent element of the natural disturbance regime (Donoso Zegers 1993; Huber *et al.* 2004). Instead, windthrow is therefore the primary natural disturbance agent, creating openings of variable size and intensity (Rebertus and Veblen 1993; Rebertus *et al.* 1997). The near complete absence of fire as an element of the forest disturbance regime came to an end in late 19th century, as European settlers began to use fire to clear the forest for domestic livestock range. In 1924, the following observation was made by an Argentine botanist:

> "The marked modification of the vegetation of those admirable regions is due to forest fire, in all the places where white man has settled, and is due to the invasion of foreign influences, which everyday further displace or annihilate the native elements." (Carlos Spegazzini, 1924, as quoted in Moore 1983).

Fire operates differently from windthrow in a number of critical aspects. Fire may volatilize and release nitrogen during combustion (Little and Ohmann 1988) and frequently induces the release of other nutrients (Alauzis *et al.* 2004). In addition, understory plants and advance regeneration of trees are frequently killed (Agee 1993).

The vegetation of Tierra del Fuego has been well described (Pisano 1977; Moore 1983), including plant species and community responses to forest management (Fernández *et al.* 1998). However, floristic inventories of burned areas are limited and fine-scale assessments of the spatial structure of plant communities in the landscape mosaic are lacking. Edge effects, for example, are known to affect the reproduction, dispersal, and persistence of both native and non-native plants (Chen and Franklin 1992; Goldblum and Beatty 1999; Harper and MacDonald 2001; Pauchard and Alaback 2006) and are likely to be significant in harsh, high-latitude environments such as Tierra del Fuego. Invasion by exotic plants has been noted in some burned areas in Patagonia (Melville *et al.* 1960) engendering the perception that these areas are largely dominated by non-native plant species. Disturbed ecosystems may be at a higher risk of invasion by non-native organisms (Davis *et al.* 2000), especially when the type of disturbance is not part of the natural disturbance regime (Westman 1990; Hobbs and Huenneke 1992; Von Holle *et al.* 2003).

Regeneration of forest trees is also of concern in burned forests in Tierra del Fuego. Tree regeneration has been observed to be sparse and largely restricted to the edges of burned areas in Patagonia (Melville *et al.* 1960; Veblen *et al.* 1996; Alauzis *et al.* 2004; Kitzberger *et al.* 2005), suggesting that anthropogenic fire may have profound influences on the long-term dynamics of these forests. Substrate or seedbed characteristics influence germination and seedling survival, both in Chilean forests (Donoso Zegers 1993; Lusk 1995; Heinemann *et al.* 2000) and in other temperate forests (Harmon *et al.* 1986; Harmon and Franklin 1989; McKenny and Kirkpatrick 1999). Furthermore, the abundance of various substrates is frequently determined by disturbance effects and may be spatially variable at the edges of disturbed areas (Hill and Read 1984; Greene *et al.* 2005). Therefore, assessing relative abundance of various substrates for plant growth, such as mineral soil, CWD, and leaf litter, is an important step in understanding the potential long-term impacts of fire on forest regeneration.

The objectives of this chapter are to characterize the community of native and exotic plant species that commonly occur in anthropogenically burned areas in Chilean Tierra del Fuego, and to assess edge-related gradients in species richness, species cover, and substrate cover in burned areas and adjacent forest. The following questions were investigated. Do forest areas differ from burned areas in composition of the flora and abundance of plant substrates? Do plant taxa and substrates show a response to distance from the edge, either in forest or in burned areas? Do exotic plants differ from native plants in cover and richness?

The hypotheses addressed in this work were:

Hypothesis 1. Forest differs from burned areas in terms of taxonomic composition.

Hypothesis 2. Abundance and richness of native herbs and shrubs are greater in forest than in burned areas.

Hypothesis 3. Exotic plants exhibit greater total abundance and richness in burned areas than in forest understories.

Hypothesis 4. Tree regeneration is most abundant near the forest edge in both burned area and forest. Regeneration will decrease in the burned area with distance from the forest edge.

Hypothesis 5. Organic substrates, including CWD, display greater abundance in forest than in burned areas. Mineral substrates will be greater in burned areas than in forest.

Hypothesis 6. Within the forests cover of native herbs and shrubs will increase with distance from the forest edge. Within burned areas cover of exotic taxa will increase with distance from the forest edge.

3.2 Methods

3.2.1 Study sites

A number of anthropogenically burned areas in southwest Chilean Tierra del Fuego were identified via interviews with local inhabitants and confirmed by the presence of charcoal throughout the burned area. Three were selected based upon accessibility and location (interior vs. coastal, Figure 3.1). All sites were deliberately burned to create pasture for domestic livestock. Campamento Puerto Arturo (CAM) and Puerto Yartou (YAR) were both relatively flat sites located at sea level on the southwestern coast of the Santa Maria Peninsula, about 100 km south of Porvenir, Chile. Cerro Cuchilla (CUC) has a northern aspect (15° slope) and was located 3 km from the eastern shore of Lago Blanco and ~20 km northwest of Estancia Vicuña. Except for a limited area at YAR, all of the sites burned during the brief dry season (December-February) with sufficient intensity to kill all overstory and understory trees. CAM and CUC burned approximately 70 years before sampling (2002) and YAR burned more recently (12 years before). The presence of burned snags and downed woody debris throughout all of the burned areas assured that all areas had supported forest prior to the fire events.

3.2.2. Field measurements

Data were collected in the austral late summer (February) of 2002. At each site, four 100-m long transects were established (Figure 3.2). Each originated 50 m within the forest and extended perpendicular to the forest edge to 50 m into the burned area. "Forest" and "burn" are considered different environments for the purposes of this study.

The edge is defined as a linear feature that follows the boles of live trees adjacent to the burned area. Transects were placed so that the north, east, south, and west edges of the burned area were each sampled by one transect (Figure 3.2). An additional 100 m transect, not contiguous with any other transect, was placed randomly at each site entirely within the burned area, extending from 50 m to 150 m into the burned area (Figure 3.2). Alongside each transect, cover (%) of each vascular plant species and substrate was sampled in 1x1 m plots spaced at 5-m intervals. Plant identification and taxonomy followed Moore (1983). Grasses (Gramineae) were measured as a group. Substrates included litter (O1: leaves and fine branches), organic soil (O2: dark, humic soil distinguished from litter by the lack of visible fibers), CWD (≥5 cm in diameter), sand, and rock (≥10 cm in minimum width). CWD was sampled by decay classes (1-5, representing least to most decayed; (Cline *et al.* 1980; Harmon and Sexton 1996)). Every 20 m (distances 0, 20, 40, 60, 80, and 100 m), a soil core was taken to assess the depth of the organic layer (O and A horizons). The corer was inserted until impossible to push further (mean depth 24.3 cm), assuring inclusion of both O and A horizons.

3.2.3 Data analysis

Two main types of analysis were conducted: comparisons between environments (forest vs. burned area) and analysis of edge effects (distance-dependent phenomena). The objective of the first type was to assess differences in response variables and overall community composition between environments, and the second was to identify finer-scale spatial patterns of response variables with respect to distance from the forest edge.

Plot data for each response variable were averaged among transects for each distance (0, 5, ... 100 m) at each site (CAM, YAR, and CUC) to create a data matrix for statistical tests and ordination. A number of summary variables were calculated at the level of each 1m x 1m plot to permit the analysis of general trends in vegetation and substrates (Table 3.1). Total plant cover and total organic substrate cover may both exceed 100% cover of any given plot, since plant species may overlap in planimetric space, and suspended woody debris may overlap other organic materials.

Table 3.1 Variables determined for each 1 x 1 m plot.

Summary variables	Calculated
Nothofagus regeneration	Cover of *Nothofagus* regeneration.
Native shrub cover	Summed cover of native shrub species.
Native herb cover	Summed cover of native herb species (including grasses).
Exotic plant cover	Summed cover of plants not native to Tierra del Fuego (according to Moore 1983).
Total cover	Total cover of all plant species (native or exotic).
Native shrub richness	Richness of native shrub species.
Native herb richness	Richness of native herb species.
Exotic plant richness	Richness of exotic plant species not native to Tierra del Fuego.
Coarse woody debris cover	Summed cover of coarse woody debris.
Mineral substrate cover	Summed cover of rock and sand.
Organic substrate cover	Total cover of coarse woody debris, litter, and exposed organic soil.

Forest vs. burned areas. Non-metric multidimensional scaling (NMS) was performed using the software PC-ORD (McCune and Mefford 1999) to assess variation in species composition attributable to location, environment (burned area vs. forest) and distance from forest edge. Only data from plots within 50 m of the forest edge were used for ordination. The distance measure employed was Euclidean distance. Correlation vectors of summary variables with the first and second axes were graphed as a joint plot. Differences in species composition between forest and burned plots were assessed with a Multi-Response Permutation Procedure (McCune and Mefford 1999). MRPP provides the *A*-statistic, which describes within-group chance-corrected agreement, which is used to make inference about differences between groups (in this case, differences in composition between forest and burned environments).

Paired-sample Mann-Whitney or Student's *t*-tests were used to examine differences in cover for each species between forest and burned areas. Mean cover values were calculated for each species for every combination of site, transect and environment (24 combinations). If the distribution of the cover data was non-normal according to the Shapiro-Wilk statistic, the non-parametric Mann-Whitney was used. Significance was assessed at both an α-level of 0.05 and adjustment for multiple tests according to the Dunn-Sidak test (Gotelli and Ellison 2004). Substrate cover variables, including cover of coarse woody debris (total and by decay class) in burned area plots and forest plots was compared using the paired-sample Mann-Whitney or Student's *t* test. The depth of the O+A horizons was compared between burned and forest environments using the Mann-Whitney test.

Analysis of edge effects. Linear regression analysis (Kutner *et al.* 2004) was used to assess edge relationships for both plant taxa and substrates in both burned areas and forests. Species cover data were averaged for each distance by site, and linear regression was performed using these means as the dependent variable and distance as the independent variable. Two linear regressions were performed for each response variable in each environment (forest or burn): one for data from plots ranging 0 to 50 m (forest), and another for plots ranging from 55 to 200 m (burned area). If a species had fewer than 10 occurrences in either burned area or forest across all sites, regression was not performed in that case. The relationship of O+A horizon depth with distance to forest edge was also assessed using linear regression in both forest and burned areas.

3.3 Results

3.3.1 Taxonomic composition of forest and burned areas

The NMS ordination was constrained to three axes following examination of the scree plot of stress (McCune and Grace 2002). The proportion of variance in the original data explained by the final ordination was 28.7% for Axis 1, 30.2% for Axis 2, and 33.5% for Axis 3 (cumulative r^2 of 92.4%). Samples representing distance from edge showed strong clustering by site and environment (forest vs. burn, Figure 3.3). Axis 1 separated sites, with the two coastal sites with high scores and CUC with lower scores. Greater separation between samples from the burned areas was observed along Axis 1, indicating greater dissimilarity among samples. Axis 2 was correlated with distance from edge in both forest and burn environments (Kendall's τ =-0.508, p<0.001). Axis 3 (not shown) separated the most recently burned site (YAR, burned 12 years prior to measurement) from the older burns (CAM and CUC, both having burned ~70 years prior to measurement).

Species composition of plots in the burned areas was significantly different from plots in forest (MRPP test, chance-corrected within-group agreement, A=0.065,

$p<0.0001$). MRPP also separated the three sites ($A=0.065$, $p<0.0001$), including all three pair-wise site-to-site comparisons (Table 3.2).

Table 3.2 Results of MRPP pairwise comparisons by site.

Pairwise Comparisons	T	A	*p*
CAM vs. CUC	-9.631924	0.06846344	0.00002608
CAM vs. YAR	-10.59515	0.07333855	0.00000803
CUC vs. YAR	-23.75377	0.18122210	0.00000000

Examination of the joint plot vectors (Figure 3.3) show that the following variables were associated with positive values of NMS axis 2 (forest): cover of organic substrates ($r=0.786$), coarse woody debris ($r=0.337$), and litter ($r=0.845$) These variables were also weakly associated with positive values of NMS axis 1 (coastal sites), with r values of 0.356, 0.116, and 0.593, respectively. Variables associated with negative values of NMS axis 2 (burn environment) were cover of mineral substrates ($r= -0.268$), exotic plants ($r= -0.448$), native herbs ($r= -0.799$), and total plant cover ($r= -0.768$). Tree regeneration and mineral substrates were associated with negative values of NMS axis 1 (i.e., more prominent in the interior site, CUC) with r values of -0.573 and -0.373, respectively. Native shrub cover was associated with mesic coastal sites (positively associated with positive values of NMS axis 1, $r= 0.309$), and was also associated with negative values of NMS axis 2 ($r= -0.471$), indicating higher levels in the burned areas than in forest.

3.3.2 Forest vs. burned areas

Abundance and richness of native herbs and shrubs. A total of 52 vascular plant taxa was identified in the plots (Table 3.3). Twenty-five of the 52 were insufficiently represented to conduct a paired-sample test or were absent in either burned area or forest. The remaining 27 taxa occurred in a sufficient number of plots to test differences in cover between burned areas and forest areas using either the t-test or Mann-Whitney test as appropriate. Eleven species displayed significant differences between forest and burned areas (Table 3.3). No individual species comparisons were significant when taking the Dunn-Sidak correction for multiple comparisons into account. In the burned areas, frequently occurring shrubs (>1% mean cover) were *Berberis buxifolia* and *Fuchsia magellanica*, and frequently occurring herbs were *Acaena ovalifolia* and *Gunnera magellanica*. In the forest, frequently occurring shrubs were *Berberis buxifolia*, *Berberis ilicifolia* and *Fuchsia magellanica*. Frequently occurring herbs in the forest were *Blechnum penna-marina* and *Acaena ovalifolia.*

Thirty-nine taxa were identified as native. Of these, only one (*Osmorhiza depauperata*) had significantly higher cover in forest, five had higher cover in burned areas, and 11 taxa showed no difference between environments. Cover of both native herbs and native shrubs was significantly higher in burned areas than in forest (Mann-Whitney test, $p<0.0001$ and $p<0.01$, respectively, Table 3.4). Total cover of native plant taxa was significantly higher in burned areas (t-test, $p<0.0001$). Richness of native herbs was significantly higher in burned areas (Mann-Whitney test, $p<0.01$ and $p<0.05$, respectively), but richness of native shrubs did not differ (Mann-Whitney test, $p=0.33$).

Abundance and richness of exotic taxa. Cover of exotic plants was significantly higher in burned areas (Mann-Whitney test, $p < 0.05$, Table 3.4) than in forest. Four exotic taxa (*Cerastium arvense*, *Hypochaeris radicata*, *Rumex acetosella*, and *Trifolium repens*) had higher cover in burned areas than in forest (Table 3). Three exotic taxa (*Cotula scariosa*, *Taraxacum officinalis*, and *Veronica serpyllifolia*) showed no significant difference in cover between burned areas and forest. Exotic plant richness at the plot level was greater in burned areas (Mann-Whitney, $p<0.0001$, Table 3.4).

Tree regeneration. Cover of tree regeneration was not significantly different between forest and burned areas for either *Nothofagus pumilio* (Mann-Whitney, $p = 0.91$) and *N. betuloides* (Mann-Whitney, $p=0.29$). No difference was found for total cover of tree regeneration between forest and burned areas (Mann-Whitney, $p=0.36$). Other tree species present in Tierra del Fuego, such as *Maytenus magellanicum* (Lam.) Hook. f. and *Drimys winteri* J.R. et G. Forst., were not observed in plots in the burned areas, and only rarely in forest plots.

Table 3.3 Plant cover and frequency in forest and burned areas

Species	*Paired Mann-Whitney p-values*	*Mean% cover (SE)*		*Occurrences in plots*		
		Burn	***Forest***	***Burn***	***Forest***	***Total***
Acaena ovalifolia	<0.05 *	4.11 (0.60)	1.67 (0.34)	103	46	149
Acaena pinnatifida	0.1551	0.98 (0.30)	0.35 (0.18)	36	10	46
Adenocaulon chilense	0.7439	0.36 (0.11)	0.52 (0.12)	27	32	59
Asplenium dareoides	0.4227	0.12 (0.06)	0.15 (0.12)	7	3	10
Berberis buxifolia	<0.05 *	19.5 (2.51)	2.93 (0.84)	74	24	98
Berberis ilicifolia	0.2863	0.30 (0.16)	2.52 (1.11)	12	21	33
Blechnum penna-marina	0.9057	1.68 (0.38)	1.73 (0.53)	40	32	72
Cardamine glacialis	NA	0.00 (na)	0.01 (0.01)	0	2	2
Carex spp.	NA	0.11 (0.07)	0.42 (0.31)	7	5	12
Cerastium arvense §	<0.05 *	0.71 (0.28)	0.03 (0.02)	29	3	32
Cerastium fontanum	NA	0.03 (na)	0.00 (na)	1	0	1
Chiliotrichum diffusum	NA	0.01 (na)	0.00 (na)	1	0	1
Cotula scariosa §	<0.05 *	0.16 (0.08)	0.05 (0.04)	10	2	12
Daucus montanus	NA	0.00 (na)	0.10 (0.08)	0	3	3
Dysopsis glechomoides	NA	0.14 (0.09)	0.04 (0.02)	3	4	7
Epilobium ciliatum	NA	0.003 (na)	0.00 (na)	1	0	1
Erigeron myosotis	NA	0.03 (0.03)	0.00 (na)	2	1	3
Fuchsia magellanica	0.4412	3.86 (1.13)	1.44 (0.61)	22	13	35
Galium aparine	0.3710	0.07 (0.06)	0.43 (0.24)	2	13	15
Galium fuegiana	NA	0.00 (na)	0.02 (na)	1	1	2
Geranium spp.	NA	0.48 (0.15)	0.32 (0.15)	19	10	29
Geum magellanicum	0.5995	0.08 (0.03)	0.09 (0.05)	12	5	17
Grasses (Gramineae)	<0.01*	50.08 (2.82)	18.58 (2.63)	142	79	221
Gunnera magellanica	<0.01*	6.75 (1.15)	0.83 (0.35)	73	12	85
Hieracium antarcticum	NA	0.04 (na)	0.00 (na)	1	0	1

Table 3.3 (cont.) Plant cover and frequency in forest and burned areas

Hymenophyllum spp.	NA	0.00 (na)	0.01 (0.01)	0	2	2
Hypochaeris radicata §	<0.05 *	0.91 (0.2)	0.01 (0.01)	32	2	34
Lebetanthus myrsinites	0.7893	0.06 (na)	0.16 (0.09)	1	8	9
Luzuriaga marginata	NA	0.05 (0.03)	0.001 (na)	3	1	4
Madia sativa §	0.3711	0.09 (0.04)	0.03 (0.01)	10	6	16
Maytenus magellanica	NA	0.00 (na)	0.01 (0.01)	0	2	2
Nassauvia spp.	NA	0.22 (0.14)	0.27 (0.19)	3	4	7
Nothofagus betuloides regeneration	0.2945	0.06 (0.06)	0.22 (0.09)	2	12	14
Nothofagus pumilio regeneration	0.91	0.01 (0.01)	0.95 (0.5)	12	13	25
Osmorhiza chilensis	0.2945	0.03 (na)	0.11 (0.06)	1	6	7
Osmorhiza depauperata	<0.05*	0.14 (0.05)	0.55 (0.16)	14	31	45
Pernettya mucronata	NA	0.00 (na)	0.31 (0.3)	0	3	3
Pernettya pumila	NA	0.35 (0.18)	0.00 (na)	10	0	10
Phacelia secunda	0.1814	0.06 (0.10)	0.10 (0.05)	11	12	23
Plantago lanceolata§	NA	0.02 (0.01)	0.01 (na)	4	1	5
Ranunculus maclovianus	<0.05 *	0.51 (0.23)	0.08 (0.08)	29	3	32
Ribes magellanicum	0.8334	0.85 (0.55)	0.62 (0.27)	9	15	24
Rumex acetosella §	<0.05*	0.68 (0.32)	0.36 (0.12)	33	20	53
Senecio spp. (including *S. patagonicus* and *S. smithii*)	0.4227	0.02 (0.01)	0.10 (0.07)	10	10	20
Taraxacum officinale§	0.1230	1.06 (0.16)	0.81 (0.22)	86	50	136
Trifolium repens §	<0.05 *	2.13 (0.58)	1.13 (0.42)	39	15	54
Veronica serpyllifolia §	0.1003	0.53 (0.18)	0.02 (na)	22	1	23
Viola spp. , including *Viola maculata*	NA	0.10 (0.03)	0.02 (0.01)	11	5	16

Results of the Mann-Whitney test for species with sufficient sample sizes (n_1 and n_2). § indicates exotic species (following Moore 1983). * indicates significance at α =0.05.

Table 3.4 Test results and cover means for calculated variables.

Variable	***Mann-Whitney or t-test p-values***	*Mean % Cover, Burn*	*Mean % Cover Forest*
Nothofagus regeneration	0.36	3.9 (2.9)	3.5 (3.0)
Native shrub cover	<0.01 *	24.7 (2.8)	8.3 (1.7)
Native herb cover	<0.0001 **	69.1 (2.8)	31.4 (3.1)
Exotic plant cover	<0.05 *	5.0 (0.8)	2.7 (0.7)
Total cover	<0.0001 **	98.5 (4.9)	46.4 (4.7)
Native shrub richness	0.33	0.8 (0.1)	0.7 (0.1)
Native herb richness	<0.0001 **	4.2 (0.2)	2.8 (0.1)
Exotic plant richness	<0.0001 **	1.4 (0.1)	0.7 (0.1)
Coarse woody debris cover	<0.01 *	11.4 (1.7)	17.1 (2.1)
Mineral substrate cover	<0.05 *	10.8 (2.3)	0.7 (0.4)
Organic substrate cover	<0.0001 **	49.3 (4.1)	88.8 (3.2)

Standard errors are given in parentheses. * indicates significance at $\alpha=0.05$. ** indicates significance following adjustment for multiple comparisons.

Substrates. Mineral cover (sand + rock) was significantly higher in burned areas (Mann-Whitney test, $p<0.05$, Table 3.4). Total organic cover (litter, exposed organic soil, and total coarse woody debris) was higher in forest (Mann-Whitney, p<0.0001, Table 3.4). Cover was significantly higher in forest for both litter and (t-test <0.001, Table 4) and total cover of coarse woody debris (t-test, $p<0.05$, Table 3.4). The only individual decay class to show a significant difference was decay class 5 (most decomposed), which had higher cover in the forest (Mann-Whitney, $p<0.05$). Mean depth of the O + A horizons was less in the burned area (2.85 vs. 3.36 cm in the forest), a marginally significant difference (Mann-Whitney test, $p=0.066$).

3.3.3 Edge effects on plant taxa and substrates

Gradients in forest. Of the taxa that occurred in the forest plots (47 of 52 taxa found in all plots), 14 were insufficiently frequent to use regression analysis. Thirty were sufficiently frequent, but the regression slopes were not significantly different from zero. Three forest species showed significant results. Cover of *Geum magellanicum* increased with distance from forest edge into the forest. In contrast, cover of *Gunnera magellanica* and *Nothofagus* regeneration decreased significantly from the edge. Tree regeneration only occurred within 30 m of the forest edge. Total plant cover decreased significantly with distance from the forest edge (Figure 3.4, Table 3.5). No significant pattern was shown in forest for native herb cover, native shrub cover, exotic plant cover, native herb richness, native shrub richness, and exotic plant richness (Table 3.5).

Total cover of organic substrates (litter, exposed organic soil, CWD) increased with distance from the forest edge. Cover of litter, CWD, and mineral (rock and sand) cover all showed no significant regression relationship to distance. Depth measurements of the O+A horizons in the forest environment likewise had no significant relationship to distance from the forest edge.

Gradients in burned areas. Of the taxa that occurred in the burned areas (46 of 52 taxa found in all plots), 14 were insufficiently frequent to use regression analysis. For 23 taxa, regression slopes were not significantly different from zero, while 9 taxa displayed a significant response to distance from the forest edge. Seven taxa showed decreasing cover with distance from the forest edge (*Acaena pinnatifida*, *Adenocaulon chilense*, *Blechnum penna-marina*, *Gunnera magellanica*, *Hypochaeris radicata*, regeneration of *Nothofagus pumilio*, and *Veronica serpyllifolia*). Grasses were the only taxa to increase with distance from the forest edge (Figure 3.4). Tree regeneration decreased significantly with distance from the forest edge into burned areas (Figure 3.4). Regeneration of *Nothofagus* spp. primarily occurred within 40 m of the edge in the burned areas, and was nearly absent beyond 50 m from the forest edge (Figure 3.4). No significant pattern was shown in burned areas for total plant cover, native herb cover, native shrub cover, exotic plant cover, native herb richness, native shrub richness, and exotic plant richness (Table 3.5).

Total organic substrate cover displayed no significant trend with distance from edge in the burned area (Figure 3.4). Cover of litter, CWD, and mineral (rock and sand) cover showed no significant regression relationship to distance from the edge. Depth of the O+A horizon likewise showed no significant relationship with distance from edge in the burned area.

Table 3.5 Regression results for transect distance vs. summary variables

Variable	*Slope*	*r*	*p-value*	*Slope*	*r*	*p-value*
Nothofagus regeneration	0.1841	0.18	0.08	-0.0663	0.35	0.0016
Native shrub cover	NS			NS		
Native herb cover	NS			NS		
Native species (herb +shrub) cover	NS			NS		
Exotic species cover	NS			NS		
Grass cover	NS			0.2676	0.11	0.0016
Total plant cover	0.6151	0.36	0.04	NS		
Native shrub taxa richness	NS			NS		
Native herb richness	NS			NS		
Native taxa (herb +shrub) richness	NS			NS		
Exotic herb richness	NS			NS		
Total taxa richness	NS			NS		
Coarse woody debris cover	NS			NS		
Litter cover	NS			NS		
Organic soil	-0.3798	0.45	0.03			
Total organic substrate cover	-0.5998	0.53	0.0015	NS		
Rock	NS			NS		
Sand	NS			NS		
Total mineral cover (rock + sand)	NS			NS		

NS= ‘not significant’.

3.4 Discussion

3.4.1 Taxonomic composition of forest and burned areas

Results from the MRPP procedure show that burned areas were dissimilar in plant composition from unburned forest. This is consistent with findings from another study of plant communities in a fire-disturbed *Nothofagus* forest (Litton and Santelices 2002). In addition, greater heterogeneity in plot composition is reflected in the greater spread of plots from burned areas along Axis 1. This may be due to the fact that burned areas in Tierra del Fuego are relatively extreme environments, and plant assemblages in these areas are likely more responsive to environmental variation due to substrate diversity, microtopography and microsites near CWD.

Examination of joint plot vectors in ordination space revealed patterns associated with site-specific and forest vs. burn factors. Organic substrates were strongly associated with forest and the mesic coastal sites, while mineral substrate was somewhat associated with burned areas and the drier site. All composite plant cover categories (exotic taxa, native herbs, native shrubs, and total plant cover) were associated with burned areas. Native shrubs and tree regeneration displayed opposite tendencies in ordination space, suggesting an inhibition effect of shrubs on tree regeneration.

3.4.2 Abundance and richness of native herbs and shrubs

Higher cover and richness of native herbs in burned areas indicated that burned areas in Tierra del Fuego are not an unfavorable environment for many native plant taxa, at least at the scale examined in this research. This suggests that some factor associated with the forest environment, possibly light levels, may be limiting. The presence of exotic plants associated with post-wildfire environments does not seem to preclude the persistence of native plants in burned areas in Tierra del Fuego. The greater species richness of native herbs also indicates the presence of biodiversity-related conservation value in existing burned areas, at least with respect to native species diversity. However, a number of native species, including both herbs and shrubs, were found only in forest (e.g., *Maytenus magellanica* or *Pernettya mucronata*), suggesting that not all native species benefit from fire disturbance.

Some plots in the burned areas had high shrub cover (usually *Berberis ilicifolia* and *Berberis buxifolia*), often with herbs in the understory. These shrub stands may create a ground microclimate more similar to interior forest conditions than elsewhere in burned environments, as evidenced by the presence of plants typical interior of forest conditions, such as *Asplenium dareoides* and *Blechnum penna-marina*. The possibility of this facilitative mechanism merits further research.

3.4.3 Abundance and richness of exotic taxa

As expected, total cover of exotic plants was higher in burned areas and four exotic species had greater individual cover in burned areas. These findings are consistent with results from other temperate Chilean *Nothofagus* forests (Litton and Santelices 2002) as well as other forested regions in North America (Brothers and Spingarn 1992; Pauchard and Alaback 2006). Some exotic taxa, such as *Veronica serpyllifolia*, *Hypochaeris radicata* and *Cerastium arvense*, were infrequent in the forest environment. However, comparability of exotic taxa richness between forest and burned areas suggests that the forest edge in Fuegian *Nothofagus* forests is not an effective barrier to invasion of exotic plants, in agreement with Fernandez et al. (1998). *Taraxacum officinale,* for example, was commonly found in forest plots, similar to observations in the Northern Rocky Mountains (Pauchard and Alaback 2006). However, greater exotic plant cover in burned areas indicates that, as in many ecosystems (Hobbs and Huenneke 1992; Davis *et al.* 2000), exotic species in Tierra del Fuego are most competitive in areas affected by disturbance events.

3.4.4 Tree regeneration

The apparent restriction of *Nothofagus* regeneration to edge environments in burned areas is consistent with findings from northern Patagonia, where anthropogenic fire, browsing pressure from exotic herbivores, and harsh climatic conditions in burned areas were identified as restricting regeneration to near forest edges (Kitzberger *et al.* 2005). Seed dispersal may also be a factor in some situations (Veblen *et al.* 1996). Most Chilean *Nothofagus* seeds fall within 30-60 m of a seed source (Donoso Zegers 1993), but may also be dispersed much further during high-wind events (Allen 1987). Facilitation of seedling survival in burned areas near to the forest edge may occur as a result of wind speed reduction by the adjacent forest, since the dessicating influence of high winds has a negative impact on *Nothofagus* regeneration (Veblen *et al.* 1996). Shrubs that have colonized the burned areas may also facilitate tree regeneration by protecting seedlings from herbivores as well as stressful abiotic conditions (Rousset and Lepart 1999). On the other hand, shrubs and other plants may compete with *Nothofagus* regeneration, especially in the more mesic environments such as coastal areas or at lower latitudes (Veblen and Schlegel 1982; Veblen *et al.* 1996). Recolonization of burned areas by *Nothofagus* in Tierra del Fuego appears to be a gradual process of infilling from the edges, as encroaching trees ameliorate the growing conditions in the adjacent disturbed area.

Within the forest, the decreasing cover of tree regeneration is likely a response to decreasing light levels. For *Nothofagus* in this environment, the edge is favorable for the germination and survival of tree regeneration. Similar patterns have been shown for tree regeneration on other systems (Chen and Franklin 1992; Burton 2002).

3.4.5 Substrates

Differences in the types and abundances of substrates between burned areas and adjacent forest have been observed in a number of temperate forest types (Litton and Santelices 2002; Greene *et al.* 2005), and these differences may influence spatial patterns of tree seedling germination and survival. Direct combustion of organic material likely is a major factor influencing the higher cover of mineral substrates in burned areas. If fire intensity is variable, seedbed diversity may be enhanced (Greene *et al.* 2005) and may be especially beneficial for ruderal species of both native and exotic origin. Coarse woody debris and snags in open areas may decompose at faster rates than in the forest due to changes in microclimate (Progar *et al.* 2000; Caldentey *et al.* 2001), which may explain the greater cover of woody debris observed in forest plots. Lower cover of woody debris in burned areas may represent a limitation on regeneration of *Nothofagus* on dry sites, since woody debris has been shown to be a moisture source for *Nothofagus* seedlings where moisture is limiting (Heinemann *et al.* 2000). Additionally, abundant woody debris may reduce the impact of herbivore browsing, since woody debris impedes large herbivores (Franklin and Dyrness 1973) such as the guanaco (*Lama guanicoe*).

Reductions in the mean depth of the O+A horizons, possibly through enhanced decomposition rates following overstory removal (Covington 1981; Boerner 1982; Caldentey 1995) or from consumption of organic material by fire (Neary *et al.* 1999), may have occurred. Reductions in O+A horizons depth may result in losses in site productivity due to decreased water-holding capacity and soil nutrient pools, especially on drier sites in Patagonia (Alauzis *et al.* 2004). The depth of the O+A horizons in burned environments may continue to decrease until trees have become re-established, reducing decomposition rates via creation of a forest microclimate and restoring pre-disturbance litterfall rates.

3.4.6 Edge effects on plant taxa and substrates

With the exceptions of tree regeneration (in forest and burned areas), cover of grasses (in burned areas) and total plant cover (in forest), most individual plant taxa did not show strong responses to edge. This result was somewhat unexpected, given the differences in composition between burned areas and the forest environment and may indicate a very sharp transition in growing conditions at the forest edge. Transitions in plant response at spatial scales of less than 5 m were not measurable with the sampling design employed in this study.

Several of the taxa that had significantly higher mean cover in the burned areas paradoxically decreased with distance into the burn (e.g., native species *Gunnera magellanicum* and exotics, *Hypochaeris radicata* and *Veronica serpyllifolia*). This ecotonal response may indicate, for these species at least, an optimum of some factor or factors may exist just inside the perimeter of the burned areas. Alternatively, there may be a shift in limiting factors. For example, the light limitations of the forest understory may be eased, but without high levels of the negative influences of harsh microclimate in the interior of the burn. The fact that two exotic species demonstrate this ecotonal response suggests that burned areas are not uniformly favorable for the invasion of exotic plants.

Within the forest, the increase in *Nothofagus* regeneration closer to the edge likely reflects increasing light availability, since *Nothofagus* is only moderately shade tolerant (Veblen 1985). The decrease in *Nothofagus* regeneration as one progresses into the burned areas may reflect one of a number of factors: increasing competition with other plants, reduced seed dispersal, or increasing exposure to harsh microclimatic conditions such as elevated wind speeds or moisture stress (Chen and Franklin 1992; Veblen *et al.* 1996). The reciprocal relationship of grass cover to tree regeneration suggests that grass species may either compete with *Nothofagus*, or can tolerate microclimatic conditions in the burn that inhibit seedling survival. Planting of *Nothofagus* and other native tree species in burned areas is therefore appropriate if accelerated restoration of forest cover is an objective (e.g., for carbon sequestration purposes). Although post-fire shrub communities do frequently succeed to *Nothofagus* stands (Veblen and Lorenz 1987), control of competing shrubs may also be appropriate in mesic coastal sites.

Only one substrate-related variable, total cover of organic substrates, showed a significant edge effect response and this response was only observed within forest. Changes in microclimate due to presence of an edge (Cadenasso *et al.* 1997; Matlack and

Litvaitis 1999) may alter decomposition rates (Chen *et al.* 2000), thus explaining the reduction in organic substrates in forest plots closer to the edge. As an alternative or additional explanation, reductions in litter inputs closer to the edge over time may decrease the amount of cover.

A significant challenge in generalizing these results is the limited number of burned sites sampled in this research. Significant burned areas exist south of Puerto Arturo, and around Lago Blanco, including the island in the middle of Lago Blanco. Since most (or all) of this island has burned, this island would present an interesting case study of post-fire regeneration at much greater distances from seed sources. In light of the small sample of burned areas, future research is needed to clarify the effects of disturbance and fully characterize the flora of burned areas in Tierra del Fuego. Time since burn is also an issue, and a pseudochronosequence approach would identify changes in composition as a function of time since disturbance. Another potential improvement of our understanding would be to assess effects related to edge orientation, which has been shown to influence the depth of edge effects (Hylander 2005). This study did not replicate sufficiently at the level of categorical aspect (N,E,S,W) to make inference at this level.

3.5 Conclusions

Anthropogenically burned areas in Tierra del Fuego, Chile are characterized by greater richness and cover of both native and exotic plant species. Exotic species do not appear to be dominating burned areas, as has been observed elsewhere in Patagonia (Gobbi *et al.* 1995). However, it may be that certain exotic plants do display higher cover in areas affected by fire disturbance than in areas disturbed by wind events. Comparison of these results with data describing the vegetation of areas disturbed by windthrow will be necessary to fully understand the impacts of anthropogenic fire in Tierra del Fuego. Fire disturbance and windthrow have different impacts on understory plants, soil biota and soil chemistry (Franklin *et al.* 2000) and greater understanding of fire effects on ecosystems in Tierra del Fuego could be gained with this comparison.

Edge effects were not shown to be especially strong in this research, but further work is warranted to identify spatial patterns. Certain taxa, such as grasses and tree regeneration, are good candidates for further examination.

It is clear that burned sites may face a prolonged early successional period due to a variety of factors. Understanding the composition and spatial patterns of the vegetation on these sites will aid forestry and conservation professionals in decision-making related to forest management, conservation of biological diversity, and values such as forest carbon storage. Anthropogenic fire in Tierra del Fuego results in a long-term reduction of carbon stored at the landscape scale due to lost sequestration and storage capacity, since trees are not occupying the site. Other environmental values associated with intact forest (e.g., watershed protection) will also be absent or reduced for an extended period on these sites. Active management activities, especially planting of native tree species, are therefore appropriate if restoration of these values is an objective.

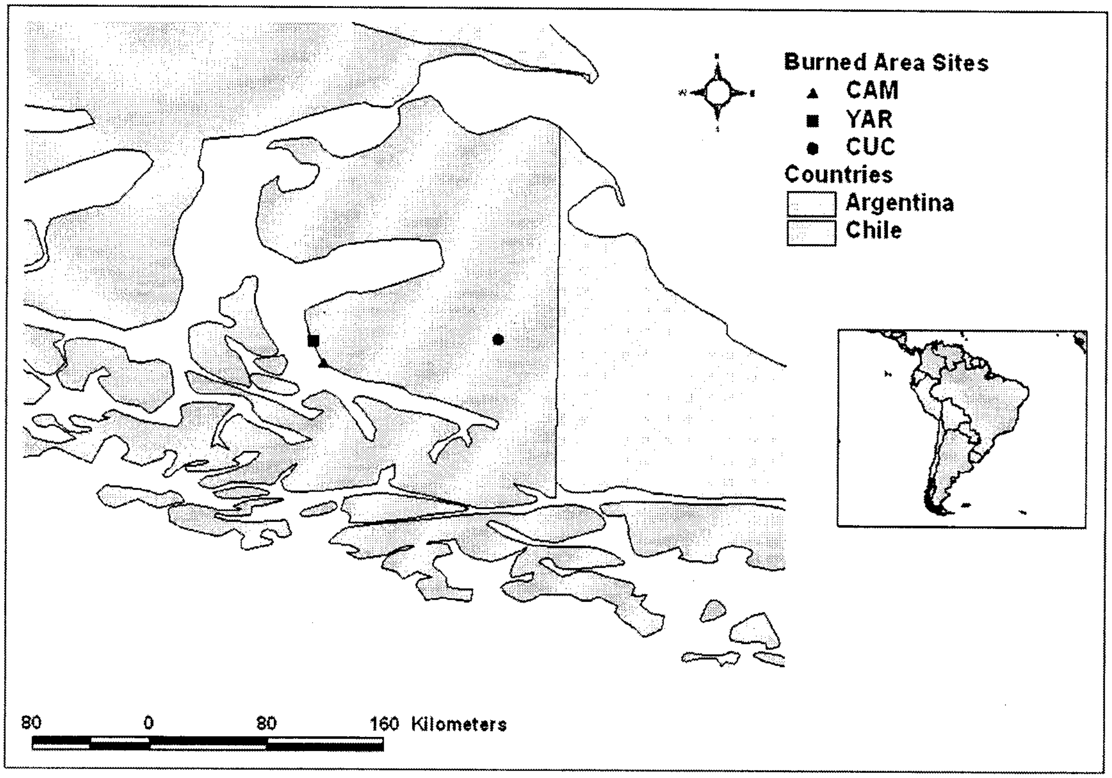

Figure 3.1 Research site locations.

CAM= Campamento site, YAR= Puerto Yartou site, CUC= Cerro Cuchilla site.

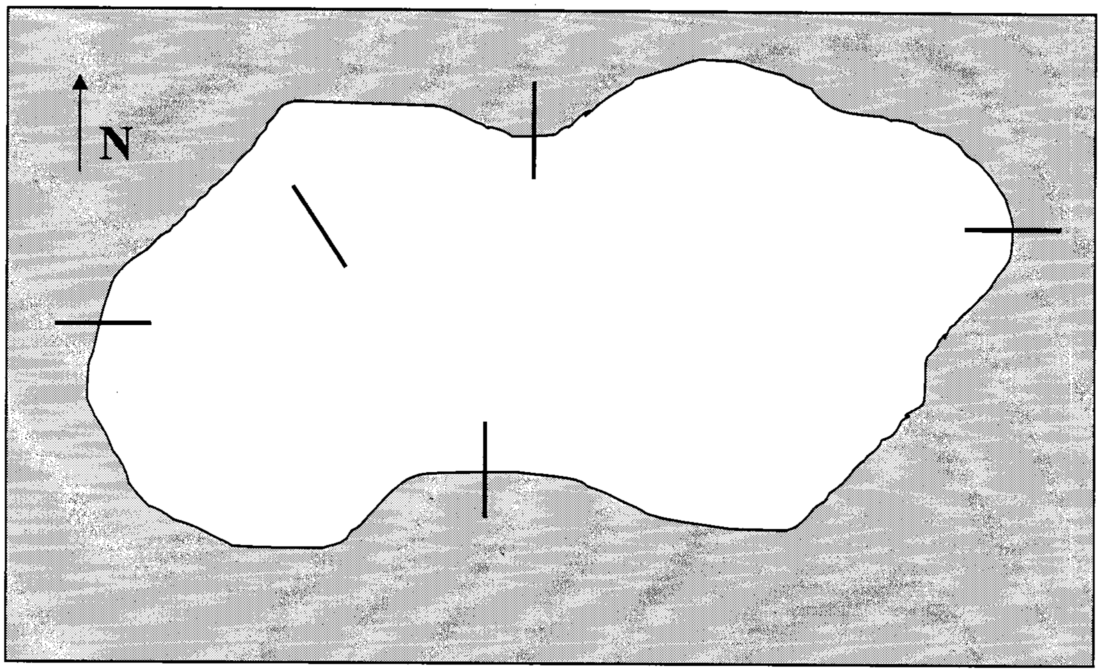

Figure 3.2 Plot setup in hypothetical burned area.

Grey = forest, white = burned area, black lines = 100 m transects. Position of 5th transect (in middle) varied by burn.

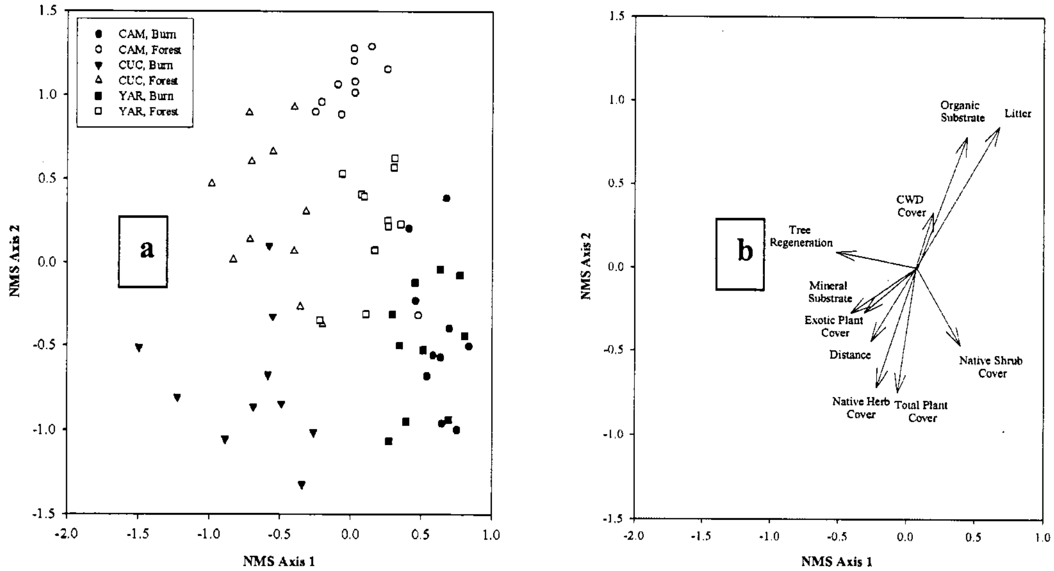

Figure 3.3 NMS ordination of plot data.

(a) represents average composition of plots at varying distances from edge and (b) displays vectors representing some response variables.

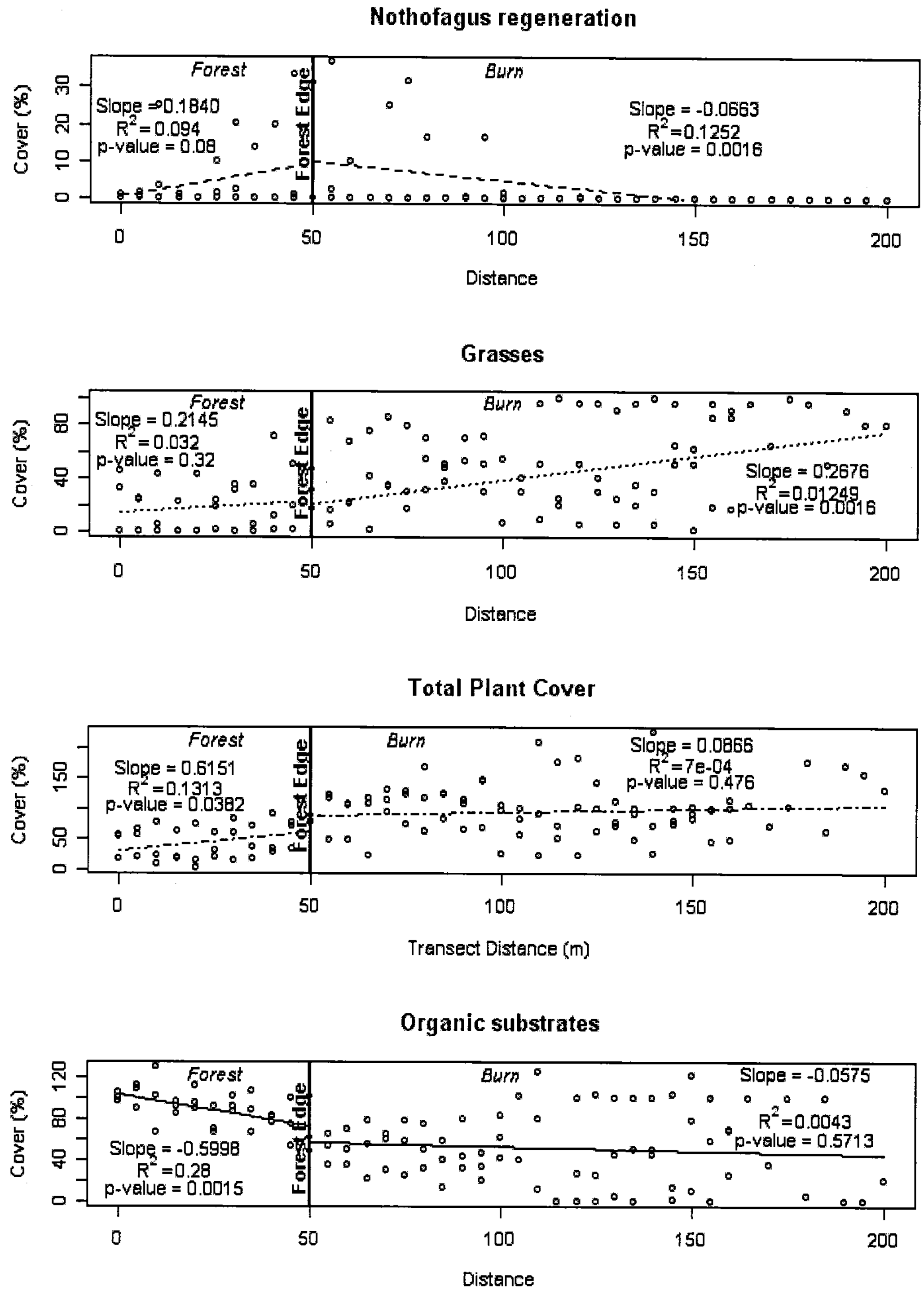

Figure 3.4 Four response variables plotted over transect distance.

Note that the y-axis varies among plots.

Chapter 4 Forest carbon at the landscape scale in Tierra del Fuego, Chile: Influences of topography and geography

4.1 Introduction

The physical relief of the Earth's surface, or topography, is a primary determinant of terrestrial ecosystem composition, structure, and function (Swanson *et al.* 1988; Turner *et al.* 2001; Kruckeberg 2002). In conjunction with lithology, the other chief element of the geophysical substrate, topography exerts a considerable influence on endogenous and exogenous processes operative in ecosystems. In forest ecosystems, topography influences patterns of primary productivity (Bolstad *et al.* 2001; McKenzie *et al.* 2003), composition (Donoso Zegers 1993; McKenzie *et al.* 2003), soil and nutrient dynamics (Woodward 1998; Tateno and Takeda 2003; Luizão *et al.* 2004; Kang *et al.* 2006) and disturbance (Boose *et al.* 1994; Foster and Boose 1995; Kushla and Ripple 1997; Kulakowski and Veblen 2002).

Topographical variables have been used either as the sole predictors of a number of ecosystem characteristics (Davis and Goetz 1990; Gessler *et al.* 1995; Iverson *et al.* 1997; Kushla and Ripple 1997), or as additional variables to increase model accuracy (Chen *et al.* 1998; Fahsi *et al.* 2000). In many landscapes, the accuracy of type classifications of satellite spectral data can be refined by including ancillary data such as soil maps and terrain variables (Iverson *et al.* 1989; Davis and Goetz 1990; Lillesand and Bolstad 1992a; Moisen and Edwards 1999). Soil attributes, such as the thickness of the A horizon, can be spatially predicted with multiple regression models including terrain variables (Moore *et al.* 1993; Gessler *et al.* 1995). The exposure of vegetation to various disturbance elements or stressors, and the corresponding effects on site productivity, have been modeled using terrain-derived indices or variables (Wilson 1984; McNab 1993; Hannah *et al.* 1995; Schulte *et al.* 2005).

At larger spatial scales, regional geography influences primary productivity (Tuhkanen 1992; Veblen *et al.* 1996), composition (Ohmann and Spies 1998), nutrient dynamics (Austin and Sala 2002), disturbance (Gonzalez *et al.* 2005) and other processes in terrestrial ecosystems. Causative factors include precipitation gradients (Austin and Vitousek 1998; Austin and Sala 2002) and temperature gradients (Mancini 2002).

The *Nothofagus* forests of Tierra del Fuego, Chile are influenced by wind disturbance (Rebertus and Veblen 1993; Rebertus *et al.* 1997), variations in temperature (Tuhkanen 1992; Veblen *et al.* 1996) and other factors whose spatial effects may be mediated by topography and regional geography. This study investigates the relationship of a number of landform and geographic variables to carbon storage in three pools: overstory trees, CWD, and the topsoil layer. Expected relationships of topographic variables are given in Table 4.1. The objectives are to 1) assess the predictive strength of individual variables, and 2) assess the maximum amount of variance in forest carbon pools explained by models constructed with selected landform variables.

Several research questions addressed in this research are focused on the utility of landform variables in predictive modeling of forest condition. How are individual landform variables related to forest carbon storage? Which combinations of landform variables are significantly related to carbon storage in the three carbon pools?

Table 4.1 Topographic variables used in terrain analysis of forest carbon.

Variable	*Expected influence on C stores*	*References*
Elevation	Cooler temperatures; shorter growing season; higher windspeeds at higher elevations	(Barry 1981; Kruckeberg 2002; McKenzie *et al.* 2003)
Slope	Greater soil loss/erosion on steeper slopes; greater influence of aspect.	(Braun *et al.* 2001)
Aspect	North aspects receive higher insolation, while west/southwest aspects may experience greater wind intensities during storm events.	(Barry 1981; Tuhkanen 1992; McCune and Keon 2002)
Distance to ridge	Proximity to ridges may increase influence of wind events and stressors.	(Kushla and Ripple 1997; Ruel *et al.* 2002)
Distance to stream	Proximity to waterways may reduce dry-season stressors, and indicate deeper accumulations of organic material.	(Moore *et al.* 1993; Gessler *et al.* 1995)
TPI250	Low values indicate lack of topographic prominence (small ravines, depressions), while high values indicate locally prominent ridges/hilltops. Higher exposure is expected to correlate with lower carbon stores.	
TPI500	Low values indicate lack of topographic prominence (small streambeds, depressions), while high values indicate locally prominent ridges/hilltops.	(Weischet 1985; Davis and Goetz 1990; Nowacki and Kramer 1998; Kramer *et al.* 2001)
TPI2000	Low values indicate lack of topographic prominence at the scale of two km, while high values indicate position on prominent ridge and peak systems.	
Distance to coast	Precipitation declines with distance to coast, inducing change in tree community.	(Tuhkanen 1992)

4.2 Methods

4.2.1 Data Collection

Forest inventory data were collected in 160 plots in three different areas across southwest Tierra del Fuego, Chile (Figure 4.1). Four plots were established in 40 stands representing different combinations of species and stand density. At the center of each plot, a variable-radius sampling method (Bitterlich 1984; Shiver and Borders 1996) was used to sample density and basal area of live and dead overstory trees. Four 25 m line intercept transects for CWD (Harmon and Sexton 1996; Shiver and Borders 1996), arranged in a square centered on the plot center. The depth of the O+A horizon (as defined in Chapter 3), the most carbon-rich segment of spodosols occurring under *Nothofagus* (Tate *et al.* 1993), was determined in four soil cores located 10 m from plot centers in each of the cardinal directions.

4.2.2 Data Analysis

Calculation of carbon stores per ha. Tree volume was calculated for each tallied live tree and snag in the variable radius plots from the equations given in (Martinez-Pastur *et al.* 1993). These volumes were expanded to per-hectare estimates by applying the expansion factors given in (Shiver and Borders 1996) to estimates of overstory tree density for each size class. Per-hectare estimates of standing tree volume were then multiplied by a carbon density estimate for either *N. pumilio* or *N. betuloides* (Mg C m^{-3}, Chapter 2) to produce an estimate of overstory carbon, or OVERC. Coarse woody debris volume estimates were calculated for each plot using the equation given for line intercept sampling by (Harmon and Sexton 1996). These volume estimates for each decay class were then multiplied by the carbon density values per decay class (Mg C m^{-3}, Chapter 2) to estimate carbon in coarse woody debris, or CWDC. O+A horizon carbon storage, or SOILC, was calculated by multiplying the O+A horizon mean depth for each plot by a carbon density value determined for *Nothofagus* forest soils (Tate *et al.* 1993). The sum of these pools is, for the purposes of this research, considered to be the total carbon stores, or TOTC, for each plot, consisting of overstory, CWD and soil values.

Calculation of topographic variables. Elevation in meters above mean sea level is provided as a co-registered layer with ASTER images (Abrams 2000). Scene characteristics of the imagery used to generate topographic variables are shown in Table 4.2. Seven plots fell in a narrow area between the ASTER images. Topographic variables for these plots were generated from Shuttle Radar Topography Mission with 90 m horizontal resolution, and comparable vertical resolution and error to ASTER DEMs (Nikolakopoulos *et al.* 2006). Slope and aspect were calculated in ERDAS Imagine using 3x3 pixel convolution windows. Aspect was used to generate two aspect-related variables, ASPECT_N and ASPECT_PS. The first variable was generated by a simple cosine transformation with no phase shift, which essentially designates north as the optimal aspect (Beers *et al.* 1966). The second variable was calculated using the method of (Stage 1976) to identify an optimum phase shift with respect to the response variables.

Topographic exposure was calculated as a Topographic Position Index (Weiss 2001), using three window widths (250, 500, and 2000 m) to capture exposure information at multiple spatial scales. Negative values of the TPI indicate pixel location in concave features such as valleys, while positive values indicate pixel locations on convexities or ridges. Values close to zero indicate a relatively flat surface (independent of angle). These calculations were performed using the Topographic Position Index extension to ArcView 3.x (Jenness 2006). The TPI at 250 m combined with TPI at 2000 m were used in a Landscape Classification procedure according to the method of (Weiss 2001). TPI can also be calculated in a 'wedge' configuration in which the metric is calculated for a specified azimuth range and distance. This permits assessment of the influence of topography in a specific direction (Jenness 2006). Eight directional TPI variables were created by calculating TPI for a 500 m, 45° azimuth range centered on each of the cardinal and subcardinal directions. The 'high ridge/mountain top' classification from the Landscape Classification procedure was used as a focal theme to generate a grid file of distance to ridges. A shapefile of perennial streams, provided by Savia Forestal, Inc. (Punta Arenas, Chile), was used to generate a grid file of distance to streams.

Calculation of Geographic Variables. Distance-to-coast in meters, or DTC, was calculated by digitizing the coastline from a Landsat scene of the region and then performing a distance-to-feature raster calculation in ArcGIS (ESRI, Redlands, California). Easting and northing coordinates in the Universal Transverse Mercator projection (WGS 1984, Zone 19S) were employed as continuous variables to capture geographic variation. Grid theme values were spatially extracted in ArcView 3.2 (ESRI Inc. 1999) to a shapefile theme of the georeferenced inventory plots and exported for analysis in the R 2.4.0 statistical programming environment (R Development Core Team 2007).

Statistical analysis. Simple linear regression (Kutner *et al.* 2004) was used to quantify relationships between continuous landform variables and carbon pool estimates.

Scatter plots of predictor and response variables were used to assess linearity and homoscedasticity and normality of residuals was visually assessed with histograms (Kutner *et al.* 2004). For categorical landform variables such as landform class, one-way analysis of variance (Zar 1999) was used to assess differences in carbon pools. Backward selecting stepwise regression (Kutner *et al.* 2004) was used to identify combinations of landform variables that predicted a maximum amount of variance in carbon pools (Kushla and Ripple 1997). A matrix of Pearson's correlation coefficients was used to identify possible issues with multicollinearity among the predictor variables. A threshold for exclusion of highly correlated predictor variables from the final multiple regression models was set at $r^2 \pm 0.70$. Variance inflation factors were also calculated to assess the contribution of each variable to model error and multicollinearity in the full model (Kutner *et al.* 2004). Variance inflation factors higher than 10 were considered indicative of inappropriate inclusion of a term in the final model.

Table 4.2 Scene characteristics of ASTER imagery used in this research.

ID Code	Scene center		Acquisition Date	Solar Elevation	Solar Azimuth
	Latitude	Longitude			
3144	53.99° S	70.12° W	02/13/2004	39.4°	51.8°
1538	54.18° S	68.88 ° W	10/02/2001	34.0 °	36.9 °

4.3 Results

4.3.1 Relationships of landform and geographic variables to carbon pools

Several variables had significant relationships with one or more carbon pools (Table 4.3). All relationships displayed acceptable linearity, homoscedasticity, and normality of residuals. Overstory carbon had the greatest number of significant relationships with terrain variables of any pool.

Table 4.3 Results of significant regression analyses.

Response variable	*Significant predictor*	*Estimate*	*P-value*	r^2
OVERC	ASPECT_PS	-12.172	0.05	0.018
	Landform ANOVA	(categorical variable)	0.0002	0.1202
	TPI 500	-1.4923	0.00325	0.0617
	TPI 2000	-0.7656	<0.0001	0.2103
	TPI W 500	-0.8480	0.0016	0.0716
	TPI NW 500	-0.3867	0.0091	0.0471
	DTC	-3.125x10-3	<0.0001	0.235
	E	-1.81x10-3	<0.0001	0.4267
CWDC	Elevation	-0.0604	0.0142	0.0395
	ASPECT_PS	11.474	<0.0001	0.120
	Distance to stream	0.02303	<0.001	0.110
	TPI N 500	0.19381	0.001	0.0790
	TPI S 500	-0.26716	<0.0001	0.1389
SOILC (O+A horizons)	ASPECT_N	-16.049	0.0354	0.033
	ASPECT_PS	-17.839	0.00625	0.061
	Distance to stream	0.04074	0.00365	0.102
	E	-5.901x10-4	0.0962	0.0042
TOTC	Slope	-3.066	0.00272	0.0736
	E	-1.451x10-3	0.1479	0.0004

Overstory carbon was significantly related to ASPECT_PS, landform type, TPI 500, TPI 2000, TPI W 500, TPI NW 500, distance to coast, and easting. Aspect values further away from the calculated optimum of 82° azimuth corresponded to lower values for overstory carbon. Overstory carbon decreased significantly across landform classes in the following order: plains, midslopes, and upper slopes (Figure 4.2). Pair-wise comparisons showed significant differences in overstory carbon between plains and midslopes (*t*-test, $p<0.05$), plains and upperslopes (*t*-test, $p<0.0001$), and midslopes and upperslopes (*t*-test, $p<0.001$). TPI 500, TPI 2000, and TPI W 500 and TPI NW 500 all were negatively correlated with overstory carbon, indicating that increasing topographic exposure is associated with lower values of this pool. Overstory carbon also decreased with Easting, indicating greater values in the western region of the study area.

Carbon in CWD was negatively correlated with elevation. This pool was positively associated with ASPECT_PS, indicating that aspects closer to the optimum of 82° azimuth corresponded to higher levels of CWD. Distance to streams was positively correlated with carbon in coarse woody debris, explaining about as much variance as ASPECT_PS. TPI N 500 and TPI S 500 had opposite relationships with respect to this pool, with exposure to the north indicating higher levels of carbon in coarse woody debris. Landform was not a significant predictor, either as a categorical variable (ANOVA, $p=0.91$) or in pair-wise comparisons (*t*-test, all $p>0.77$, Figure 4.2).

Carbon in the O+A horizons was negatively related to both ASPECT_N and ASPECT_PS, indicating a deeper combined O+A horizon on slopes oriented to the south, and those slopes facing the prevalent storm wind direction. The most variability in this pool was explained by distance to streams, with Oa horizon carbon increasing with distance from streams. Easting explained very little variance, but was also significant.

Total carbon displayed a negative relationship with slope. The regression with easting was significant, but explained almost no variation in total carbon. Due to the spatial distribution of plots in the study area, Northing was highly correlated with Easting (r^2= -0.973, p<0.0001), and was dropped from further analysis.

Table 4.4 Results of stepwise regression analyses involving landform variables. N indicates the number of plots with sufficient data on the pool and topography to conduct the analysis. R^2_a is the adjusted R^2

Predicted C pool	*N*	*Model*	R^2_a	p
Overstory	123	OVERC = 580.3 -0.00094(E) - 0.2993(TPI2000)	0.4935	<0.0001
Coarse woody debris	123	CWDC = 44.350 -0.05525(Elevation) +10.642(ASPECT_PS) +0.01824(D_STREAM)	0.2383	<0.0001
O+A horizons	75	SOILC = 711.9 -0.00103(E) - 1.836(SLOPE) -21.71(ASPECT_PS) -0.0112(D_RIDGE)	0.2433	<0.0001
Total	75	TOTC = 928.0 -0.00127(E) -1.947(SLOPE) +0.05016(D_STREAM)	0.2662	<0.0001

4.3.2 Multiple regression analysis

The four carbon pools responded to different combinations of topographical variables when examined with stepwise regression (Table 4.3). Overstory carbon decreased with easting and TPI2000. Coarse woody debris decreased with elevation and distance to streams and was positively correlated with ASPECT_PS. Oa horizon carbon stocks decreased with easting, slope, and distance from ridges, and was negatively associated with ASPECT_PS values (i.e., increased to windward slopes). Total carbon decreased with easting, decreased with slope, and increased with distance from streams.

The overstory carbon pool had the largest amount of variance explained by the final regression model (49.35%, **Table 4.4**). The models for coarse woody debris, Oa horizon, and total carbon pools were similar in terms of variance explained, ranging from 23.83% to 26.62% (**Table 4.4**). These were relatively weak patterns, and therefore no real relationship can be inferred from these data.

4.4 Discussion

Phase-shifted aspect was the only variable that explained variability in both overstory and woody debris pools, indicating its utility as a predictor variable in forest modeling. The phase shift determined from the plots is almost 180° from the prevalent storm wind direction, which in Tierra del Fuego is from the southwest (Tuhkanen 1992; Rebertus *et al.* 1997). Surprisingly, elevation was not a strong predictor variable. It is probable that this variable would become more prominent if the analysis could be constrained to a particular stage of forest development. Landform class, as determined using a combination of a topographic index calculated at a larger and a smaller spatial scale (Weiss 2001), performed well at predicting overstory carbon storage. This type of multiple-scale landform classification has great promise in wind-disturbed systems, where exposure at several spatial scales may influence both disturbance frequency and growing conditions.

Carbon stocks in the overstory responded to a regional variable, easting, and a local topographic variable, TPI2000. These may reflect the influences of factors operating at two separate spatial scales: regional influences of precipitation and continentality of temperature vs. local influences of topographic exposure. The relatively large amount of variance explained by the model for the overstory pool (49.35%) suggests that this pool is most responsive to geographic variation and topography compared to the other pools. The forest overstory may be more responsive to topography-mediated climatic variables because of its relative exposure to atmospheric and solar conditions. Since the overstory ameliorates microclimatic conditions for the other pools (Chen *et al.* 2000; Caldentey *et al.* 2001), it may additionally reduce the sensitivity of the other pools to topography-mediated climatic variables. This interpretation would help explain the higher proportion of variance explained in the overstory model compared to the other pools. This distinction also may account for the result that overstory carbon was responsive to landform class, but CWD was fairly constant over landform class.

Carbon stocks in CWD decreased with elevation, an interesting result given that this variable did not appear in the model explaining overstory carbon. Phase-shifted aspect was a significant predictor of CWD carbon in the final model, with lee slopes (as indicated by the phase-shift) corresponding to higher stocks. (Kramer *et al.* 2001) showed that topography may influence the spatial distribution of wind disturbance regimes and stand structures over a single landscape, with gap-phase development more common on lee slopes and stand-replacement events occurring on windward slopes. Stands of montane lenga may develop more frequently on exposed windward slopes and have low levels of woody debris biomass until a stand-replacement windthrow event. Distance to stream emerged as a positive coefficient in the equation predicting woody debris stocks, which is reasonable given that streamside stands are frequently topographically better protected and have deeper total soil profiles in most landscapes (Donoso Zegers 1981; Singer and Munns 1996), which may enhance rooting strength of mature trees. This relationship may be the reason why distance to stream shows a positive sign in the equation predicting total carbon storage, which was contrary to prediction.

Greater slope angles were negatively correlated with lower carbon storage in the O+A horizons and total carbon pools. Steep slopes experience progressively greater influence from solar angle-related phenomena up to an incidence angle of 90° (Stage 1976). Soil moisture, a key determinant of site productivity, generally decreases on steeper slopes, with corresponding decreases in site productivity (Iverson *et al.* 1997). Steep slopes likewise generally experience increasing rates of soil loss through gravity-related erosive forces such as soil creep (Braun *et al.* 2001). This may limit overall soil depth, reducing site productivity and litter production, thus negatively influencing the overall combined O+A horizon depth.

Easting emerged as a significant predictive variable for three of the four pools considered in this study. Tierra del Fuego has strong regional precipitation and continentality gradients that are oriented southwest-northeast (Tuhkanen 1992). The negative relationship of overstory carbon with distance to coast likely reflected an increasingly continental climate further inland. Continental climates tend to be drier, experience moisture limitations in the summer and have colder winters. The southern part of the study area has a significant mountain range, the Cordillera Santa Maria, which probably enhances continentality in the Vicuña area due to orographic precipitation on the southern slopes of the range.

A major limitation of this research is the fact that stand age was not measured. The wood of *Nothofagus* species is relatively hard and difficult to core. In addition, as many as half of the trees in mature *Nothofagus* stands in Tierra del Fuego may have a central rot column from the activity of pathogenic fungi (Cwielong and Rajchenberg 1995). This means that the variation in carbon storage associated with stand age was not accounted for in this research. However, statistical relationships that do emerge, such as between TPI2000 and overstory carbon storage, are likely to be strongly significant once variation in stand age is incorporated into the model.

Three separate crews worked on the field sampling portion of this research, but sampling was sufficiently standardized among these crews to reduce variation in data collection.

The estimates of soil carbon were derived from research located in a southern beech forest in New Zealand. Unfortunately, little work has been done on forest soils in Tierra del Fuego. However, the depth of the combined O+A horizon in this work was used to directly estimate per-hectare volume of this horizon and associated carbon stores. Therefore, the general relationships to topographical variables should be preserved, even if predictions of upper-horizon soil carbon are not accurate due to differences between forest soils in Tierra del Fuego and those of New Zealand.

The methodology employed in this paper is correlative in nature, and is not explicitly tied to disturbance, climatic variables, and other actual mechanisms of topographic influence on carbon stores. This is a limitation in that it does not explain actual mechanistic influences, but an advantage in that an empirical statistical model may be used to predict landscape-scale carbon storage without the need to regionalize climate variables (Schulz *et al.* 2002). The weak statistical relationships obtained for the CWD and soil pools may be improved upon with sampling methodologies that are designed to isolate topographic variables.

4.5 Conclusions

Three different carbon pools in the *Nothofagus* forests of Tierra del Fuego, Chile, and the sum of these pools, were analyzed in this research. Only one pool, the overstory, was even marginally significant in terms of variance explained by a stepwise regression equation. The significant predictor variables in this equation were easting, slope, and distance to streams. Slope, aspect, and easting appeared in two or more of the regression equations, suggesting that these variables be included in future investigations of landform and forest carbon storage. This observational study highlights the potential for topographic variables to be employed in predictive spatial modeling of ecosystem structure and corresponding functions such as carbon storage. However, this potential can only be realized with specific sampling to capture variability related to topographic patterns. Further research on carbon storage in *Nothofagus* forests should either incorporate or control for the effects of topographic and geographic variables.

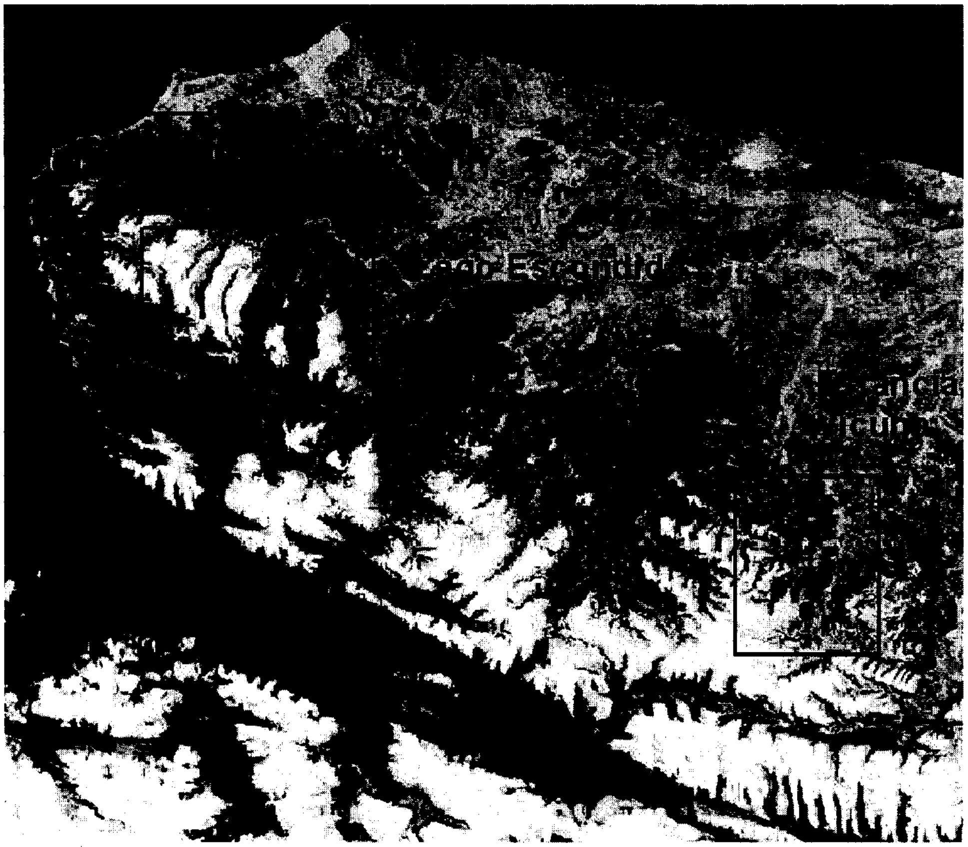

Figure 4.1 Location of research areas and plots.

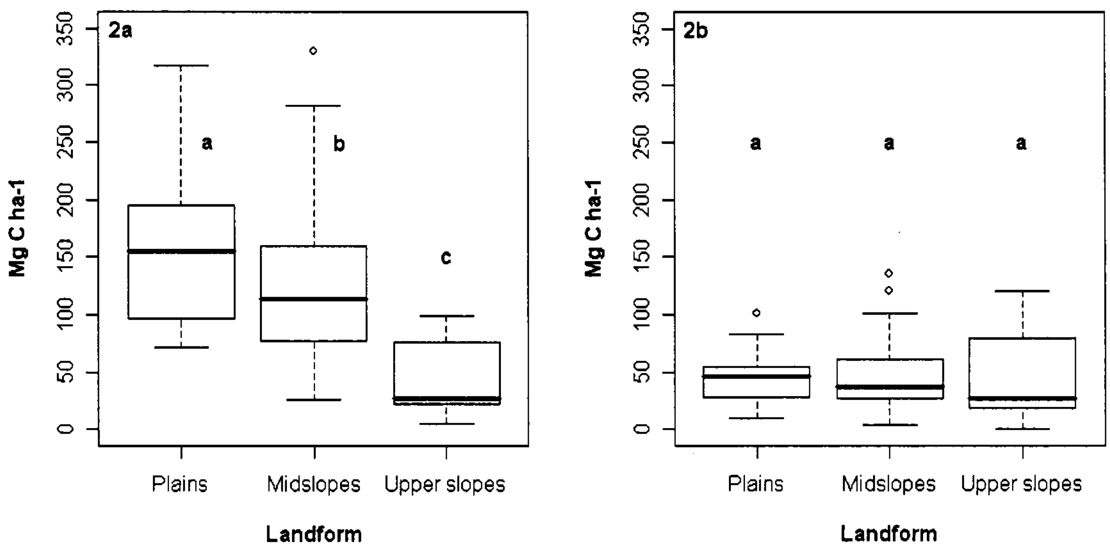

Figure 4.2 Overstory carbon stores (a) and coarse woody debris carbon stores (b) as related to Weiss' (2001) landform classes.

Letters indicate significant differences according to pair-wise *t*-tests (α=0.05, all p<0.05).

Chapter 5 Modeling the effects of alternative management strategies on forest carbon in the Nothofagus forests of Tierra del Fuego, Chile

5.1 Introduction

The sequestration and storage of atmospheric carbon is being increasingly recognized as a valuable environmental service performed by forest ecosystems. As interest increases in the various physical and biological factors influencing climate change, so does interest in understanding how human activities relate to these factors. Human activities associated with forests, including forest management, have been recognized as significant forces in the terrestrial carbon cycle (Whittaker and Likens 1975; Bramyrd 1979). As carbon dioxide and other carbon-containing gases in the atmosphere have become recognized as greenhouse gases, the role of forests in sequestering and storing carbon has become an important element in the policy debate regarding anthropogenic climate change (Brown *et al.* 1996).

Forest management activities have the ability to influence the amount of carbon stored in forested stands and landscapes, through both intermediate stand interventions (Garcia-Gonzalo *et al.* 2007) and general timber harvest regimes (Harmon *et al.* 1990; Cohen *et al.* 1996). Since forest carbon cannot be feasibly measured across broad areas, approaches such as remote sensing and landscape models are necessary to scale stand-level carbon estimates to the landscape and region level (Cohen *et al.* 1996).

Much is known about management of the forest carbon resource in the Pacific Northwest of North America (Harmon *et al.* 1990; Turner *et al.* 1995; Harmon *et al.*

2004), but many ecosystems remain to be addressed in terms of necessary considerations for optimal balance of the values associated with carbon storage with other forest values.

The objective of this research was to employ a simulation modeling approach to examine the effects of timber harvest activities on forest carbon storage at the landscape scale in the southern beech (*Nothofagus* Blume) forests of Tierra del Fuego, Chile, in terms of changes to forest carbon pools. The disturbance regime in these forests is dominated by small to medium-scale windthrow events (Rebertus and Veblen 1993), creating a shifting landscape mosaic of even and unevenaged stands (Rebertus *et al.* 1997). The response of forest carbon pools to the addition of a forest harvest regime to this wind disturbance regime has not been quantified for this ecosystem.

The LANDIS-II model (Gustafson *et al.* 2000; Scheller *et al.* 2007) was used to simulate natural disturbance, timber harvest, regeneration, growth, decomposition, and other processes. The simulation modeling addressed the following hypothesis: increasing intensity of timber harvest will result in reduced forest carbon storage in both overstory and coarse woody debris pools (snags and downed wood) at the landscape scale when compared to the natural background disturbance regime. It was also hypothesized that, due to the extreme environment and the poor dispersal of *Nothofagus* species, clearcut harvesting will result in greater reductions of carbon than an overstory retention system.

5.2 Methods

5.2.1 Simulation landscape

The western portion of the Santa Maria peninsula (53°30' S, 69°30'W) in southwestern Tierra del Fuego, Chile was selected as the simulation landscape (Figure 5.1).

5.2.2 Generation of a land cover map using ASTER imagery

The LANDIS model is designed to accept classified imagery as a spatially-explicit input for the modeling of actual landscapes. For this research, this input was derived from satellite imagery from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER). This imagery was obtained from the Department of Earth and Space Sciences, University of Washington. ASTER is a remote sensing instrument that captures high-resolution earth-reflected radiation in three visible and near-infrared bands, six short-wave infrared bands, and five thermal bands (Abrams 2000). In addition to these 14 nadir-looking bands, a 27.6° off-nadir, backward-looking radiometer captures a parallax image for the generation of high-resolution elevation datasets (Abrams 2000).

An ASTER scene was utilized to provide image cover of the study area. Level 1B data were utilized, meaning that radiometric calibration and geometric co-registration were performed on images (ERSDAC 2005). Topographic correction was performed on the visible, near infrared, and shortwave infrared ASTER bands using the SCS+C algorithm. This algorithm avoids the over-correction problems presented by the cosine correction and other topographic correction methods (Soenen *et al.* 2005). A square sampling grid of points (20 km by 20 km, with 1 km between points in each axis) was generated and used to extract the cosine of light incidence values (cos(i)) and grid values for each uncorrected band. The slope and intercept constants from linear regression models of uncorrected relectance in each band and cos(i) values were used as inputs for calculation of the correction constant C (Teillet *et al.* 1982). Correction was performed using ERDAS Imagine 9.1 (Leica Geosystems Geospatial Imaging, LLC) with the SCS+C algorithm implemented using the Spatial Modeling Language. Visual comparisons between corrected and uncorrected images confirmed the desired flattening of reflectance values (Figure 5.2).

An unsupervised classification (Lillesand and Kiefer 1994) was performed to identify areas of *Nothofagus* forest and non-forest such as water, bare ground/rock, grassland (pampa), and Magellanic tundra. Non-forest cover types were masked with a Boolean process and a second unsupervised classification was performed on the masked imagery to identify distribution of *Nothofagus* forest types. These included stands dominated by coigüe (*Nothofagus betuloides*), lenga (*N. pumilio*), and ñirre (*N. antarctica*). This classification layer (Figure 5.3) was used as a map of initial community distribution to parameterize LANDIS-II.

5.2.2 Description of the LANDIS-II Model

The functional architecture of the LANDIS model is shown in Figure 5.4. The LANDIS-II model provides an environment in which the combined effects of timber harvest and the natural disturbance regime (wind, fire, and endogenous mortality) on forest biomass may be assessed (Gustafson *et al.* 2000; Scheller and Mladenoff 2004).

LANDIS-II is a spatially-explicit, temporally discrete simulation model for forest disturbance dynamics (Mladenoff 2004; Scheller *et al.* 2007) and incorporates extension modules for simulating many processes, including timber harvest regimes (Gustafson *et al.* 2000; Mehta *et al.* 2004) and wind disturbance (Scheller and Mladenoff 2004). The extensible nature of LANDIS-II increases the number of ecology and management-oriented questions that can be addressed (Scheller *et al.* 2007). LANDIS-II operates on landscapes represented by a raster, or lattice of square cells. Within each cell, processes such as regeneration, growth, mortality and decomposition are modeled according to a set of user-defined parameters. Some processes modeled by LANDIS-II, such as wind and fire disturbance, operate at spatial scales larger than the cell, and the spatial behavior of these processes may also be parameterized. For example, the minimum, mean, and maximum size of windthrow events may be set, as well as the probability of a windthrow event spreading from the cell of origin to adjacent cells. The biomass module calculates biomass values for live and dead pools for each cell (Scheller and Mladenoff 2004) as a function of time since disturbance, the maximum aboveground net primary productivity and the number of cohorts that have established in a cell. The maximum cohort biomass is determined by multiplying the maximum aboveground net primary productivity by a factor of 30 (Brown and Schroeder 1999; Scheller and Mladenoff 2004). Growth of a cohort and endogenous mortality are both functions of time since disturbance, expressed as functions of the fraction of the species' lifespan (Scheller and Mladenoff 2004). As the cohort approaches the maximum possible age, aboveground net primary productivity asymptotically approaches the maximum possible value. Mortality is a sigmoidal function of species lifespan, low at first, increasing exponentially, and then asymptotically approaching the maximum possible. The LANDIS-II model output is comprised of spatially-explicit raster maps in .gis format, corresponding to each time-step for the process in question, of live overstory woody biomass, biomass of CWD (which in LANDIS-II consists of downed woody debris and snags), areas disturbed by wind, harvested units, and stand age. The maps of biomass were opened in ArcMap (ESRI, Redlands, CA) and the attribute table was exported for analysis. The contents of the attribute table were used to determine the amount of live overstory and CWD in each site or pixel in the study landscape. The sum of these provides an estimate of landscape-scale biomass.

5.2.3 Parameterization of LANDIS-II

Specification of management areas and harvest units. Five management areas were digitized in ArcGIS: non-forest (inactive, consisting of water, grassland/moorland, and alpine), a large wetland complex in the southeastern part of the management unit (inactive), the Rio Condor floodplain (active, but not designated for harvest), interior forests (active), and coastal forests (active). Using the management area map as a base layer, 572 designated timber harvest units were created with a mean area of 194 ha (sd=108.2). Harvest unit boundaries were created by dividing the two active management areas into smaller units based on the presence of roads, streams, forest types, and boundaries between forest and non-forested areas. No riparian buffers were employed in these simulations, but the floodplain of the Río Cóndor was reserved from harvest. The management areas and stand boundaries are shown in Figure 5.5.

Species characteristics. Longevities of *N. pumilio* and *N. betuloides* in Tierra del Fuego are approximately 400 and 440 years, respectively (Rebertus and Veblen 1993) and these values were employed as maximum cohort ages for these simulations. Onset of sexual maturity in *Nothofagus* genera is not usually earlier than 25 or 30 years (Donoso 1996; Read and Brown 1996) and a value of 25 years was used in the model runs. Both *N. pumilio* and *N. betuloides* are moderately shade-tolerant (Veblen *et al.* 1996), but a slightly higher shade tolerance was assigned for *N. betuloides*. Seed dispersal of Chilean *Nothofagus* is relatively poor (Donoso Zegers 1993; Veblen *et al.* 1996) and effective seed dispersal of 40 m and maximum seed dispersal values of 100 m were used as model parameters. The probability of vegetative reproduction is very low for *N. betuloides*, and slightly higher for *N. pumilio* (Veblen *et al.* 1996).

Ecoregion definitions. LANDIS incorporates variation by allowing the user to specify 'ecoregions' or areas where site productivity, disturbance, regeneration probability, and other factors are expected to operate in a similar fashion. Six ecoregions were defined for the study area. Ecoregions were defined by the initial communities (Figure 5.3), since the spatial distribution of tree species and their relative proportions are constrained by environmental gradients in Tierra del Fuego (Gutiérrez *et al.* 1991). Species-specific establishment probabilities for lenga and coigüe that maintained their relative proportions in the current landscape were specified as model parameters for these simulations (Table 5.1). Annual net primary productivity (ANPP), a critical parameter in LANDIS-II, was also parameterized by ecoregion. Since ANPP data have only been gathered for a few sites in Tierra del Fuego, ANPP was assumed to decrease from the coast to the interior for *N. betuloides*. ANPP for *N. pumilio* was assumed to increase from the coastal ecoregions to the mixed *N. betuloides*/*N. pumilio* ecoregion, and then decrease again into the drier *N. pumilio* ecoregions (Table 5.1).

Table 5.1 Characteristics of ecoregions.
Establishment probability is the probability of establishment of the species in a site (pixel) during a given time-step. ANPP units are kg biomass ha^{-1}.

Ecoregion	Est. prob., NOBE	Est. prob., NOPU	ANPP, NOBE	ANPP, NOPU	Wind return interval, yrs.
1. Coigue (NOBE)	0.9	0.01	700	450	147
2. Coigue/Lenga	0.8	0.3	600	550	147
3. Coigue/Lenga, even	0.6	0.6	500	650	147
4. Lenga/Coigue	0.2	0.85	400	600	147
5. Lenga (NOPU)	0.01	0.95	300	600	147

Disturbance regime. A mean wind disturbance return interval of 147 years (Rebertus *et al.* 1997) was used for all ecoregions. Probabilities of wind disturbance were parameterized in the Base Wind extension using 50 year integrals of the Weibull probability density function described by Rebertus *et al.* (1997,Table 5.2). Minimum and maximum wind disturbance areas were set to 1 and 150 ha, respectively (Veblen *et al.* 1996; Rebertus *et al.* 1997). Fire is not included as a disturbance type in the model runs for this research, since fire in southwest Tierra del Fuego is primarily an anthropogenic disturbance.

Table 5.2 Probabilities of wind disturbance during time in age class based on a Weibull probability density function.

Cohort age class (years)	Probability of wind disturbance (%)
0 to 50	0.03
50 to 100	12.4
100 to 150	61.9
150 to 200	25.3
200 to 250	0.07
250 to 350	0.03

Biomass Succession. The Biomass Succession (v. 1.1) extension of LANDIS-II was used to generate biomass estimates for calculation of carbon stores. This extension estimates overstory, woody debris, and leaf litter biomass. Woody debris decay constants for *N. pumilio* and *N. betuloides* were calculated using the equations from (Frangi *et al.* 1997) which describe the relationship of the decay constant k with diameter of woody debris for each species. Mean diameters of woody debris for each species were calculated from line-intercept data (Chapter 2). A mean diameter of 19.1 cm for *N. betuloides* corresponded to a decay constant of k=0.070, and a mean diameter of 15.8 cm for *N. pumilio* corresponded to a decay constant of k=0.022. Leaf longevity values were 1 year for the deciduous *N. pumilio* and 7 years for the evergreen *N. betuloides* (Gutiérrez *et al.* 1991). Maximum aboveground net primary production (ANPP) values were taken from the range of values reported by Gutierrez et al. (1991) for *N. pumilio* and *N. betuloides*-dominated forest, and adjusted for ecoregions. A leaf litter decay rate of k=0.38 for *N. pumilio* was taken from Caldentey et al. (2001) and a slightly lower value of k=0.30 was assigned to *N. betuloides* to reflect lower nitrogen concentration and higher lignin concentration. In LANDIS-II, ANPP increases sigmoidally as a function of cohort age, finally approaching a maximum at a value of 30 x ANPP (Scheller and Mladenoff 2004). This maximum is based upon a regression relationship between measured ANPP and maximum observed biomass for broadleaf forests (Brown and Schroeder 1999).

Scenario design. Since age data were not available for the landscape, a single long-term simulation (1600 years) was run to create a steady-state landscape under the specified wind disturbance frequency and extent parameters. The resulting landscape was combined with the ecoregion map constraining species distribution and the resultant map was used as the initial communities map for all model runs. Individual simulation length was set at 800 years (arbitrarily assigned the years 1600-2400). The first 400 years, or pre-harvest period, was intended to demonstrate an equilibrium condition for all model runs, with the last 400 years, or harvest period, being the focus of comparisons among management scenarios.

The major variables differentiating scenarios were the silvicultural method, harvest rotation, and regeneration method. Two different silvicultural methods were tested: clearcutting and an overstory retention harvest where the oldest cohort of trees is retained. In most of the cells, this was generally a cohort from between 250 to the maximum age of either lenga or coigüe. Two harvest rotation lengths were used: 100 and 200 years. Choices of regeneration method depended upon the silvicultural method. Clearcut units were allowed to regenerate naturally according to the resprouting probabilities and Ward Seed Dispersal model implemented in LANDIS-II (Ward *et al.* 2004), or they were replanted uniformly at time of harvest.

Table 5.3 Scenarios run in the LANDIS-II model.

Scenario	Silvicultural Method	Rotation	Regeneration
No harvest (NOH)	None	None	Natural
CC200N	Clearcut	200	Natural
CC200RP	Clearcut	200	Planting
CC100N	Clearcut	100	Natural
CC100RP	Clearcut	100	Planting
OR200	Overstory retention	200	Natural
OR100	Overstory retention	100	Natural

Seven different management scenarios (Table 5.3) were simulated: no timber harvest (NOH), clearcutting without replanting on 200 year rotations (CC200N), clearcutting and replanting on 200 year rotations (CC200RP), clearcutting without replanting on a 100 year rotation (CC100N), clearcutting and replanting on a 100 year rotation (CC100RP), overstory retention on a 200 year rotation (OR200), and overstory retention on a 100 year rotation (OR100). Woody biomass reduction at timber harvest was set at 50%. This parameter estimate is based upon personal observations of residual structure in harvest units in Tierra del Fuego, where many felled trees are not recovered due to a high incidence of heart rot (J. Franklin, *personal communication*). Three replicates of each simulation were run. This low number of replicates was considered sufficient for comparing model outcomes, given the relatively low stochastic variability in the LANDIS-II model design (Scheller and Mladenoff 2005). The time interval for biomass outputs was set at 40 years, which was sufficient temporal resolution to display trends over an 800-year simulation run. Output from the model consists of spatially-explicit pixel maps with cell values representing biomass for a given pool. For example, Figure 5.7 shows live overstory biomass (Mg per 0.36 ha pixel) for the NOH scenario. Biomass estimates for each pixel were converted to carbon estimates using conversion factors from *Nothofagus* (Chapter 2). Carbon removed as a result of harvest was calculated as a function of stand age at harvest and area harvested (number of hectares harvested in each harvest operation multiplied by the per-hectare carbon storage in live overstory stem wood).

5.2.4 Statistical Analysis

For all scenarios, mean landscape carbon levels for each pool (overstory, CWD, and total) in the harvest period were compared to pre-harvest levels with a Student's *t*-test, correcting for multiple comparisons with the Dunn-Sidak correction (Gotelli and Ellison 2004). Significance of the test was set at α=0.05. Analysis of variance (Zar 1999) was used to assess the significance of management alternative and time period in predicting carbon pools. Graphs were produced for visual comparison.

5.3 Results

The classification process produced a map of forest cover types (Figure 5.3). Non-forested areas were spectrally distinct, and were easily identified for subsequent exclusion from both classification and modeling by the Boolean mask. The second unsupervised classification, conducted on the masked data, clearly identified the west-to-east decrease in the prevalence of coigüe, and the corresponding increase in lenga, through separation of the forest into several classes representing species mixtures.

The spatial pattern of landscapes varied greatly depending upon the silvicultural system (clearcutting vs. overstory retention) and the regeneration method (natural regeneration vs. replanting). Figure 5.7, Figure 5.8, Figure 5.9, and Figure 5.10 show the NOH, CC100N, CC100RP, and OR100 scenarios in simulation year 2360.

Both period (pre-harvest and harvest) and rotation length were significant factors in predicting landscape carbon (ANOVA, p<0.0001 for both factors). The interaction effect (period*rotation) was also significant (p<0.0001). Carbon removed from the landscape through harvest per hectare over the course of the harvest period varied by treatment (Table 5.4). The highest levels of removal occurred in the 100-year rotation scenarios where regeneration was uniform, either from planting or from natural seeding from a retained overstory.

The no-harvest scenario maintained similar equilibrium amounts of carbon in the forest overstory, CWD, and the total pool (Table 5.5, Figure 5.11, Figure 5.12, Figure 5.13). The similarity of the pools throughout the simulation confirms its utility as a steady-state control for comparison with timber harvest scenarios.

Table 5.4 Harvest-related removals of C for each scenario.

Scenario	**Mg C per ha, 400-yr period**	**Mg C per ha, annual removal**
NOH	0	0
CC200N	273.3	0.68
CC200RP	316.7	0.79
CC100N	299.2	0.75
CC100RP	489.8	1.22
OR200	219.9	0.55
OR100	421.67	1.05

The CC200N scenario resulted in reductions in overstory carbon beginning at the initiation of harvesting activities, and apparently continuing throughout the scenario (Figure 5.11). CWD had more variable behavior, experiencing an immediate reducation at the initiation of harvest, and another about 200 years into the harvest period (Figure 5.12). Total carbon decreased gradually over 100 years, reaching a new equilibrium at a mean level of about 160 Mg C ha^{-1} (Figure 5.13). Overstory, CWD and total carbon were all reduced (Table 5.5).

Overstory carbon in the CC200RP scenario was initially reduced for a period of about 150 years in the harvest period, but increased to levels greater than the wind disturbance-dominated system (Figure 5.11). Carbon in CWD exhibited greater variability over time, but also was reduced for the first 200 years, but recovered to relatively high levels (Figure 5.12). Total carbon increased to levels 5.6% higher than in the NOH scenario (Figure 5.13, Table 5.5).

Table 5.5 Mean carbon stocks in studied landscape over each simulation period. Units are Mg C ha^{-1}. Test significance according to Dunn-Sidak-corrected: α=0.0034.

Scenario	**Pool**	**1600-2000**	**2000-2400**	**% Change**	***t*-test**
No harvest	Overstory	207.5 (2.1)	207.6 (1.7)	0.04	NS
	CWD	53.0 (5.7)	53.8 (5.7)	1.7	NS
	Total	260.5 (6.2)	261.5 (6.2)	0.37	NS
CC200N	Overstory	207.6 (2.0)	148.7 (19.8)	-28.3	*p<0.0001*
	CWD	51.5 (5.3)	26.4 (9.8)	-49.0	*p<0.0001*
	Total	259.3 (5.8)	175.1 (27.4)	-32.5	*p<0.0001*
CC200RP	Overstory	207.6 (2.2)	219.3 (22.5)	+5.7	NS
	CWD	52.6 (7.6)	55.5 (13.9)	+5.4	NS
	Total	260.2 (7.3)	274.8 (34.4)	+5.6	NS
CC100N	Overstory	207.6 (2.0)	142.5 (20)	-31.3	*p<0.0001*
	CWD	53.0 (5.0)	24.7 (11)	-53.4	*p<0.0001*
	Total	260.5 (5.8)	167.2 (29.8)	-35.8	*p<0.0001*
CC100RP	Overstory	207.5 (2.3)	170.1 (10.6)	-18.0	*p<0.0001*
	CWD	52.6 (5.5)	35.1 (11.9)	-33.3	*p<0.0001*
	Total	260 (5.8)	205.2 (19.3)	-21.1	*p<0.0001*
OR200	Overstory	207.5 (2.2)	199.1 (2.9)	-4.0	*p<0.0001*
	CWD	51.9 (5.0)	46.8 (8.4)	-9.8	NS
	Total	259.4 (5.1)	245.9 (9.4)	-5.2	*p<0.0001*
OR100	Overstory	207.5 (2.3)	194.4 (4.1)	-6.3	*p<0.0001*
	CWD	52.0 (7.8)	44.7 (8.0)	-14.0	*p<0.0001*
	Total	259.5 (7.5)	239.1 (8.8)	-7.9	*p<0.0001*

The CC100N scenario experienced the greatest decreases in carbon in all scenarios, although it was not markedly different from the CC200N scenario. Overstory carbon in the CC200RP scenario decreased to a new equilibrium over about 100 years (Figure 5.11). Carbon in CWD displayed a similar trend, but with minor increases towards the end of the scenario run (Figure 5.12). Total carbon followed the same temporal pattern as overstory carbon, with a new equilibrium 35.8% lower than the undisturbed landscape (Figure 5.13,Table 5.5).

Overstory carbon in the CC100RP scenario achieved a new equilibrium relatively quickly, with minimal subsequent variation (Figure 5.11). Carbon in CWD was highly variable. This pool decreased sharply in the early harvest period, but increased slightly in the latter half of the 400-year harvest period (Figure 5.12). Total carbon varied around an equilibrium -21.1% lower than in the NOH scenario (Figure 5.13,Table 5.5).

The overstory retention scenarios (OR200 and OR100) were very similar in terms of pattern and the magnitude of reductions. Total carbon in OR200 and OR 100 declined relatively rapidly to a new equilibrium, with total reductions of 5.2% and 7.9% in the harvest period, respectively (Figure 5.13). CWD for both was more highly variable than the overstory pool. In the OR200 scenario, the CWD pool experienced an increase throughout the harvest period. The overstory retention scenarios resulted in the least reduction in the carbon pools among all scenarios (Table 5.5).

5.4 Discussion

Only two rotation lengths were tested in this research, which does not provide a complete picture of the response of the landscape to harvest frequency. However, it may be seen that the 200-year rotation did facilitate higher carbon storage on the landscape, but there was not a strong difference. The greatest difference attributable to rotation length was between the two clearcut-and-replant scenarios (Figure 5.14). A number of factors incorporated into the model account for this response. Of primary importance is that as the landscape is converted to predominantly younger stands through timber harvest, and younger stands have greater growth per time step than older stands. Figure 5.6 tracks changes in a single stand over the course of a CC100RP scenario. The quick recovery of the stand following timber harvest helps to explain overall model behavior. The response of the CWD pool to time following harvest also aids in understanding the overall model behavior. CWD is reduced following timber harvest due to a lack of inputs and continued decomposition. It reaches a low point about 40 years into the rotation, and then begins to recover as inputs from the overstory resume. This provides a compensation factor for the loss of older forest with higher biomass. Another important factor is that young stands (less than 80 years of age) in Fuegian Nothofagus forests are less susceptible to windthrow (Rebertus *et al.* 1997). Consequently, a landscape dominated by younger stands has high productivity and lower windthrow losses. Total carbon, however, is less than the no-harvest scenario because of the lower mean biomass in younger stands.

Removals of C through harvesting activities were highest where tree establishment was relatively immediate, either through seeding from a retained overstory or through planting. This allowed stands to reach harvestable age, and have relatively uniform biomass across the harvest unit. The low removals observed in the CC100N scenario can be explained by lower levels of biomass at harvest age due to regeneration encroaching slowly on the harvest unit.

The results of this modeling exercise indicate that spatial and temporal patterns of tree regeneration play a key role in long-term, landscape-scale carbon storage. When regeneration is immediate over the extent of a harvest unit, as in a uniform replanting, long-term carbon storage is enhanced. However, such successful planting, as implemented in the LANDIS-II model, is rare in real-world forest management. For the purpose of interpreting model results, the clearcut-and-replant scenarios at both 100 and 200-year rotations must be regarded as upper-bound estimates of what is possible in the Fuegian landscape. Browse by guanacos (Cavieres and Fajardo 2005), summer desiccation (Weischet 1985), competing vegetation such as grasses and shrubs (Chapter 3 of this dissertation), and other factors would likely reduce the actual efficacy of artificial regeneration in the Fuegian landscape. Another variable that could not be incorporated into these model runs was the inclusion of the patchy advanced regeneration that may be found in Chilean *Nothofagus* forests (Donoso Zegers 1993; Rebertus and Veblen 1993; Veblen *et al.* 1996).

Seed dispersal has the ability to influence model outcomes in LANDIS-II and other ecological models (He and Mladenoff 1999), justifying further research on this topic in *Nothofagus* forests. The results presented here are likely fairly sensitive to the mean and maximum seeding distance parameters, since there was such a great difference between the replanting scenarios and the scenarios where regeneration was dependent on seed dispersal.

LANDIS-II, like all models, require numerous assumptions and is limited by how much detail can be incorporated into simulations of actual landscapes (Turner *et al.* 2001). For example, partial wave disturbance, a pattern of the wind disturbance regime observed in Tierra del Fuego (Rebertus and Veblen 1993), is not represented by the wind disturbance module in LANDIS-II. However, small gap formation (Rebertus and Veblen 1993) could be incorporated to an acceptable degree into the model runs by setting the minimum wind event size to the level of the pixel (60m by 60m, or 0.36 ha). The mean area of wind disturbance events calculated from Rebertus and Veblen (Rebertus *et al.* 1997) was 11 ha, which means that a number of wind events were relatively small (1-11 ha). This would capture some of the intra-stand variation due to windthrow that is characteristic of Fuegian forests.

Clearcutting blocks of the size utilized in the simulation runs had variable impacts on carbon storage. The influence of clearcutting mostly depended on the type of regeneration to follow harvest. If managers relied on natural regeneration, then landscape-scale reductions in carbon storage were most drastic with the clearcutting option. An overstory-retention approach retained both stored carbon and assimilative potential in the standing trees, retained a source of future coarse woody debris, and maintained a seed source spatially distributed over the harvest unit. Other research has demonstrated that partial harvesting instead of clearcutting can enhance forest carbon storage. For example, (Neilson *et al.* 2006) showed that carbon assimilation was enhanced in a partial cut in comparison to a clearcut in boreal mixed forest.

The carbon pool represented by CWD was relatively variable compared to the overstory carbon pool. This may be related to the stochastic nature of windthrow in the LANDIS-II model. The long term proportions of stand biomass represented by CWD produced by the model are consistent with observations of actual *Nothofagus* stands in Tierra del Fuego (Gutiérrez *et al.* 1991). The amount of CWD in landscapes depends upon species-specific primary productivity, decay resistance, and mortality patterns, in addition to exogenous disturbance factors (Harmon *et al.* 1986). All of these factors can be parameterized in LANDIS, and reproduction of observed CWD levels by the model is an important validation of the model for the Fuegian landscape, given the number of processes influencing CWD.

The results of this modeling exercise indicate that CWD is more responsive to forest management activities than the overstory. This is likely related to the changing susceptibility of forest stands in the model to windthrow as a function of stand age. A shift in the age class distribution in the landscape may change the proportion of the landscape in the 100-150 year age class, where windthrow (and therefore CWD inputs) is highest. CWD has been demonstrated by other investigators to be responsive to different forest management regimes, including in boreal forests (Sturtevant *et al.* 1997; Rouvinen *et al.* 2002), conifer forests in the Pacific Northwest (Franklin *et al.* 2002; Janisch and Harmon 2002), and *Nothofagus* forest in other parts of Chile (Carmona *et al.* 2002). While this modeling exercise demonstrates the potential for forest management to influence CWD levels, it is critical that field research be carried out in the future to determine actual dynamics of CWD in response to timber harvest and other management activities.

The poor dispersal characteristics of *Nothofagus* (Donoso 1996) had important consequences for carbon storage, since clearcut units slowly filled in from the edges. It may be argued that planting would accelerate this process. However, harsh microclimatic conditions in Tierra del Fuego frequently cause regeneration mortality in the center of disturbed areas (Kalin-Arroyo 1996), so that the spatial pattern of regeneration may well be dominated by encroachment even with planting efforts. The overstory retention scenario avoided this problem by maintaining a seed source on site in all units. In the actual landscape, the protective effects of a retained overstory would also enhance survival and productivity (Martinez-Pastur *et al.* 1997), but this phenomenon could not be incorporated into LANDIS-II at the time of this research. The shelterwood scenario results can therefore be considered conservative.

An important limitation of this research is that climate will almost invariably undergo changes over the temporal scales represented in the simulations. Primary productivity and decomposition rates are temperature- and moisture-sensitive processes (Harmon *et al.* 2004), and climate shifts that can occur on the scale of centuries may significantly influence net carbon balances (Goulden *et al.* 1998; Larocque *et al.* 2006). Wind disturbance may also be affected by climate change (Dale *et al.* 2001) influencing the distribution of age classes on the landscape and consequently altering carbon storage. Although not incorporated into the model scenarios in this research, fire (anthropogenic or naturally ignited) may also play an increasingly important role in the future carbon dynamics of Tierra del Fuego. The frequency and intensity of fire is at least partially dependent upon climate (Gedalof *et al.* 2005) and anticipated climatic warming may result in a greater importance of fire in the Fuegian landscape, likely reducing long-term carbon storage.

The results suggest that timber harvest can influence forest carbon storage at the landscape level in the *Nothofagus* forests of Tierra del Fuego, Chile. In addition, the frequency of harvest is an important factor in determining the equilibrium level of forest carbon storage in the harvested landscape, but other factors, such as spatial pattern of harvest, regeneration method and retention of structures, may be equally important. Conversion of landscapes to a regulated, continuously harvested state may cause this equilibrium to move to a new steady state with lower amounts of carbon retained in the landscape. Reductions in carbon storage with the initiation of a harvest regime have been observed at the stand level (Harmon *et al.* 1990), but it is important to be able to assess carbon-related impacts on larger spatial scales (Kurz *et al.* 2002). With the possible emergence of a forest carbon market as a result of the Kyoto Protocol and related policy measures, it may become important to quantify the impacts of timber harvest on forest carbon storage. The results of a modeling exercise such as this one can be used to guide decision-making regarding the type and frequency of timber harvest in a landscape if management of the forest carbon resource is among the landowner's objectives.

5.5 Conclusions

The imposition of a timber harvest regime on a natural wind disturbance regime leads to changes in both specific woody carbon pools such as live overstory and CWD, and in the average amount of carbon stored on a per-hectare basis. CWD was relatively responsive to management effects, which suggests that it is an important pool to consider in both modeling and in ecosystem monitoring. The simulations in this research also indicated the importance of tree regeneration, both natural and artificial, in long-term carbon storage. Assumptions of successful artificial regeneration may lead to overestimates of potential carbon storage, however.

Furthermore, this research clarified the necessity of accurate information on disturbance regimes, the autecology of primary tree species, and productivity and mortality to predict the effects of timber harvest on a forested landscape. A spatially and temporally-explicity model such as LANDIS-II can be a powerful tool for understanding the relative impacts of management decisions on landscape carbon balance.

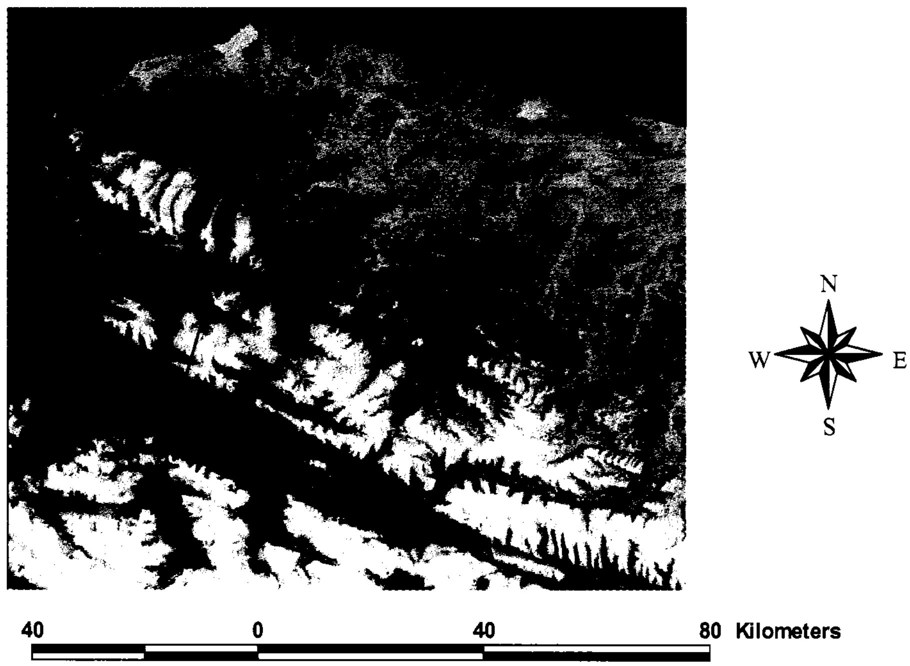

Figure 5.1 Southwest Tierra del Fuego, Chile, with area used for LANDIS modeling outlined in red.

Figure 5.2 Sample of imagery corrected with SCS+C topographic normalization procedure.

ASTER Band 3 (NIR, 0.76-0.86 μm). Image on left is uncorrected image. Image on right has been corrected.

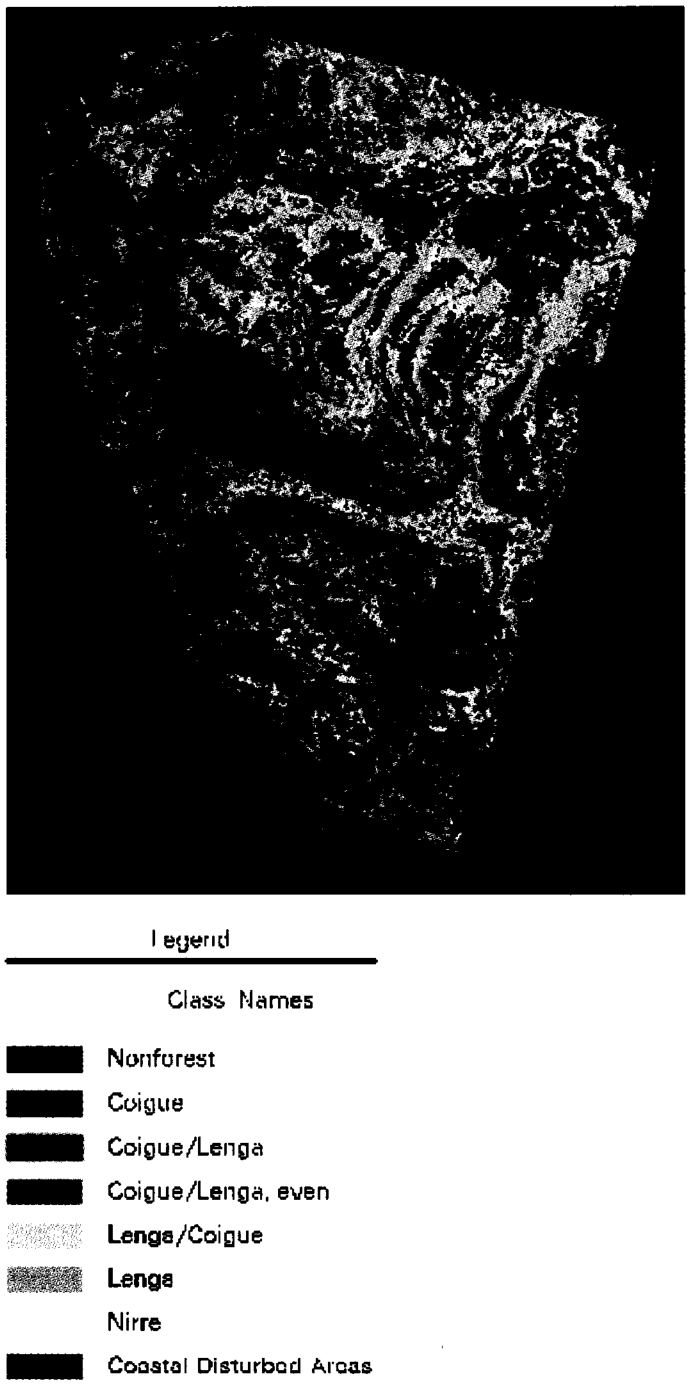

Figure 5.3 Initial community composition from unsupervised classification. These were used to define ecoregions.

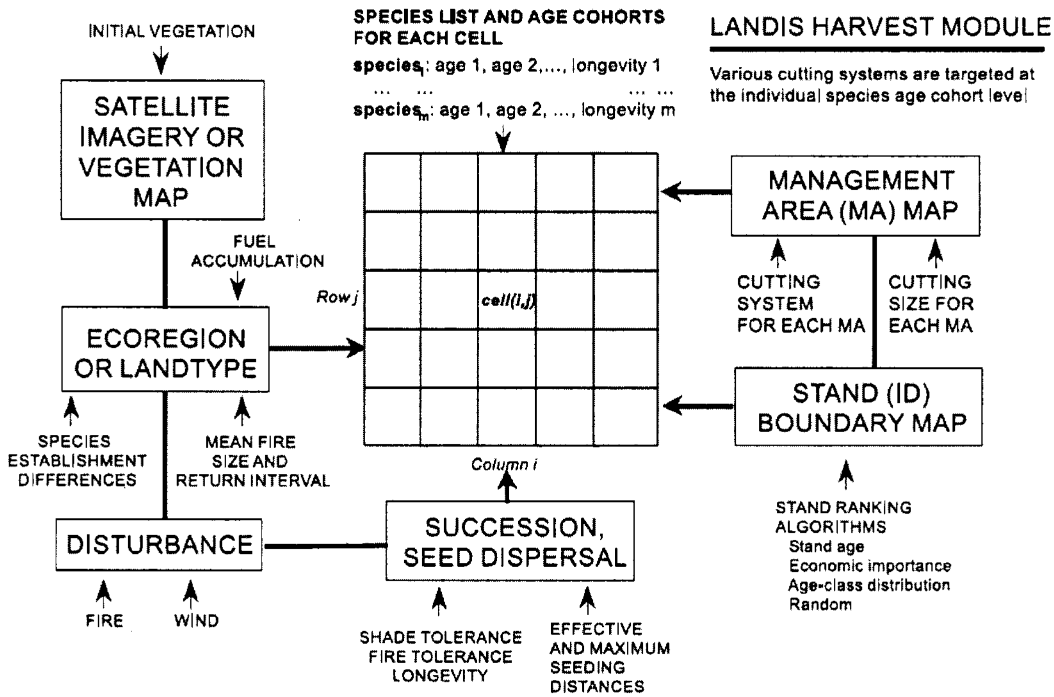

Figure 5.4 LANDIS-II model architecture.

Reproduced from (Gustafson *et al.* 2000).

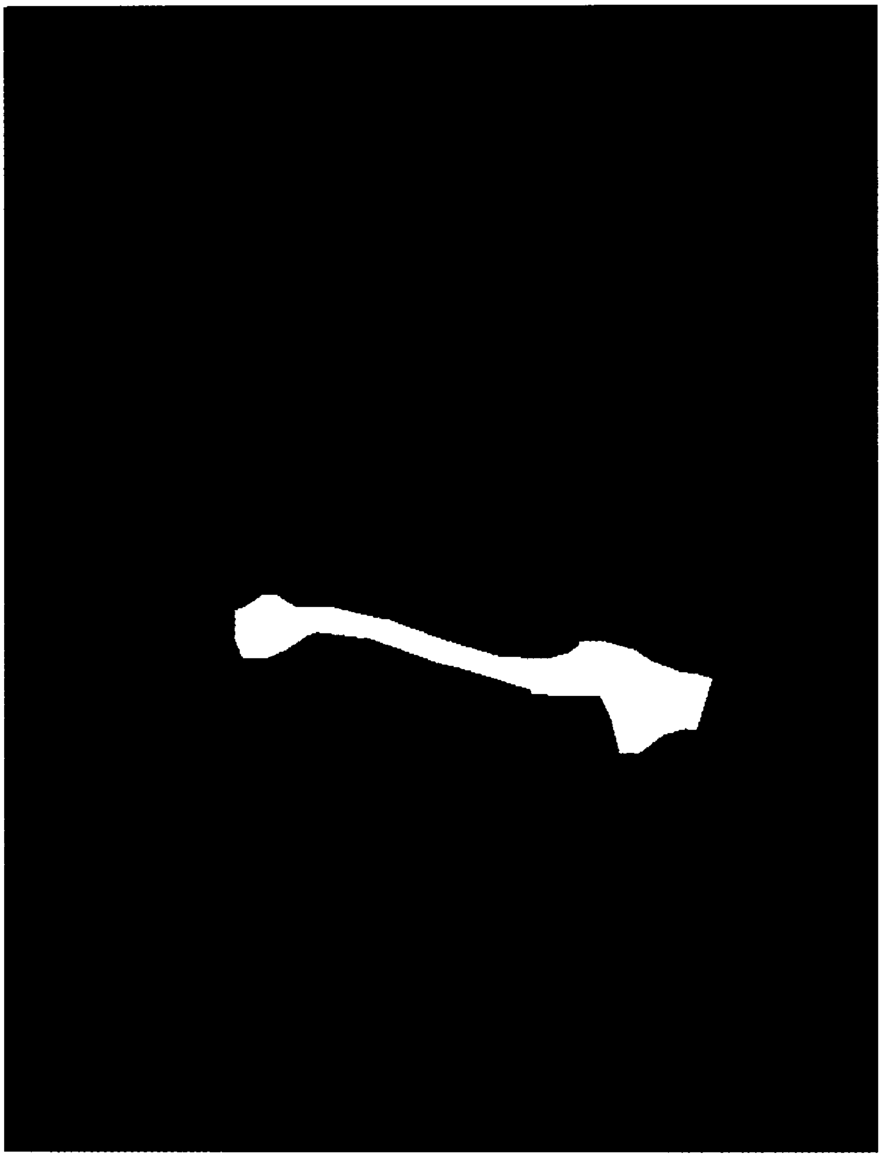

Figure 5.5 Division of landscape into stands and management areas.

Stands are delineated by black lines. Dark green = coastal management area. Light green = interior management area. Yellow = Río Condor floodplain (no harvest). Orange = Magellanic moorland (no harvest).

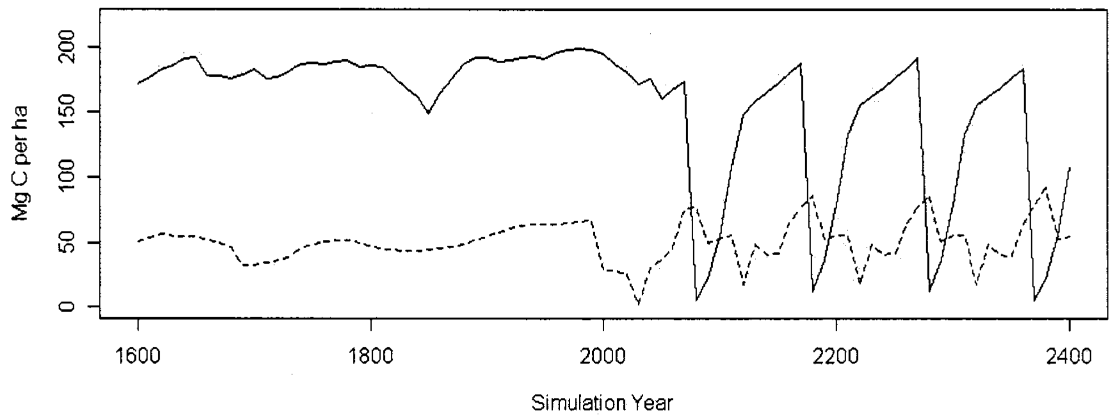

Figure 5.6 Overstory and CWD carbon in a single coastal coigue stand over the course of a simulation run.

Solid line represents carbon in live trees. Dashed line represents carbon in CWD (downed wood + snags).

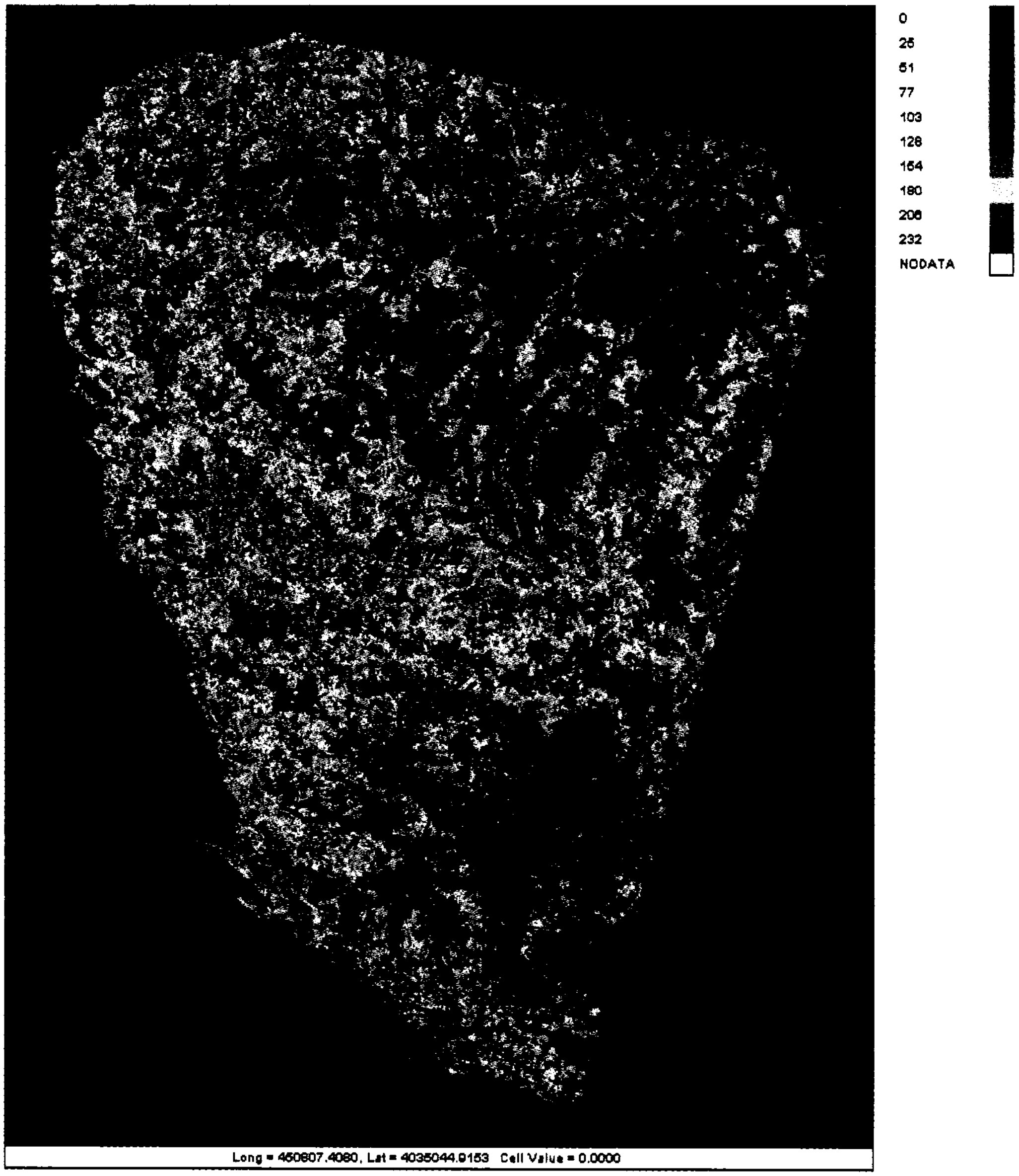

Figure 5.7 Output map for overstory (converted to carbon). NOH scenario.

Simulation year 2360. Units are Mg biomass per 0.36 ha pixel.

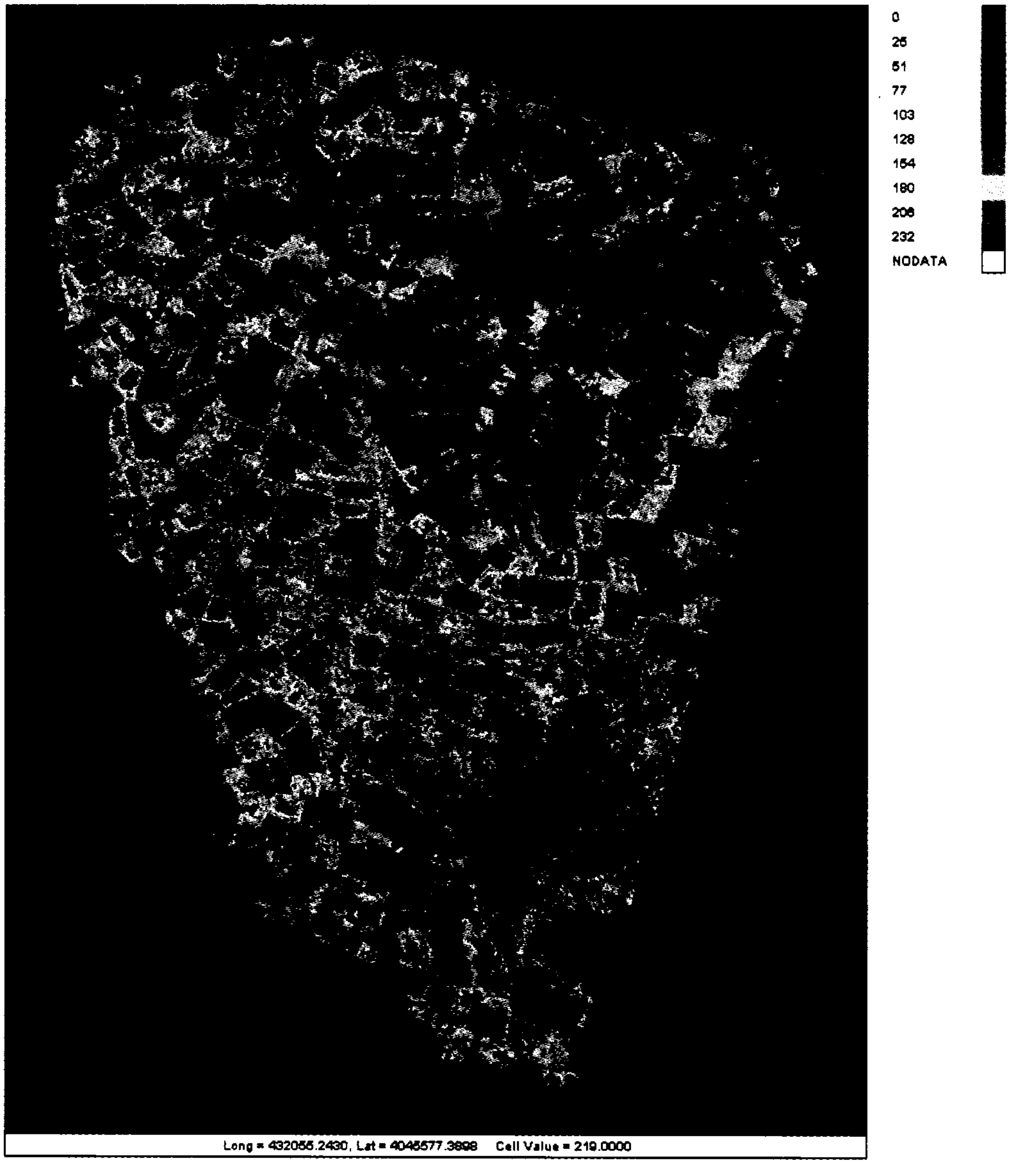

Figure 5.8 Output map for overstory biomass. CC100N scenario.

Simulation year 2360. Units are Mg biomass per 0.36 ha pixel.

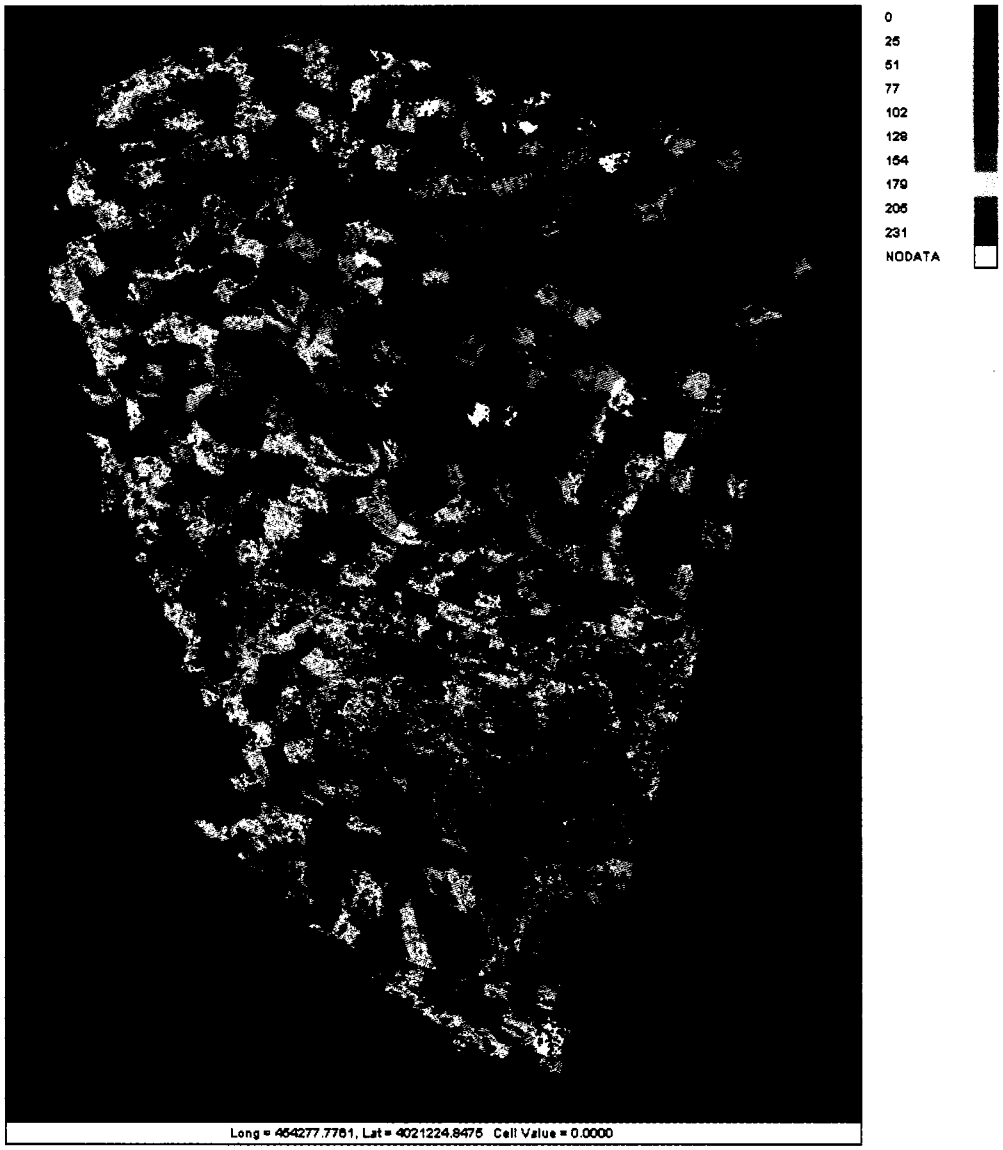

Figure 5.9 Output map for overstory biomass. CC100RP scenario. Simulation year 2360. Units are Mg biomass per 0.36 ha pixel.

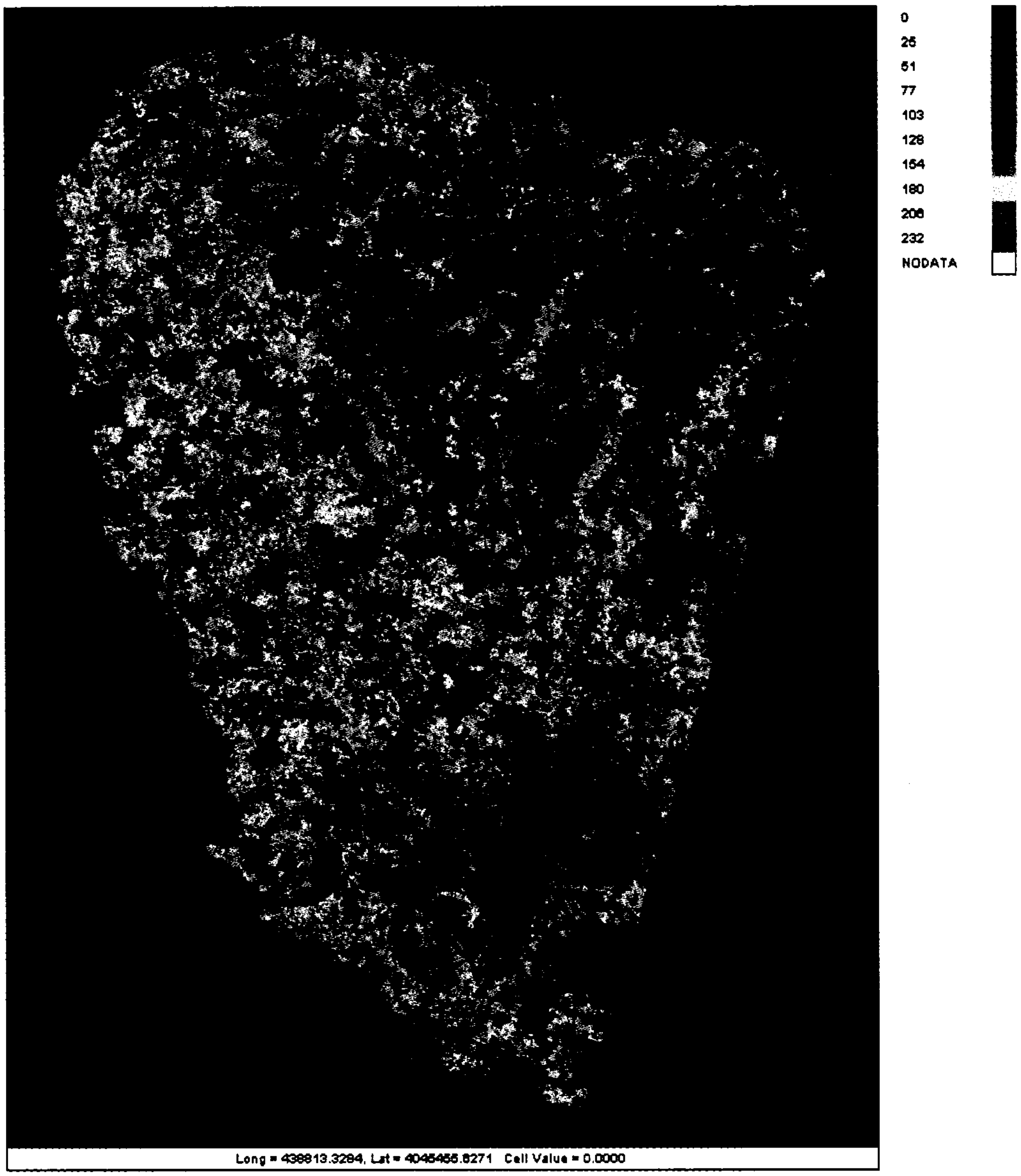

Figure 5.10 Output map for overstory biomass. OR100 scenario. Simulation year 2360. Units are Mg biomass per 0.36 ha pixel.

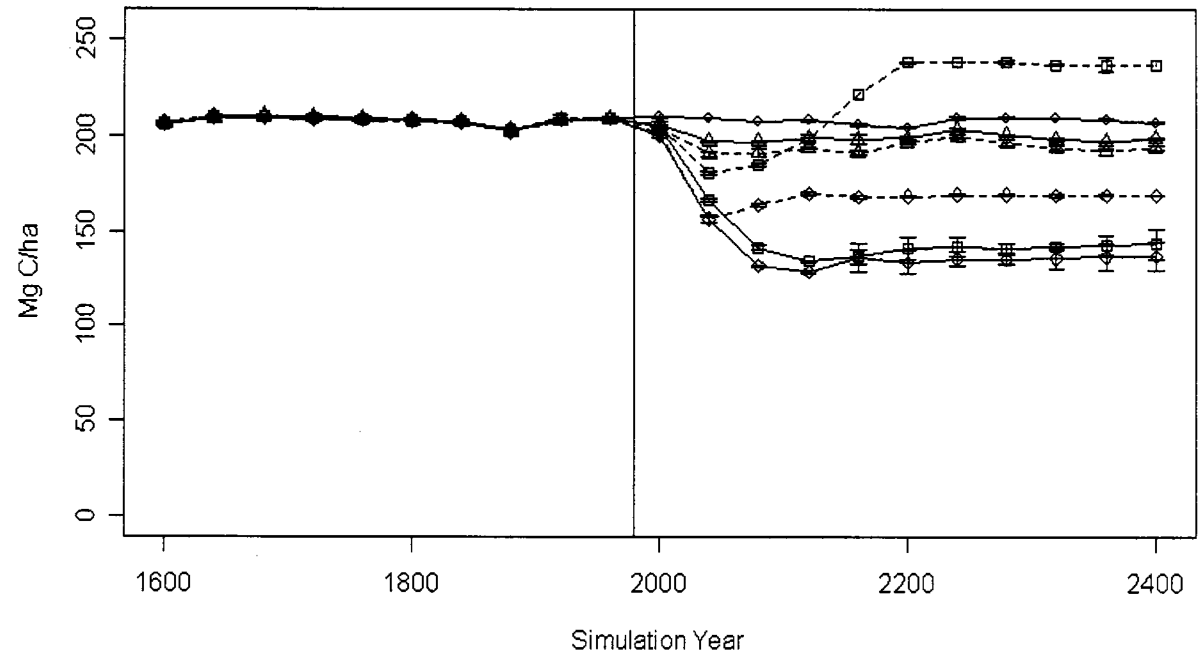

Figure 5.11 Overstory carbon stocks, average per hectare.

NOH: circles. CC200N: squares, solid line. CC200RP: squares, dashed line. CC100N: diamonds, solid line. CC100RP: diamonds, dashed line. OR200: trianges, solid line. OR100: triangles, dashed line. Error bars represent ±1 standard deviation.

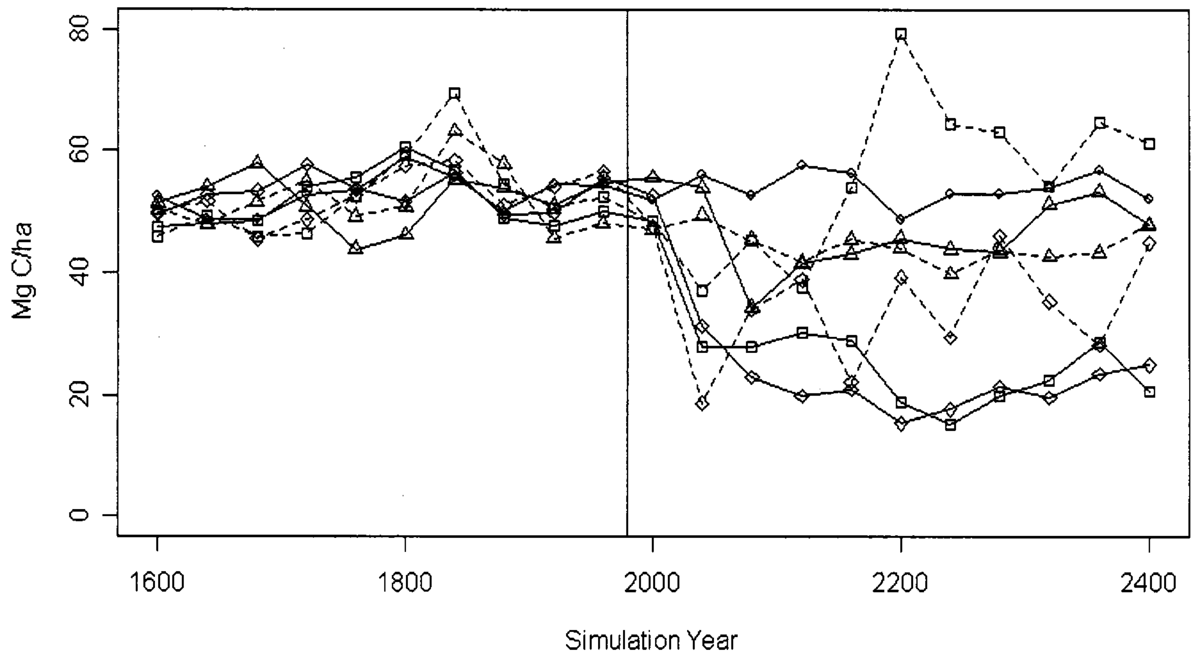

Figure 5.12 CWD carbon stocks, average per hectare.

NOH: circles. CC200N: squares, solid line. CC200RP: squares, dashed line. CC100N: diamonds, solid line. CC100RP: diamonds, dashed line. OR200: trianges, solid line. OR100: triangles, dashed line. Error bars omitted for clarity.

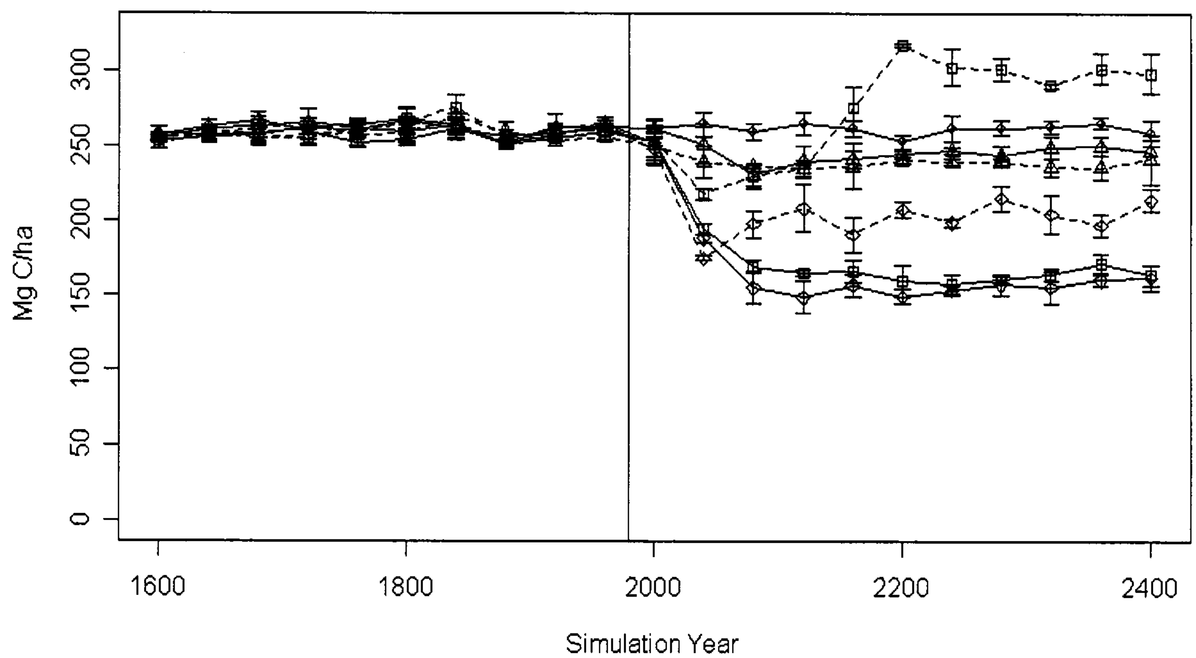

Figure 5.13 Total (live overstory + downed wood/snags) carbon, average per hectare.

NOH: circles. CC200N: squares, solid line. CC200RP: squares, dashed line. CC100N: diamonds, solid line. CC100RP: diamonds, dashed line. OR200: trianges, solid line. OR100: triangles, dashed line. Error bars represent ±1 standard deviation.

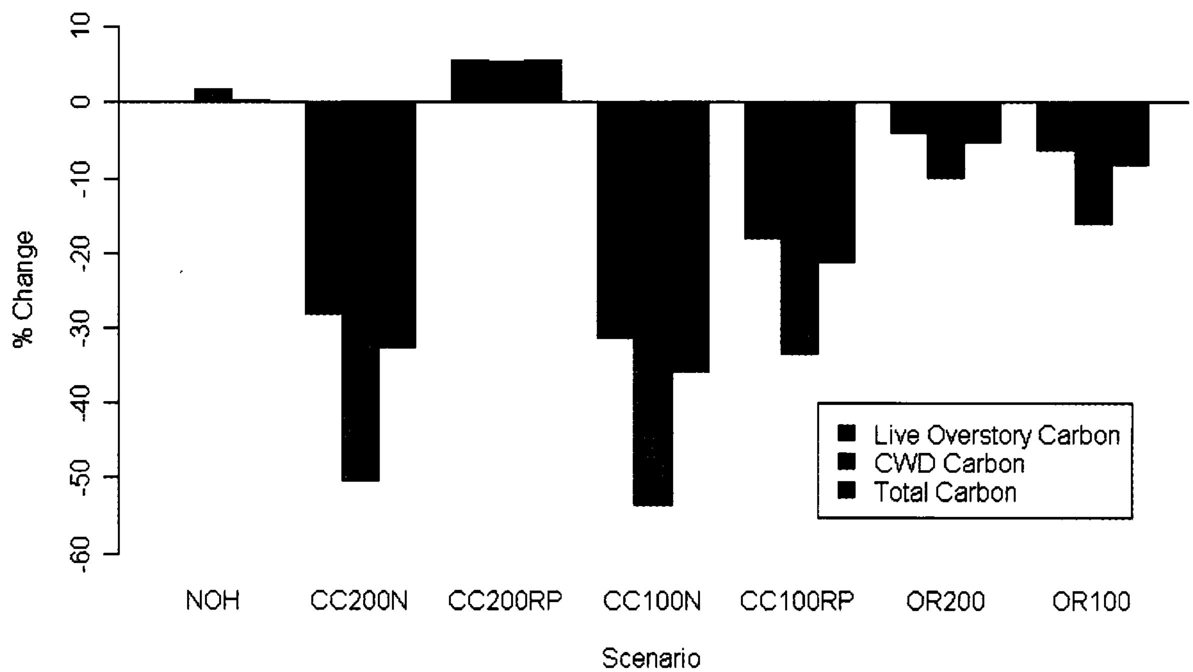

Figure 5.14 Percent change in carbon pools under different management scenarios over a 400-year treatment period.

Chapter 6. Concluding Remarks

This research is comprised of four studies addressing different aspects of the characteristics of forest carbon in the *Nothofagus* forests of Tierra del Fuego. The scope of the analysis presented ranges spatially from the scale of the individual piece of CWD to entire landscapes, and temporally from an instantaneous sample of current forest landscape carbon to projections of forest carbon over hundreds of years of disturbance and timber harvest. The results of each individual research segment make a contribution towards understanding forest carbon and its management in the *Nothofagus* forests of Tierra del Fuego.

In Chapter 2, I addressed the amount of carbon stored in natural stands, stored in three separate pools: overstory, CWD, and the organic layer of the soil. The results suggest that CWD is an important pool of carbon and other nutrients in these forests, and that the structure of the woody debris pool reflects overstory dynamics. Values for tissue density, carbon content, and nutrient content of woody debris produced in this research may be utilized in future work in this regionally important forest type. Some of the results of this work, for example, provided data for the analysis in chapters 3 and 4.

In Chapter 3, I assessed edge effects in anthropogenically burned areas in Tierra del Fuego, examining plant species composition and substrates of three representative locations. Regeneration of forest trees is progressively limited with distance from the forest edge into burned areas. This suggests that burned areas face a protracted recovery to closed forest, indicating a lost opportunity for storing carbon over time on these sites.

In Chapter 4, I established the importance of topography as an influence on forest carbon storage. The approach employed may be used in any forested landscape with significant relief to determine the magnitude of changes in forest carbon storage over space.

In Chapter 5, I demonstrated the potential changes in forest carbon storage resulting from various forest management scenarios. The small-medium scale nature of disturbance in the *Nothofagus* forests of Tierra del Fuego means that the landscape may be considered to exist in a relative steady state, offering an opportunity for examination of departures from this steady state as a function of management.

Several major themes recurred in this dissertation. Coarse woody debris is an important structure in Fuegian *Nothofagus* forests, and merits consideration in planning for the optimization of many forest values, including managing for carbon sequestration. Regeneration is relatively limited in large disturbed areas when compared to many other ecosystems, and seed dispersal and other issues related to the spatial pattern of regeneration must be understood to predict long-term ecosystem dynamics.

Further research is needed on a number of topics. Greater understanding of *Nothofagus* regeneration dynamics is needed, especially in response to silvicultural treatments. Spatial patterns of regeneration, in particular, merit further research. Long-term permanent plot observations will be needed to partially validate the results of the modeling exercise.

Climate change and its impact on ecosystems is a major societal concern. Understanding the nature of carbon storage in the forest ecosystems of the world, and the impacts of human activities on this important ecosystem service, is a key component of strategies to mitigate the forcing factors involved in climate change. This research represents one method of approaching this task.

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Appendix A. Concentrations (μg g^{-1}) of major nutrients for the two primary *Nothofagus* species on Tierra del Fuego.

Nothofagus betuloides (Mirb.) Oersted. Coigüe de Magallanes; coihue; guindo.						
Decay Class	*P*	*K*	*Ca*	*Mg*	*Na*	*S*
1	306.0 ±46.2	663.8 ±154.1	2619.5 ±727.6	316.3 ±47.3	157.4 ±56.1	133.3 ±6.8
2	339.6 ±288.9	862.0 ±836.5	2565.8 ±521.2	340.4 ±113.0	215.3 ±119.1	134.3 ±54.1
3	127.6 ±20.6	234.7 ±51.4	805.7 ±227.2	170.3 ±66.5	118.0 ±15.9	135.4 ±24.8
4	279.1 ±239.6	714.2 ±374.7	4359.3 ±1704.7	1355.3 ±558.9	319.6 ±25.1	443.4 ±350.8
5	187.8 ±69.7	780.0 ±361.2	2520.4 ±151.5	712.2 ±255.9	434.4 ±341.8	281.8 ±61.2
Nothofagus pumilio (Poeppig & Endl.) Krasser. Lenga; roble de Magallanes.						
Decay Class	*P*	*K*	*Ca*	*Mg*	*Na*	*S*
1	112.4 ±127.8	324.9 ±396.5	392.3 ±195.2	90.4 ±78.2	377.4 ±42.3	122.7 ±14.0
2	35.2 ±39.3	126.5 ±63.5	402.8 ±280.2	121.9 ±91.1	432.7 ±48.7	117.3 ±21.2
3	49.8 ±65.7	424.7 ±327.4	629.3 ±524.6	145.8 ±128.3	508.0 ±59.4	147.5 ±71.5
4	231.1 ±129.6	619.0 ±159.6	3261.3 ±1448.6	676.2 ±470.4	669.7 ±192.3	337.8 ±125.8
5	344.4 ±178.0	563.1 ±191.3	2479.3 ±1134.8	506.3 ±245.8	544.1 ±95.2	367.0 ±139.4

All values are means, ± one standard deviation.

VITA

Mark Ellyson Swanson was born in Redlands, California. Both parents served with pride and distinction in the United States Air Force, and the family moved frequently during the first half of Mark's life. Mark graduated from high school in Cupertino, California, and earned a Bachelor of Science in Forest Management from the University of Washington, Seattle, Washington. After a year of work as a science technician, he enrolled in the Master of Science program in Forest Ecosystem Analysis. With permission of his committee and the College of Forest Resources, he extended this degree program into a doctorate. His work has ranged from the study of post-disturbance plant communities to the use of geospatial technologies in forest science and management.