

AN ABSTRACT OF THE THESIS OF

Laura Angélica Fuentes-Rodríguez for the degree of Master of Science in Forest Ecology presented on December 2, 1993.  
Title: Factors Influencing Growth of Young Douglas-fir and Red Alder in the Oregon Coast Range: Interference, Nitrogen Availability, and Animal Damage.

Abstract approved: \_\_\_\_\_  
Dr. Timothy B. Harrington

Red alder (Alnus rubra Bong.) is a common associate and a potentially severe competitor of Douglas-fir (Pseudotsuga menziesii var. menziesii [Mirb.] Franco) in the Oregon Coast Range. However, because it fixes nitrogen and increases rates of soil nutrient cycling, red alder has the potential to benefit Douglas-fir. The objective of this study was to quantify and attempt to explain differences in growth of young Douglas-fir and red alder, growing in mixed and pure stands, by analyzing six-year trends in survival, growth, animal damage of saplings, cover of understory vegetation, and foliar and soil nutrients.

In March 1986, a replacement series study was established by planting Douglas-fir and red alder at 3-m spacing in 0.073-ha plots with the following species

proportions (Douglas-fir/red alder): 1/0, 0.9/0.1, 0.7/0.3, 0.5/0.5, 0.25/0.75, 0/1. Each proportion was replicated three times in a randomized complete block design. Six annual measurements (fall 1986-1991) of survival, growth, and animal damage and one measurement of stand yield (1991 basal area, volume, and predicted biomass) were used in response surface analyses to test for significant polynomial relationships ( $\alpha=0.05$ ) between tree response and species proportion.

Relationships of Douglas-fir height increment to red alder proportion varied from positive linear (year 2) to no relationship (years 3-4) to negative linear (years 5-6). Relationships of Douglas-fir diameter increment to red alder proportion varied from no relationship (years 2-3) to negative linear (year 4) to negative quadratic (years 5-6).

In the sixth year, competition from red alder caused relative yield (relative to monoculture yield) of Douglas-fir volume index and predicted biomass to be significantly less than the yield that would be expected in the absence of intraspecific competition (expected yield). Increasing proportion of Douglas-fir decreased intraspecific competition of red alder, and as a result, relative yield of basal area and predicted biomass for red alder was significantly greater than its expected yield.

Two measurements (March 1986 and 1991) of mineralizable nitrogen ( $\text{NH}_4$  and  $\text{NO}_3$ ); total N, P, and C; and pH from 3 soil depths (0-15, 15-30, and 60-90 cm) were

used in analysis of variance to test for significant differences ( $\alpha=0.05$ ) in sixth-year amount and five-year change in these variables among three species proportions (Douglas-fir/red alder): 1/0, 0.5/0.5, and 0/1. There was no net N accretion; however, there was higher mineralizable N as  $\text{NH}_4$  in pure Douglas-fir stands than in mixed stands. One explanation for these results is that possibly the more open conditions of Douglas-fir stands increased rates of N mineralization. Douglas-fir foliar N and P also were significantly higher in pure stands than in mixed stands, probably because of the increased ability of large, vigorous saplings growing in absence of red alder to absorb soil nutrients rather than because of greater supplies of soil nutrients. The effect of increased Douglas-fir vigor and size in enhancing nutrient uptake was more prominent for P than for N.

These data indicate that the effects of red alder on Douglas-fir can range from positive to neutral to negative. In general, competition was the most important factor limiting survival and growth of Douglas-fir; animal damage and understory vegetation under red alder canopies caused further limitations in Douglas-fir response. In addition, results of this research suggest that red alder competition can be tolerated with little loss of Douglas-fir survival and growth through an age of 4 years.

Factors Influencing Growth of Young Douglas-fir and Red  
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Availability, and Animal Damage  
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Laura Angélica Fuentes-Rodríguez

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Signature redacted for privacy.

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Professor of Forest Science in charge of major

Signature redacted for privacy.

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Head of Department of Forest Science

Signature redacted for privacy.

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Dean of Graduate School

Date thesis is presented December 2, 1993

Typed by Laura Angélica Fuentes-Rodríguez

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Factors Influencing Growth of Young Douglas-fir and Red Alder in the Oregon Coast Range: Interference, Nitrogen Availability, and Animal Damage

I. Introduction

A. Statement of the Problem

1. High Productivity of Oregon Coast Range Results in Extreme Competition Between Douglas-fir and Red Alder

Competing vegetation is believed to be one of the most important factors influencing the survival and growth of Douglas-fir (Pseudotsuga menziesii var. menziesii [Mirb.] Franco) seedlings in western Oregon (Cleary et al. 1978 from Wagner and Radosevich 1991b). Management of competing vegetation has become a routine silvicultural practice to ensure successful establishment of conifer plantations in the Pacific Northwest (Walstad and Kuch 1987). In this region, artificial regeneration of Douglas-fir is often limited or completely replaced by its common associate, red alder (Alnus rubra Bong.) (Hermann and Lavender 1990).

Red alder is the major hardwood species in the coastal forests of the Pacific Northwest. Its rapid occupation of

disturbed forest land and fast early growth make it appear as an unwelcomed competitor of the highly valued Douglas-fir (Bormann and DeBell 1981). When red alder reproduces naturally on upland sites, where it is unlikely to attain commercial size, it may seriously impede establishment of other tree species (Tarrant 1961). On sites of average productivity, Douglas-fir and red alder can attain the same height at an age of about 45 years (Harrington 1990).

## 2. Both Douglas-fir and Red Alder are Commercial Species

For more than a century, Douglas-fir has been the principal tree species used by the forest industry in the coastal Pacific Northwest. Old-growth logs provided a superior raw material, especially for sawmills and plywood plants (Tarrant et al. 1983). Periodic recurrence of catastrophic wildfires created vast, almost pure stands of coastal Douglas-fir throughout its range north of the Umpqua River. Although logging has mostly eliminated the original old-growth forest, clearcutting combined with slash burning, and artificial regeneration have helped maintain Douglas-fir as the major component in second-growth stands.

Red alder is a fast growing pioneer species in forested areas of the Pacific Northwest. It has invaded many areas after disturbances, and in 1988 it covered about 13 percent of the commercial forest land in western Oregon and Washington (Resch 1988). Over the last two decades, the value of red alder lumber has increased and the hardwood industry has expanded (Puettmann et al. 1993).

### 3. Red Alder is a Nitrogen-Fixing Species with Potential to Benefit Douglas-fir

In the majority of Douglas-fir stands in the Pacific Northwest, growth is limited by the amount of available nitrogen in the soil. Productive Douglas-fir stands apparently require 40 to 100 kg N/ha per year. Nitrogen in the soil of commercial forests ranges from 2,000 to more than 20,000 kg/ha, but practically all of this is in living organic matter or organic residues and is not readily available to plants. Each year, a small fraction of this is mineralized to inorganic nitrogen which is available to plants, as well as competing micro-organisms (Miller et al. 1976).

Red alder is a nonleguminous, nitrogen-fixing tree species (Tarrant et al. 1969). Because of its characteristics of rapid juvenile growth, ability to

improve soil fertility and structure, a presumed capacity for rapid genetic improvement, and suitability for a wide range of products, red alder has a potential value in intensively managed forests (Tarrant et al. 1983).

Miller and Murray (1978) studied the long-term effects of off-site red alder which were interplanted with 4-year-old Douglas-fir in 1933. They found increases in height and diameter of Douglas-fir because of the associated red alder. Interplanting of red alder seems to be a possible silvicultural treatment for increasing yields of Douglas-fir on nitrogen-deficient sites. Miller and Murray (1978), Binkley (1982), and Binkley and Greene (1984) have shown that red alder increased Douglas-fir growth and foliar nitrogen content on nitrogen-deficient sites. However, on nitrogen-rich sites Douglas-fir growth was reduced and foliar nitrogen content was not affected (Cole and Newton 1986).

## B. Objectives

Although the nitrogen accretion by red alder in mixed stands has been extensively studied (Tarrant 1961, Tarrant et al. 1969, Bollen and Lu 1968, Miller and Murray 1978, Binkley et al. 1982, Binkley 1984), the relationship between Douglas-fir foliar nitrogen and soil nitrogen in the presence and absence of red alder is not well known. In addition, limited research exists in which the effects of a range of Douglas-fir/red alder species proportions are studied using a systematic design, such as a replacement series. This study attempts to explain the reasons for observed differences in growth of young mixed stands of Douglas-fir and red alder. Hypotheses tested relate to causes of these growth differences and can be grouped into those due to: (1) competition between trees and with understory vegetation, (2) tree injury due to deer and elk browse, and (3) soil nitrogen accretion by red alder. Therefore, the specific objectives of the study were to:

1. Quantify the effects of red alder species proportion and understory vegetation on survival and growth of Douglas-fir.

2. Determine if deer and elk damage was an important factor in limiting growth of Douglas-fir and red alder.



3. Determine if differences in growth of young Douglas-fir are associated with increases in soil nitrogen from the presence of red alder.

4. Test relationships of foliar nitrogen and phosphorus content of Douglas-fir to indices of soil nitrogen, phosphorus, carbon, and pH which may have been influenced by the presence of red alder.

## II. Influences of Interference and Animal Damage on Survival and Growth of 1- to 6-year-old Douglas-fir and Red Alder in the Oregon Coast Range

### A. Introduction

During early succession, growth of coastal Douglas-fir can be strongly influenced by associated woody and herbaceous vegetation, depending upon vegetation abundance, size, and proximity (Wagner and Radosevich 1991a). Red alder is one of the tree species most commonly found in association with Douglas-fir due to its characteristic ability to rapidly invade sites following disturbances such as logging and fire (Harrington 1990).

Clearcutting is a common harvesting method for Douglas-fir. Clearcuts, usually 40-60 acres in size, are generally slash-burned and then planted, providing opportunities to, at least partially, control the composition of the new stand. These harvested areas are generally reforested by planting of bare-root Douglas-fir seedlings, resulting in survival rates that often exceed 80% (Tesch and Helms 1992).

Disturbances associated with logging and burning favor the establishment of red alder (Harrington 1990). In fact, the largest concentration of red alder stands in western

Oregon is found on mesic sites with a history of scarification or fire (Newton et al. 1968). Red alder is one of the most widely distributed hardwoods in the Douglas-fir region of the Pacific Northwest. It occurs as pure stands and attains merchantable size on moist bottom-land sites. On upland sites at elevations above 3,000 feet, it is also abundant throughout the region as a noncommercial tree (Tarrant 1961). A potential advantage of red alder is its nitrogen-fixing ability, which may lead to significant accretion of this element in soils where nitrogen is limiting tree growth (Cole et al. 1978).

### 1. Successional Relationships

In the moist Oregon Coast Range, overtopping vegetation is considered a severe obstacle to Douglas-fir regeneration on clearcut sites. In some cases, the fast-growing red alder and salmonberry (Rubus spectabilis) overtake the Douglas-fir trees (Chan and Walstad 1987). The suppression of Douglas-fir which can result from red alder competition may outweigh any positive effects of red alder on soil availability (Cole and Newton 1986, 1987).

Red alder's juvenile height growth is more rapid than the initially slower-growing conifer species (Miller and Murray 1978). On good sites, first-year red alder

seedlings may be 18 inches tall (Worthington 1957, from Tarrant 1961). Five-year-old alders may be 15 feet in height, and within 10 years their height may reach 35 to 40 feet (Worthington 1957, from Tarrant 1961). By age 20, their height may exceed 80 feet (Harrington and Curtis 1986). Both Douglas-fir and red alder can attain the same height at about 45 years of age on an average site (Harrington 1990).

On well-stocked sites of high quality, mean annual increments may approach 150 ft<sup>3</sup> per acre for 20- to 40-year rotations (Tarrant et al. 1983). In the Oregon Coast Range, a 12-year-old stand of red alder averaged 5.4 inches in dbh (diameter at breast height) (Tarrant et al. 1983), while unmanaged natural stands do not normally reach this size until an age of about 20 years. Twenty-six-year-old trees in western Washington, thinned to a spacing of 16 ft. by 16 ft. at age 7, averaged 11.2 in. in diameter. However, trees in natural stands typically do not attain this size until they are about 36 years old (Tarrant et al. 1983).

## 2. Factors Affecting Growth

The availability of resources on a site and the ability of trees to use them determines a tree's growth rate. Thus, both intraspecific and interspecific competition can decrease resource availability, reducing tree growth below that of trees existing without competition (Cole and Newton 1987). Intraspecific competition has been shown to reduce leaf area, height, basal diameter and biomass of red alder (Giordano 1990). Bormann and Gordon (1984) found that red alder density affects average tree dimensions. Average dbh, volume, branch surface area, and number of shoots were greatest in trees growing in open stands. High densities limited allocation of photosynthates to  $N_2$  fixation.

The performance of Douglas-fir in mixture with red alder varies with site fertility and species proportions (Binkley 1984). Binkley (1984) found that Douglas-fir stem growth per unit of leaf area was increased by its association with interplanted Sitka alder (Alnus sinuata) and red alder. Miller and Murray (1978) studied the long-term effects of off-site red alder which were interplanted with 4-year-old Douglas-fir in 1933. They found increases in height and diameter of Douglas-fir because of the associated red alder. Their results suggested that interplanting of red alder could be a possible

silvicultural treatment for increasing yields of Douglas-fir in nitrogen-deficient soils. While on nitrogen-deficient sites red alder increased Douglas-fir growth and foliar nitrogen, on nitrogen-rich sites Douglas-fir growth was reduced and foliar nitrogen content was not affected by mixtures with red alder (Miller and Murray 1978, Binkley 1982).

Often the rapid juvenile growth of red alder is responsible for the failure of associated conifers to acquire and maintain a position of height dominance. Therefore, Douglas-fir success may depend on a delay in the establishment of red alder from 4 to 9 years or having both species with such spacing that Douglas-fir will be from 8 to 10 years old before encroachment by red alder occurs (Newton et al. 1968). In young Douglas-fir stands, maximum height growth may not occur at the spacing characterized by maximum biomass of individual trees. Although severe crowding decreases height growth, there is some evidence that a minor degree of crowding may stimulate allocation of resources toward height growth (Cole and Newton 1987).

Substantial increases in ecosystem production in mixed conifer/alder stands were noted by Binkley and Greene (1984), when compared with pure conifer plots on infertile sites. Little change in ecosystem production was found in mixed stands on fertile sites, because conifer growth was reduced proportionately to the increase in alder growth.

Binkley (1984) noted that relative densities in mixed stands may alter the performance of each species, but experimental density plantings were not available for such evaluations (Binkley 1984).

A study of juvenile growth of different types of Douglas-fir planting stock showed that overtopping vegetation slowed the height and diameter growth of the trees and may interfere with establishment of a new stand (Howard and Newton 1984). Under a red alder canopy, Douglas-fir trees were shorter than red alder (Cole and Newton 1987). Overtopping caused the Douglas-fir trees to have a greater proportion of shade needles, which is a useful adaptive strategy in an understory situation (Hamilton 1969; Kira et al. 1969, in Cole and Newton 1986). Shade needles have a greater photosynthetic efficiency at low light intensities than sun needles (Kramer and Kozlowski 1979).

Shainsky and Radosevich (1992), in a study of the mechanisms of competition between Douglas-fir and red alder seedlings, found that red alder was the dominant competitor and overtopped the Douglas-fir. Increasing alder leaf area reduced the light reaching the understory Douglas-fir. In contrast, increasing Douglas-fir leaf area increased the light penetrating through the alder overstory, due to Douglas-fir's ability to suppress alder leaf area.

One of the major difficulties of establishing mixed plantations of Douglas-fir and red alder is that early height growth of red alder often exceeds that of Douglas-fir. Consequently, fast growing red alder usually overtop nearby, equal-aged Douglas-fir, often for as long as 25 years (Fowells 1965, Newton et al. 1968, Miller and Murray 1978).

Knapp et al. (1984) and Walstad and Kuch (1987) consider overtopping vegetation to be a severe obstacle to Douglas-fir regeneration in the moist Oregon Coast Range. This observation is supported by Chan and Walstad (1987) who found that as the amount of overtopping brush increased, sapling growth generally decreased in the Oregon Coast Range. However, some studies have shown that herbaceous plants develop better in pure alder and mixed stands than in pure conifer stands only (Franklin and Pechanec 1967).

Wagner and Radosevich (1991a) examined the influence of abundance measures, height, distance, and spatial arrangement of nonconiferous woody plants on survival and growth of neighboring individual saplings of Douglas-fir. They found that the best interspecific competition index for predicting Douglas-fir height and stem diameter of individual Douglas-fir was initial tree size and the total percent cover of all woody species within a 2.1-m radius. An interaction which existed between the competition index



and tree age indicated that the negative effect of interspecific competition on Douglas-fir increased with time. Douglas-fir stem diameter was more sensitive to neighboring woody plants than was height. Regression models describing height, stem diameter, stem volume index, and crown volume index of individual 4- to 9-year-old saplings were developed. The models indicated that tree age, competing vegetation, animal damage, and initial seedling size respectively had a dominant influence on the performance of Douglas-fir saplings, while prescribed burning and topography were of relatively minor importance.

In an study of a 5-year-old Douglas-fir plantation with variable competition, Cole and Newton (1986) inferred that grass competition with Douglas-fir was primarily for moisture until crown closure eliminated the grass, while competition from red alder trees reduced available light and moisture for Douglas-fir (Cole and Newton 1986). Animal damage in the Pacific Northwest is an important concern for forest land managers. Damage to planted conifers from deer-browsing in the Douglas-fir region is widespread and often severe. If damage to seedlings can be minimized for the first 3 or 4 years after planting, browsing is usually not a limiting factor (Campbell and Evans 1975). Crouch (1968) found that deer started browsing Douglas-fir shortly after bud burst and continued for about 1 month. Douglas-fir was eaten despite abundant

new growth on many other plant species that deer prefer in late spring and early summer. The beginning and ending of tree browsing was not related to any visual growth-stage characteristic except bud burst.

Deer and reforestation interact mainly during regeneration after wildfire or logging. In the Douglas-fir region, numbers of black-tailed deer increase dramatically after forests are logged or burned in response to improved forage supplies. Here, browsing on planted trees in clearcuts lowers forest productivity by reducing growth and occasionally contributes to plantation failures (Crouch 1976).

### 3. Scope, Objectives and Hypotheses

Research on the interactions between Douglas-fir and red alder was conducted to study the survival and growth responses of individual trees and stands during early succession. Mixed stands of fixed density but with varying species proportions (i.e., a replacement series) were grown for six years in the Oregon Coast Range. The objectives of this research were to:

1. Determine if survival, size and growth of individual trees and yield of stands of Douglas-fir and red alder varied with species proportion.

2. Determine if proportionate browsing of Douglas-fir and red alder, and abundance and size of associated shrub and herbaceous vegetation varied with species proportion.

This study tested the null hypothesis that, for a plantation of 3-m spacing, species proportion had no effect on survival, growth, yield, or proportion browsed of Douglas-fir and red alder, and on abundance and size of understory vegetation.

## B. Methods

### 1. Site Description and Treatments

The experiment was conducted on the Cascade Head Experimental Forest near Otis, Oregon. The study site is located at T6S R10W S15 and S22 and has an elevation of 330 m above sea level. In the summer of 1985, the previous 120-year-old stand of Sitka spruce (Picea sitchensis) and western hemlock (Tsuga heterophylla) was clearcut harvested and the site was broadcast burned in the fall. The soil varies from very dark grayish brown loams, to silt loams. Slopes are between 0 to 50 percent. The site occurs within the Pacific Coast fog belt. The average minimum temperature is 20.2°C and the average maximum temperature is 20.9°C. Average annual precipitation is 2500 mm. The distribution of the high precipitation is between October and May, often in form of cloud condensation. Low precipitation occurs during June through September with only 3 to 4 weeks without rainfall.

The study was accomplished in an existing Douglas-fir/red alder replacement series experiment that was planted in March 1986. Vegetation plots in a replacement series have a fixed plant density but varying species proportion (Radosevich and Holt 1984). The size of each

plot was 0.073 ha (27 X 27 m), and the trees were planted on a 3- X 3-m spacing. Seedling mortality was replaced during each of the first three growing seasons. Each plot consisted of 81 saplings (9 X 9 rows), and the two outermost rows were designated as border rows, and therefore were not included in the tree measurements.

The following species proportions (Douglas-fir/red alder) were studied: (1) 1.0/0.0, (2) 0.9/0.1, (3) 0.7/0.3, (4) 0.5/0.5, (5) 0.25/0.75, and (6) 0.0/1.0 (Figure 2-1). Each proportion was replicated three times in a randomized complete block design.

## 2. Vegetation Measurements

Growth measurements of Douglas-fir and red alder were taken annually at the end of the 1986-91 growing seasons. During 1986-90, six saplings per species (when present) were measured in each plot. In 1991, all saplings in the central 5 X 5 grid of seedlings in each plot were measured (Figure 2-1). Stem diameter was measured to the nearest 1 mm at 2 cm height, and when possible, at 137 cm (dbh) above ground. Dbh of each stem for multi-stemmed trees was measured in 1991. Basal diameter of red alder was measured only in 1986-87; in subsequent years dbh was measured. Height to the tip of the dominant meristem and crown width

Figure 2-1. Systematic arrangement of Douglas-fir (X) and red alder (O) in various species proportions (Douglas-fir/red alder; shown below in parentheses) of the replacement series experiment.

```
X X X X X X X X X X
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X X X X X X X X X X
X X X X X X X X X X
X X X X X X X X X X
X X X X X X X X X X
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(1.0/0.0)

```
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X X X X X X X X X X
O X O X O X O X O
X X X X X X X X X X
X X X X X X X X X X
X X X X X X X X X X
X X X X X X X X X X
O X O X O X O X O
X X X X X X X X X X
X X X X X X X X X X
```

(0.9/0.1)

```
O X O X O X O X O
X X X X X X X X X X
O X O X O X O X O
X X X X X X X X X X
O X O X O X O X O
X X X X X X X X X X
O X O X O X O X O
X X X X X X X X X X
O X O X O X O X O
```

(0.7/0.3)

```
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
X O X O X O X O X
O X O X O X O X O
```

(0.5/0.5)

```
O X O X O X O X O
O O O O O O O O O
O X O X O X O X O
O O O O O O O O O
O X O X O X O X O
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O X O X O X O X O
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(0.25/0.75)

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O O O O O O O O O
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O O O O O O O O O
```

(0.0/1.0)

were measured to the nearest 1 cm. Stem-volume index, a commonly used predictor of tree biomass (Zavitkovski and Stevens 1972, DeBell et al. 1989, Shainsky and Radosevich 1992), was calculated as height X (stem diameter)<sup>2</sup>.

Crown coverage of understory vegetation was determined in June of 1986, 1988 and 1989 using the line transect method (Mueller-Dombois and Ellenberg 1974). A single transect (38 m), located as the diagonal of each plot, was sampled for species, height, and cover. Cover (%) was estimated as the total length of transect that was intersected by the crown of a given species divided by total transect length X 100. Browsing and other injuries from deer and elk were coded as 1 if present, or 0 if absent, during the growth measurements.

In order to predict total above-ground biomass for saplings in the study, a total of 44 Douglas-fir and 43 red alder were destructively sampled from 1987 to 1991. These saplings were selected to represent a range of sizes and species proportions from extra plots that were established adjacent to the study. In the field, each sapling was measured for basal stem diameter (at 2 cm height), dbh (at 137 cm height), height, and crown width. Each tree was severed at groundline and returned to the laboratory where foliage and woody components were separated, dried at 70°C to a constant weight, and weighed.

### 3. Statistical Analysis

A response surface analysis (Petersen 1985) was used to evaluate the relationships of tree sapling and understory vegetation responses to species proportion. The following quadratic model was tested on responses from each of the 1986-91 growing seasons using the Statistical Analysis System (SAS 1988):

$$Y_i = b_{0i} + b_{1i} (P) + b_{2i} (P^2) \quad (1)$$

were  $Y_i$  is the plot mean ( $n=6$ ) for a given dependent variable (tree sapling and understory vegetation responses) measured in a given growing season,  $b_{0i}$  is the regression intercept, and  $b_{1i}$  and  $b_{2i}$  are regression slopes that quantify the linear and quadratic effects, respectively, of species proportion ( $P$ ), hereafter referred to as red alder proportion. Significant response-surface models were chosen on basis of  $\alpha=0.05$ , after a backward elimination technique was used to eliminate non-significant parameters. To predict 1991 height of each stem for multi-stemmed trees, which was used in calculations of stand volume, a regression equation was developed having the form of:

$$\log(H) = b_{0i} + b_{1i} \log(D) \quad (2)$$



where H is the sapling height (cm),  $b_{0i}$  and  $b_{1i}$  are the regression coefficients, and D is the dbh (mm). For Douglas-fir, 328 saplings were used in the regression analysis, while for red alder, 619 saplings were used (Table 2-1). The regression coefficients were estimated by multiple regression analysis in which three models were tested:

$$H = b_0 + b_1 * D \quad (3)$$

$$\text{Log } H = b_0 + b_1 * D \quad (4)$$

$$\text{Log } H = b_0 + b_1 * \text{Log } (D) \quad (5)$$

The best model to describe the data was chosen on the basis of the highest adjusted  $R^2$  (from regressions of predicted H vs. observed H) and the lowest mean-squared error.

The premise of the replacement series experiment (substitutive experiments) is to determine the yields of mixtures by comparing them to monoculture yields (Radosevich 1987). Relative and total yields were calculated for basal area ( $\text{dm}^2/\text{ha}$ ), volume index ( $\text{dm}^3/\text{ha}$ ), and predicted biomass ( $\text{kg}/\text{ha}$ ). Multiple regression analyses (SAS 1988) were used to develop allometric equations to predict total aboveground biomass (Table 2-2). When non-homogenous variance was detected in scatterplots of residual versus predicted values,

Table 2-1. Regression coefficients for predicting height (cm) from dbh (mm) for multi-stemmed saplings of Douglas-fir and red alder. Values reported for  $S_{y,x}$  and adjusted  $R^2$  were calculated using untransformed dependent variables.

Dependent variable	Regression Coefficients <sup>1</sup>		$S_{y,x}$	Adjusted $R^2$	n
	$b_0$	$b_1$			
Height	Douglas-fir		0.0807	0.8904	328
	4.4752	3.631E-1			
Height	Red alder		0.1198	0.9348	619
	4.2203	5.571E-1			

<sup>1</sup>Equation:  
 $\text{Log}(Y) = b_0 + b_1 * \text{log dbh}$

Table 2-2. Regression coefficients for predicting foliage and wood biomass (g) of Douglas-fir and red alder. Values reported for  $S_{y,x}$  and adjusted  $R^2$  were calculated using untransformed dependent variables.

Dependent variable	Eq. #	Regression Coefficients				$S_{y,x}$	Adjusted $R^2$	n
		$b_0$	$b_{01}$	$b_1$	$b_{11}$			
Douglas-fir								
Totfol	2	4.727	-6.276E-1	8.133E-1	----	43.977	.942	44
Totwood	2	5.385	----	9.073E-1	----	52.925	.988	44
Red alder								
Totfol	1	3.981	4.212E+1	----	----	32.048	.851	43
Totwood	1	2.328	1.333E+2	----	----	43.101	.970	43
Totfol	3	4.120	3.842E-1	----	----	.583	.920	26
Totwood	3	5.224	4.169E-1	----	----	.525	.922	26
Totfol	Total foliage biomass							
Totwood	Total wood biomass							

<sup>1</sup>Equations:

$$1. Y = b_0 + b_{01} * \text{overtop} + b_1 * \text{volindx1} + b_{11} * \text{overtop} * \log \text{volindx1}$$

Weighted least squares were used to estimate parameters for model 1.

$$2. \log(Y) = b_0 + b_{01} * \text{overtop} + b_1 * \log \text{volindx1} + b_{11} * \text{overtop} * \log \text{volindx1}$$

$$3. \log(Y) = b_0 + b_{01} * \text{volindx2}$$

Where  $\text{volindx1} = (\text{basal diameter (dm)})^2 * \text{height (dm)}$ ,

$\text{volindx2} = (\text{dbh (dm)})^2 * \text{height (dm)}$ ,

and  $\text{overtop} = 1$  if Douglas-fir proportion  $\leq 0.5$ , else  $\text{overtop} = 0$

regression coefficients were estimated via weighted least squares (SAS 1988). Relative yields for each species were calculated as yield for each proportion divided by the mean monoculture yield (Radosevich and Holt 1984).

A response surface analysis was performed to determine whether competitive interactions occurred between Douglas-fir and red alder. The null hypothesis was that observed responses in relative yield of Douglas-fir or red alder did not deviate from noninteraction as indicated by the competitive equivalence line in a replacement series diagram (Harper 1977). Tests for significant lack of fit from the competitive equivalence lines were used to indicate whether the null hypothesis could be rejected and that competition occurred between Douglas-fir and red alder.

## C. Results

### 1. Average Sapling Size and Growth

At the end of each of the 1986-91 growing seasons, the average heights of Douglas-fir seedlings were, respectively, 29, 34, 73, 118, 166, and 213 cm. There were no significant ( $p>0.05$ ) response functions detected for the first five years of the study (1986-90). However, a linear response function was found to be significant in the sixth year ( $p=0.05$ ,  $R^2=0.27$ ), in which Douglas-fir at 0.3 and 0.1 red alder proportions had greater average heights (226 and 234 cm, respectively) with respect to the other proportions of red alder (Table 2-3 and Figure 2-2a).

For red alder there were no significant ( $p>0.05$ ) response functions for total height during the first five years, as found for Douglas-fir. In the sixth year, there was a significant linear response, with a consistent increase in height with increasing red alder proportion ( $p=0.009$ ,  $R^2=0.44$ ) (Table 2-3 and Figure 2-2b). In the 0.1 red alder proportion, height of red alder saplings averaged 214 cm less than for saplings in the 1.0 proportion.

Average basal diameter for Douglas-fir saplings during the first three years did not vary significantly ( $p>0.05$ ) with red alder species proportion (Figure 2-3a). In the

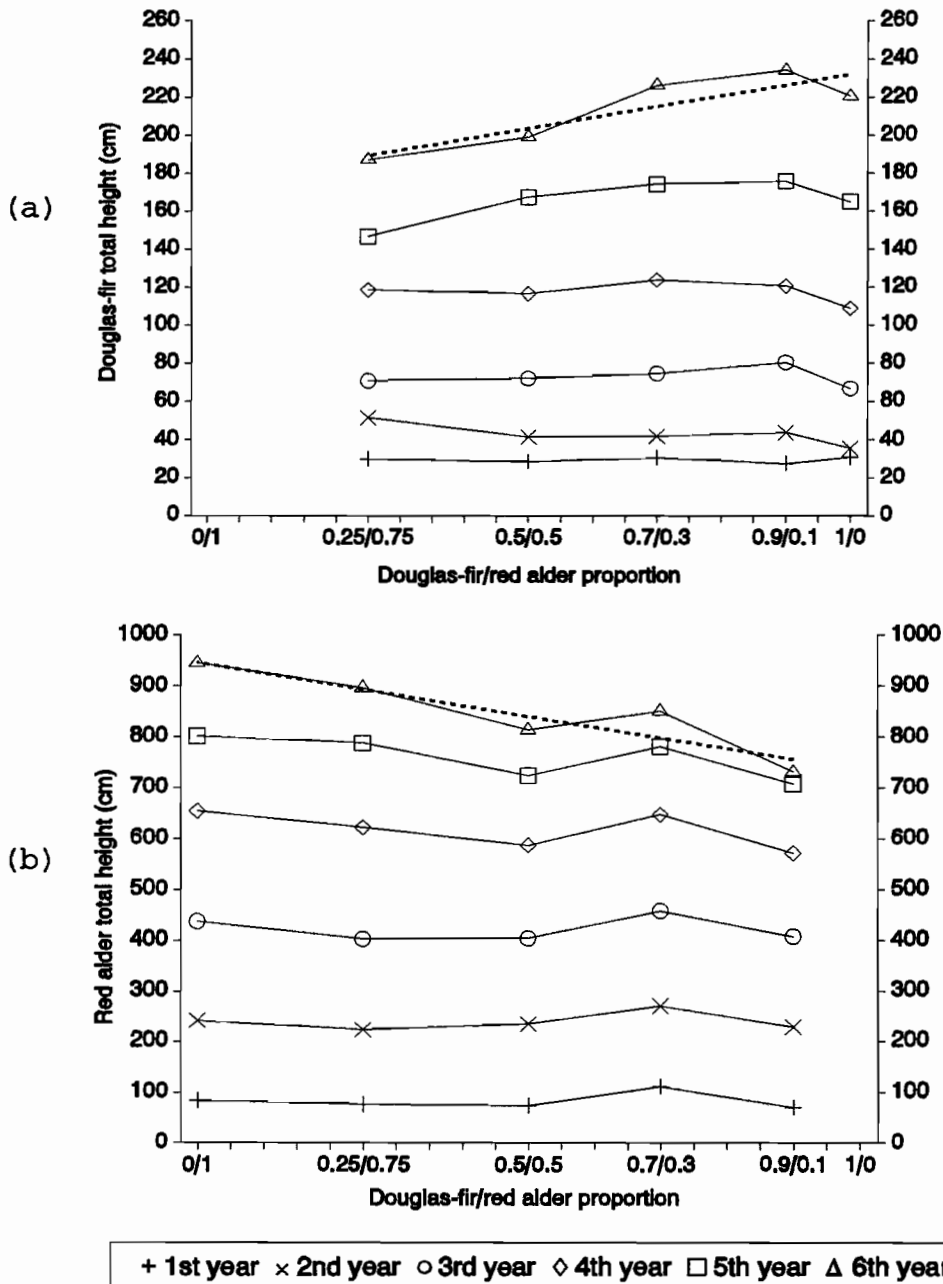
Table 2-3. Regression coefficients for the significant polynomial response functions ( $p \leq 0.05$ ) of Douglas-fir and red alder.

Dependent variable	year	Regression Coefficients <sup>1</sup>			$S_{y.x}$	Adjusted $R^2$	n
		$b_{01}$	$b_{11}$	$b_{12}$			
Douglas-fir							
Height (cm)	6	2.322E+2	-5.703E+1	----	2.796E+1	0.27	15
Diameter (mm)	4	2.063E+1	-0.692E+1	----	0.323E+1	0.29	15
	5	3.220E+1	-1.722E+1	----	0.488E+1	0.53	15
	6	4.534E+1	-4.400E+1	2.028E+1	0.702E+1	0.62	15
Height increment (cm)	2	0.938E+1	-1.780E+1	----	0.536E+1	0.52	13
	5	6.882E+1	-4.221E+1	----	1.084E+1	0.60	13
	6	5.528E+1	-4.047E+1	----	1.368E+1	0.53	13
Diameter increment (mm)	4	0.740E+1	-0.606E+1	----	0.201E+1	0.46	15
	5	1.280E+1	-1.672E+1	0.825E+1	0.282E+1	0.57	15
	6	1.245E+1	-2.470E+1	1.359E+1	0.367E+1	0.60	15
Proportion Browse	1	8.104E+1	-2.156E+2	2.503E+2	2.473E+1	0.36	15
	6	0.468E+1	-4.523E+1	1.090E+2	0.716E+1	0.77	15
Proportion Surviving	6	9.792E+1	5.073E+1	-1.108E+2	0.503E+1	0.85	15
Red alder							
Height (cm)	6	7.662E+2	-2.105E+2	----	8.385E+1	0.44	15
Height increment (cm)	4	1.508E+2	7.952E+1	----	2.674E+1	0.52	15
Herbaceous Vegetation							
Crown volume ( $m^3 ha^{-1}$ )	4	9.054E+1	1.625E+2	-1.899E+2	3.019E+1	0.44	18

<sup>1</sup>Equation:

$$Y = b_{01} + b_{11} * \text{red alder proportion} + b_{12} * (\text{red alder proportion})^2$$

Figure 2-2. Total height responses of (a) Douglas-fir and (b) red alder saplings one to six years (1986-1991) after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.



fourth and fifth years, basal diameter of Douglas-fir decreased linearly ( $p \leq 0.05$ ) with increasing red alder proportion (Table 2-3 and Figure 2-3a). In the fourth year the basal diameter means ranged from 14.7 mm in the 0.75 red alder proportion to 20.12 mm in the 0.1 red alder proportion, with an average of 18.34 mm ( $p = 0.04$ ,  $R^2 = 0.28$ ). In the fifth year, the average mean was 26.5 mm, with a maximum of 31.4 mm in 0.1 red alder proportion, and a minimum of 18.9 mm in the 0.75 red alder proportion ( $p = 0.003$ ,  $R^2 = 0.53$ ). In the sixth year, basal diameter of Douglas-fir decreased quadratically ( $p = 0.001$ ,  $R^2 = 0.61$ ) with increasing red alder proportion (Figure 2-3a). During this time, diameter ranged from 31.42 to 19.94 mm for the red alder proportions, 0.9 to 0.0, respectively.

There were no significant ( $p > 0.05$ ) response functions for basal diameter of red alder in the first and second years (Figure 2-3b), although diameter in the 0.3 red alder proportion exceeded that for all other species proportions.

Height increment of Douglas-fir varied little with increasing red alder proportion during the first four years of the study (1986-89) (Figure 2-4a). In the first, third and fourth years, response functions for Douglas-fir height increment were not significant ( $p > 0.05$ ). In the second year, height increment of Douglas-fir varied as a positive linear function with red alder proportion ( $p = 0.004$ ,  $R^2 = 0.52$ ) (Table 2-3 and Figure 2-4a). During this time,



Figure 2-3. Basal diameter responses of (a) Douglas-fir and (b) red alder saplings one to six years (1986-1991) after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.

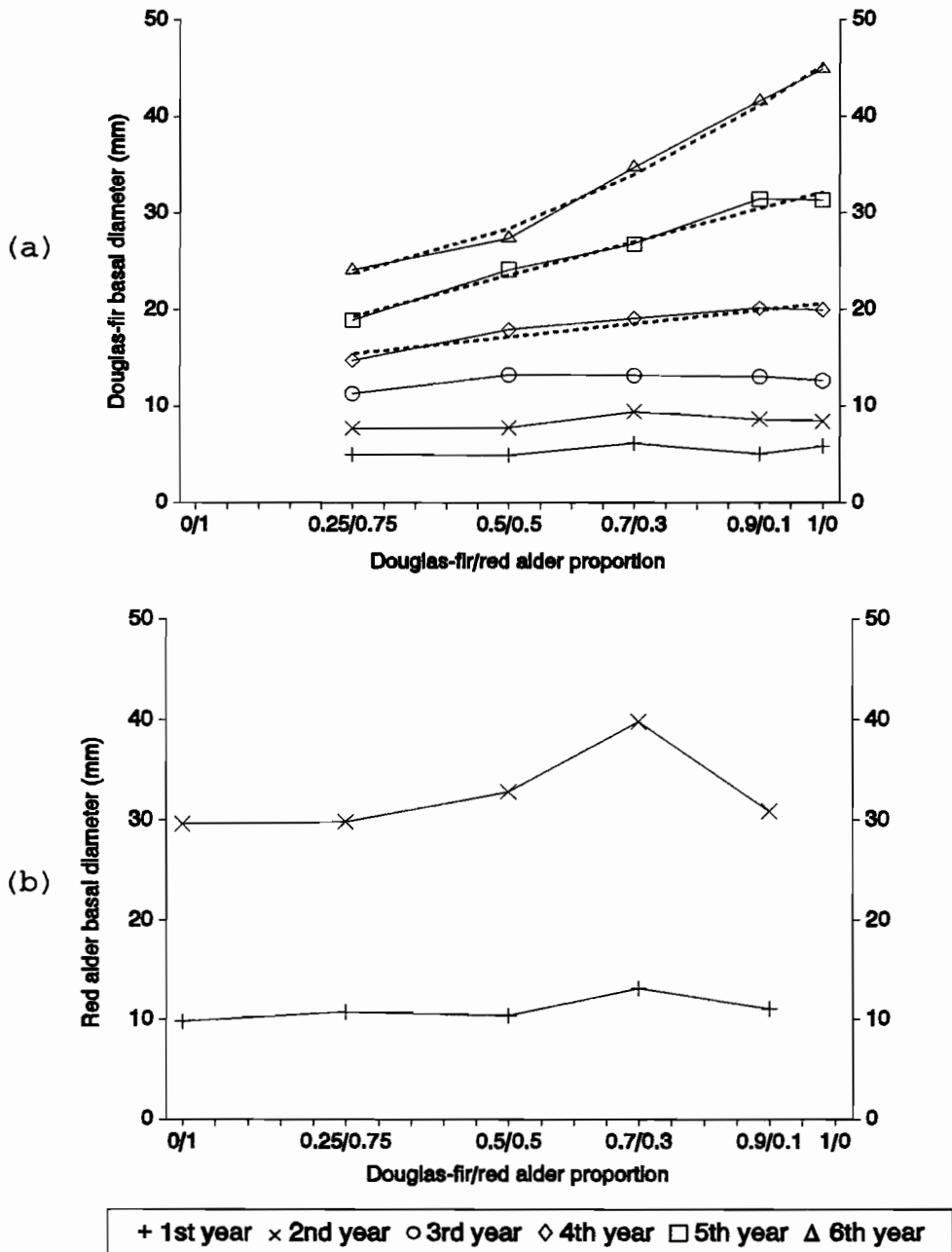
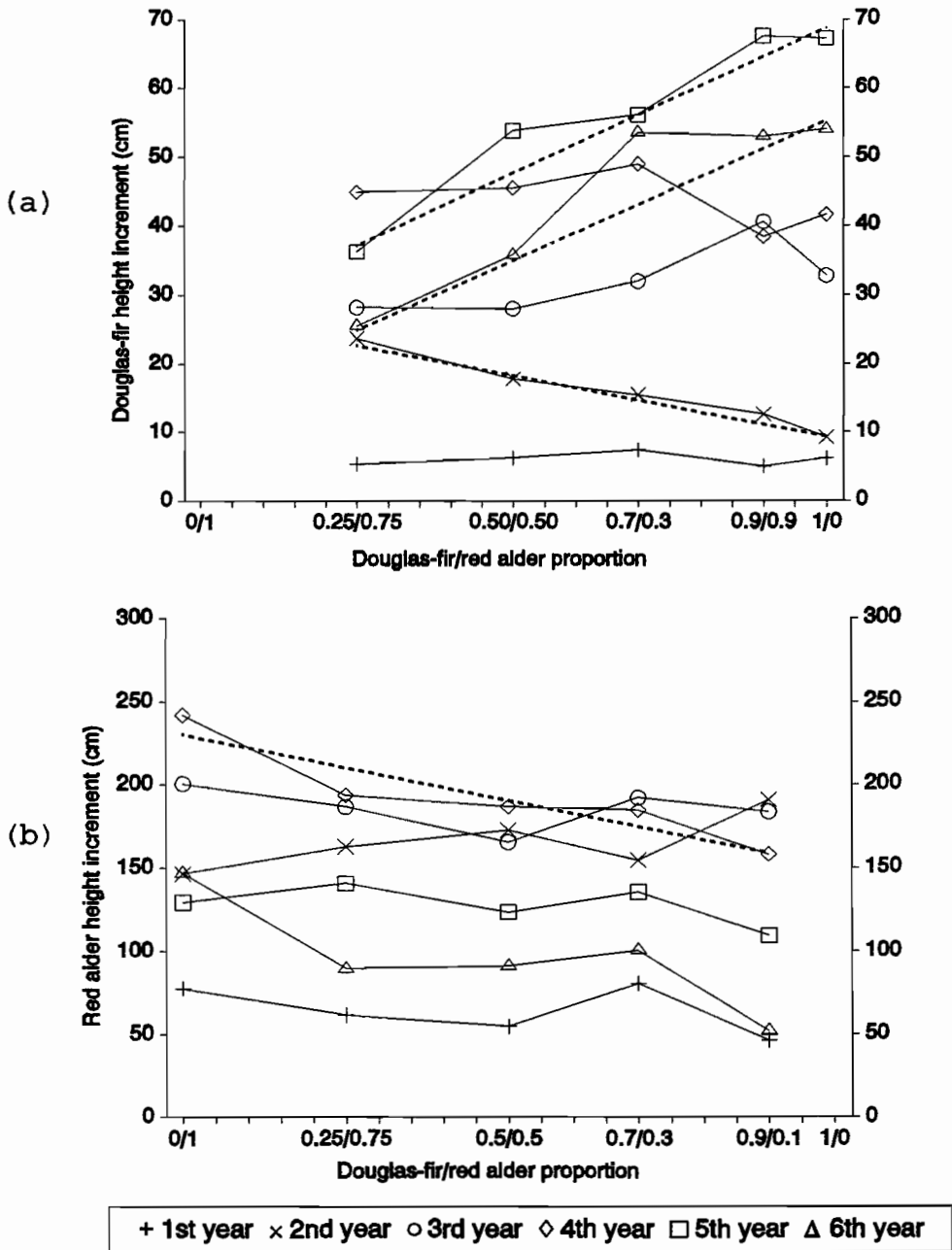


Figure 2-4. Height increment of (a) Douglas-fir and (b) red alder saplings one to six years (1986-1991) after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.

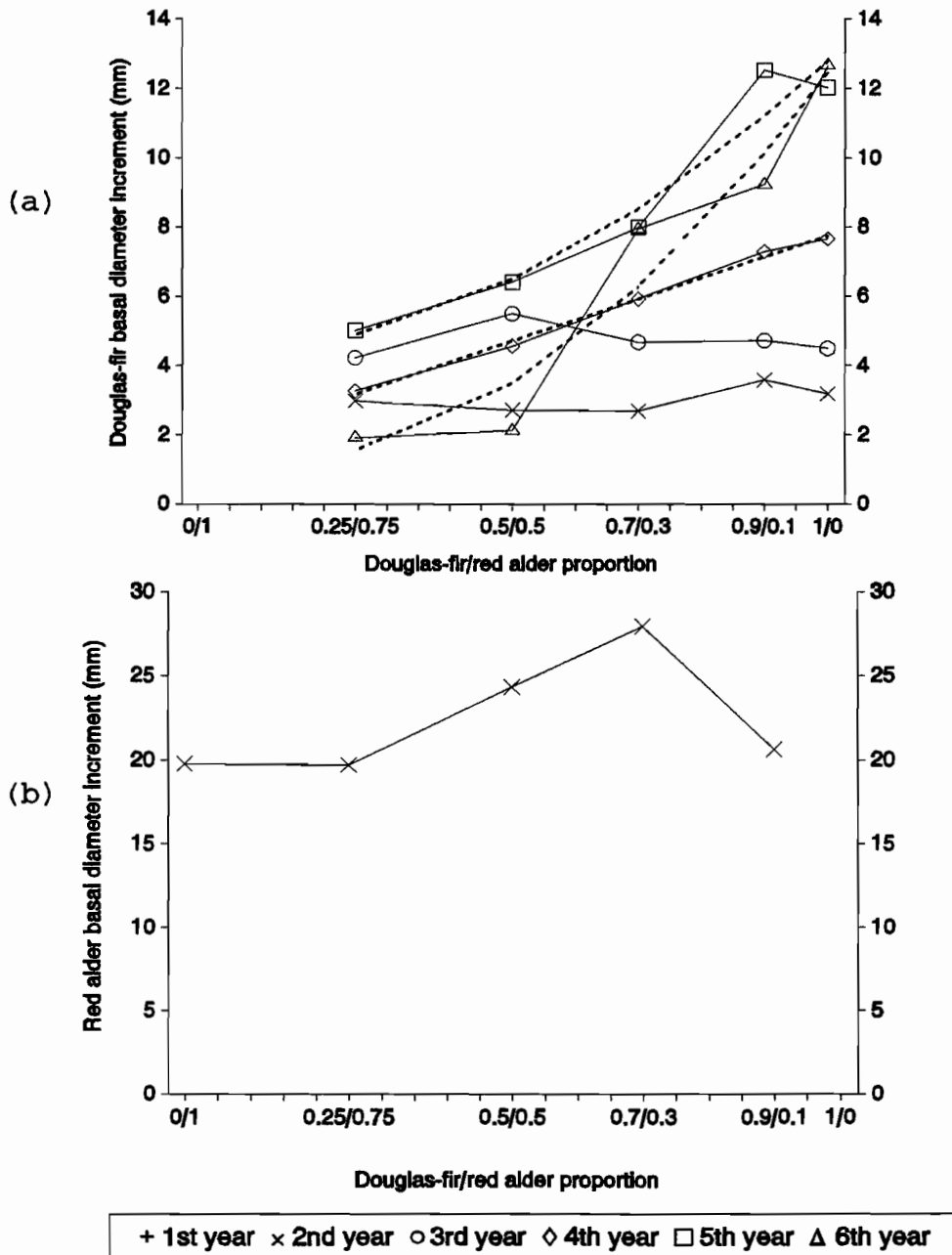


the height growth ranged from 23.7 cm in the 0.75 red alder proportion to 9.2 cm in the 0.0 red alder proportion, with an average of 15.75 cm. Height increment of Douglas-fir varied as a negative linear function with red alder proportion in the fifth ( $p=0.002$ ,  $R^2=0.60$ ) and sixth years ( $p=0.009$ ,  $R^2=0.53$ ) (Table 2-3 and Figure 2-4a). Mean height increment of Douglas-fir for the fifth year was 56.2 cm, with a maximum of 67.54 cm in the 0.1 red alder proportion, and a minimum of 36.28 cm in the 0.25 red alder proportion. In the sixth year, the maximum height increment was found in the 0.0 and 0.1 red alder proportions, with means of 54 cm and 53 cm respectively, while in the 0.75 red alder proportion the lowest Douglas-fir height increment (25.5 cm) was observed (Figure 2-4a).

For height increment of red alder, the only significant response function found was in the fourth year ( $p=0.003$ ,  $R^2=0.52$ ), in which the maximum was 241.98 cm in the 1.0 red alder proportion, and a minimum of 158 cm in the 0.1 red alder proportion (Table 2-3 and Figure 2-4b).

Response functions for basal diameter increment of Douglas-fir were significant ( $p \leq 0.05$ ) in the fourth, fifth and sixth years (Table 2-3 and Figure 2-5a). In the fourth year, a significant linear function ( $p=0.008$ ,  $R^2=0.45$ ) was found, in which the lowest diameter increment was in the 0.75 red alder proportion (3.27 mm), and the highest in the 0.0 red alder proportion (7.65 mm). A significant

Figure 2-5. Basal diameter increment of (a) Douglas-fir and (b) red alder saplings one to six years after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.



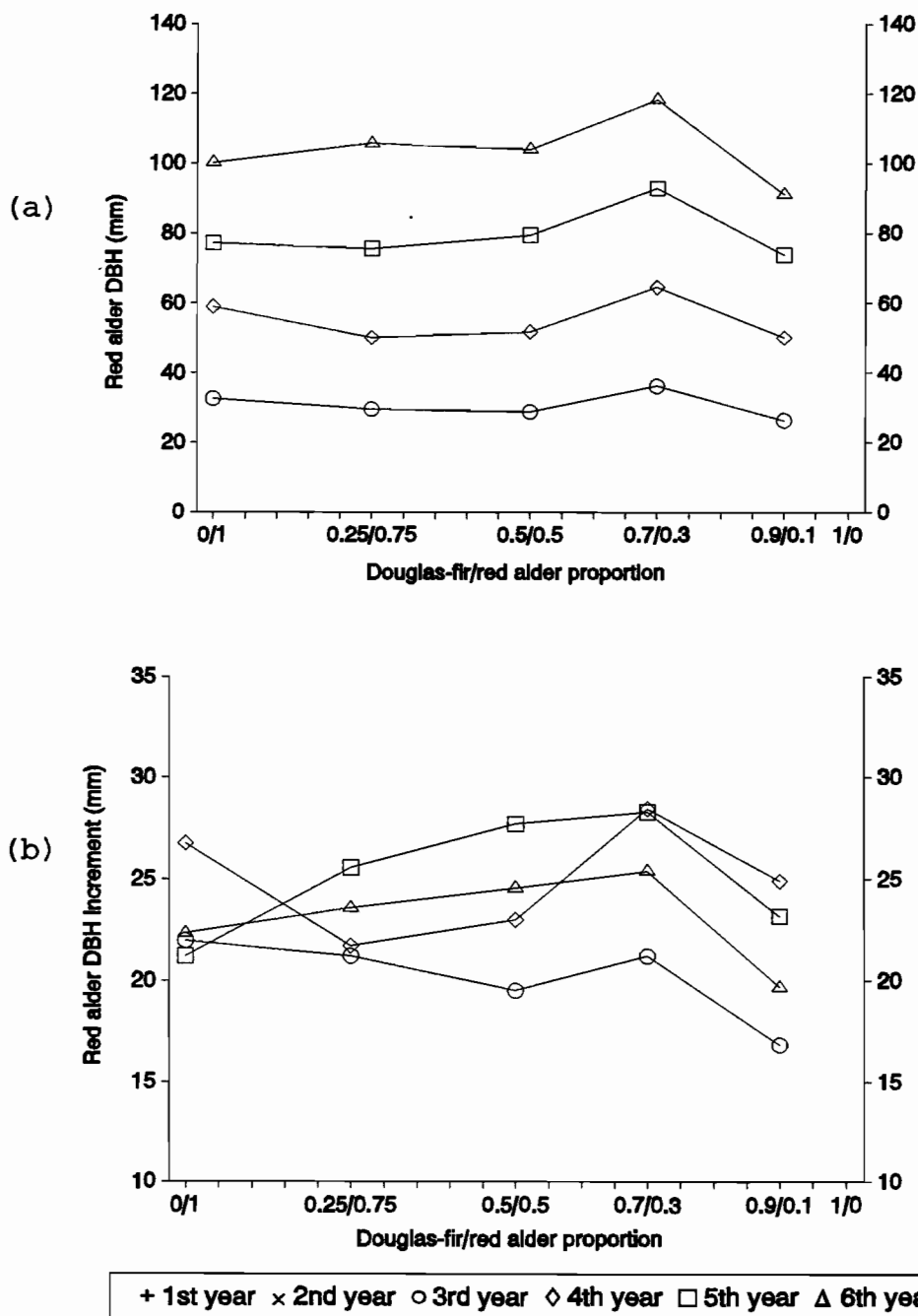
quadratic response function ( $p=0.002$ ,  $R^2=0.57$ ) was found in the fifth year. In this case, basal diameter increment of Douglas-fir in the 0.75 red alder proportion was the lowest (5.01 mm), and the highest was in the 0.0 red alder proportion (12 mm). For the sixth year ( $p=0.001$ ,  $R^2=0.60$ ) the highest increment in basal diameter was also in the 0.0 red alder proportion (12.66 mm), and the lowest was in the 0.75 red alder proportion (1.92 mm).

Only red alder had a sufficient number of dbh measurements to permit a response surface analysis. There were not any significant response functions ( $p>0.05$ ) for absolute size or increment in dbh during the four growing seasons (1988-1991) (Figure 2-6a,b). Average values for dbh were 30, 55, 80, and 104 mm for the fourth, fifth, and sixth growing seasons, respectively. Although response functions were not significant ( $p>0.05$ ), dbh of red alder in the 0.3 red alder proportion exceeded that for other treatments in each year of the study. Average values for dbh increment of red alder were 20, 25, 25, and 23 mm for the fourth, fifth, and sixth growing seasons, respectively.

## 2. Stand Basal Area, Volume, and Predicted Biomass

Stand values for basal area, volume, and predicted biomass of each species were largely determined by the

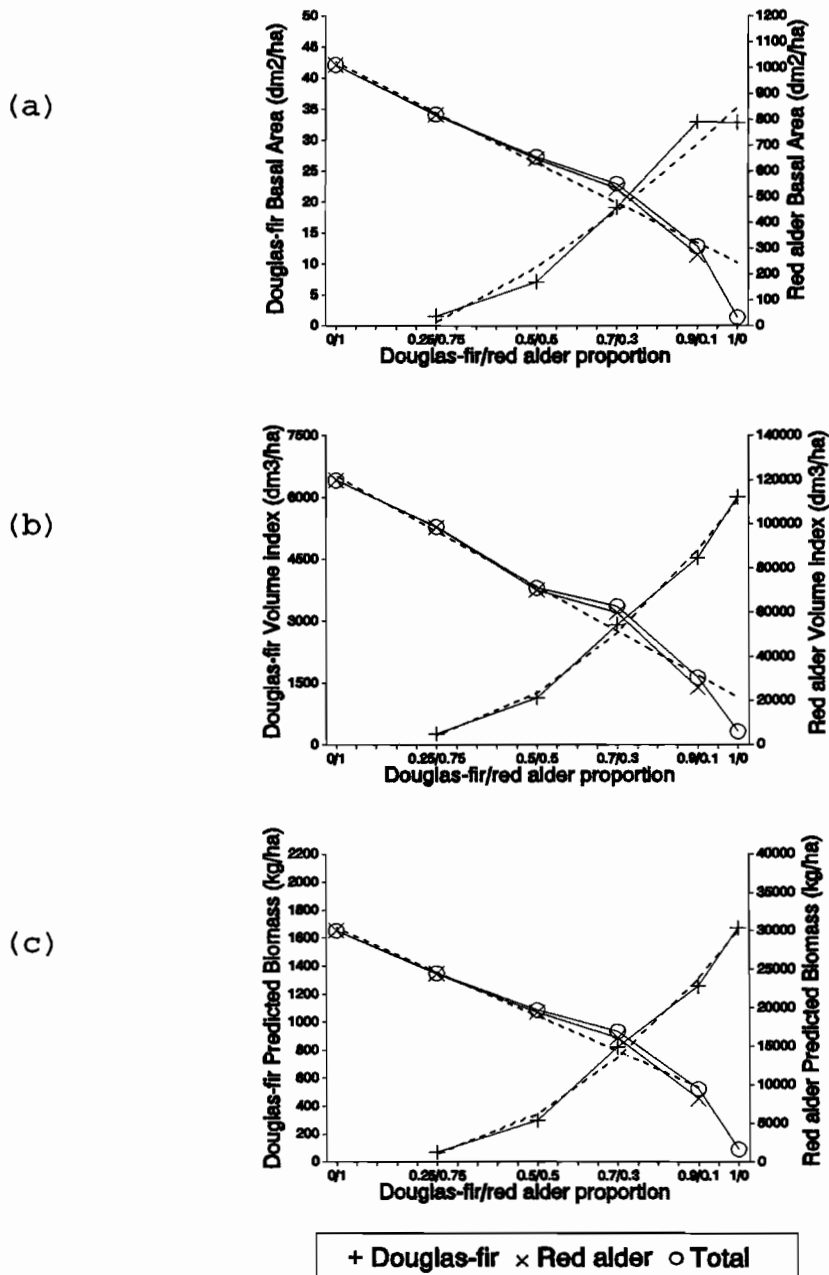
Figure 2-6. DBH responses in (a) absolute size and (b) increment of red alder saplings three to six years (1988-1991) after planting in a replacement series experiment in the Oregon Coast Range.



proportion of the stand occupied by that species. For example, basal area of red alder ( $p=0.000$ ,  $R^2=0.85$ ) and that for Douglas-fir increased ( $p=0.000$ ,  $R^2=0.77$ ) with increases in their own proportion (Figure 2-7a). For Douglas-fir, the response function was quadratic, while for red alder, it was linear. Average basal area of Douglas-fir ranged from 1.58 dm<sup>2</sup>/ha (0.75 red alder proportion) to 32.97 dm<sup>2</sup>/ha (0.1 red alder proportion), while that of red alder varied from 274.46 dm<sup>2</sup>/ha (0.1 red alder proportion) to 1011.55 dm<sup>2</sup>/ha (1.0 red alder proportion). Volume index (Figure 2-7b) of Douglas-fir ( $p=0.000$ ,  $R^2=0.70$ ) and red alder ( $p=0.000$ ,  $R^2=0.81$ ) also increased with increases in their own proportion. Average volume index for Douglas-fir ranged from 258.96 dm<sup>3</sup>/ha in the 0.75 red alder proportion to 6,011.84 dm<sup>3</sup>/ha in the 0.1 red alder proportion, while for red alder it ranged from 25,960 dm<sup>3</sup>/ha in the 0.1 red alder proportion to 119,877 dm<sup>3</sup>/ha in the 1.0 red alder proportion.

Douglas-fir ( $p=0.000$ ,  $R^2=0.89$ ) and red alder ( $p=0.000$ ,  $R^2=0.82$ ) predicted biomass increased according to their own respective proportions (Figure 2-7c). Average biomass for Douglas-fir ranged from 70 kg/ha in the 0.75 red alder proportion to 1,670 kg/ha in the 0.0 red alder proportion, while for red alder it ranged from 8,253 kg/ha in the 0.3 red alder proportion to 30,066 kg/ha in the 1.0 red alder proportion.

Figure 2-7. Sixth-year (1991) (a) basal area (dm<sup>2</sup>/ha), (b) volume index (dm<sup>3</sup>/ha), and (c) predicted biomass (kg/ha) responses of Douglas-fir and red alder to varying species proportion. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given species.



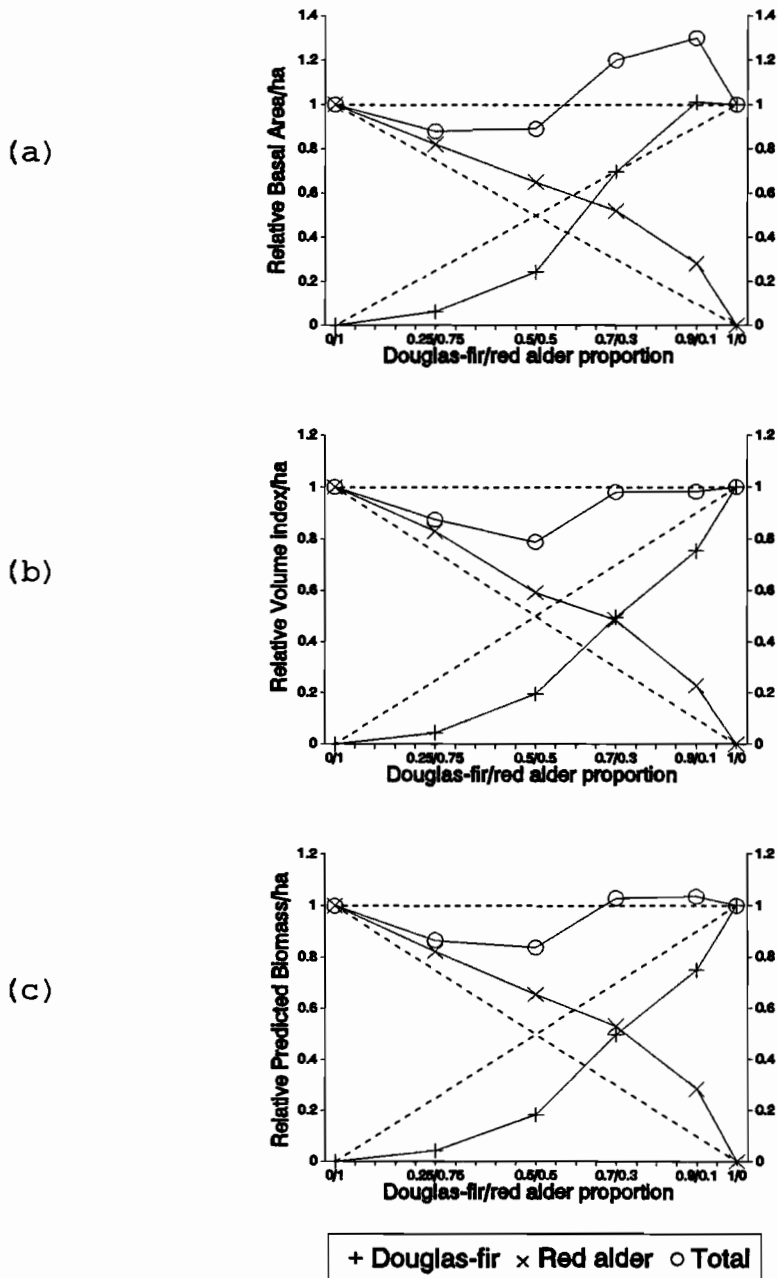


### 3. Stand Relative Yields

In the replacement series experiment, values for the relative yield total for basal area, volume index, and predicted biomass did vary significantly ( $p \leq 0.05$ ) from 1 in some cases (Figures 2-8a,b,c). Evidently, the two species were competing for the same resources (Radosevich and Holt 1984). The relative yield values indicate the competitive ability of the two species. Two straight dotted lines in Figure 2-8 ( $45^\circ$  and  $315^\circ$  with respect to the x-axis) indicate a situation in which the ability of the two species to compete is equivalent. If these lines were concave or convex, this indicates that one species is more competitive than the other and gains resources at the other's expense (Harper 1977).

The relative yields for basal area, volume index, and predicted biomass of Douglas-fir did not differ significantly ( $p > 0.05$ ) from the expected yields (Figure 2-8a,b,c). However, each of these variables for red alder were significantly ( $p \leq 0.05$ ) greater than the expected yields (Figure 2-8a,b,c), indicating the presence of competition between the two species and that red alder was the superior competitor. For relative yield totals (RYT), volume index was significantly ( $p = 0.001$ ) less than 1 (Figure 2-8b), while basal area and predicted biomass did not differ significantly ( $p > 0.05$ ) from 1 (Figure 2-8a,c).

Figure 2-8. Sixth-year (1991) relative yields of Douglas-fir and red alder and relative yield totals for (a) basal area, (b) volume index, and (c) predicted biomass. Dotted lines indicate the expected yields in the absence of intraspecific competition.



Values of RYT for volume index in the 0.75 and 0.5 red alder proportions were 0.87 and 0.79, respectively, indicating that the observed increases in relative yield of red alder did not compensate fully for decreases in relative yield of Douglas-fir.

#### 4. Understory Vegetation Responses

In the fourth year (1989), crown volume of herbaceous vegetation was quadratically related ( $p=0.02$ ,  $R^2=0.44$ ) to red alder proportion (Figure 2-9a). For this year, crown volume varied from 71 to 147 m<sup>3</sup>/ha for the 0.5 and 0.75 red alder proportions, respectively. Cover or height of herbaceous vegetation (Figure 2-9b,c) or variables describing abundance and size of woody understory vegetation (data not presented) were not significantly ( $p>0.05$ ) related to red alder proportion.

#### 5. Browsing and Survival Responses

Browsing of Douglas-fir stems and foliage was observed on almost all red alder proportions. No differences were found in the proportion of red alder that were browsed (Figure 2-10b), but for Douglas-fir saplings, proportion

Figure 2-9. Herbaceous vegetation (a) crown volume, (b) crown coverage, and (c) height from 1986, 1988 and 1989 in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.

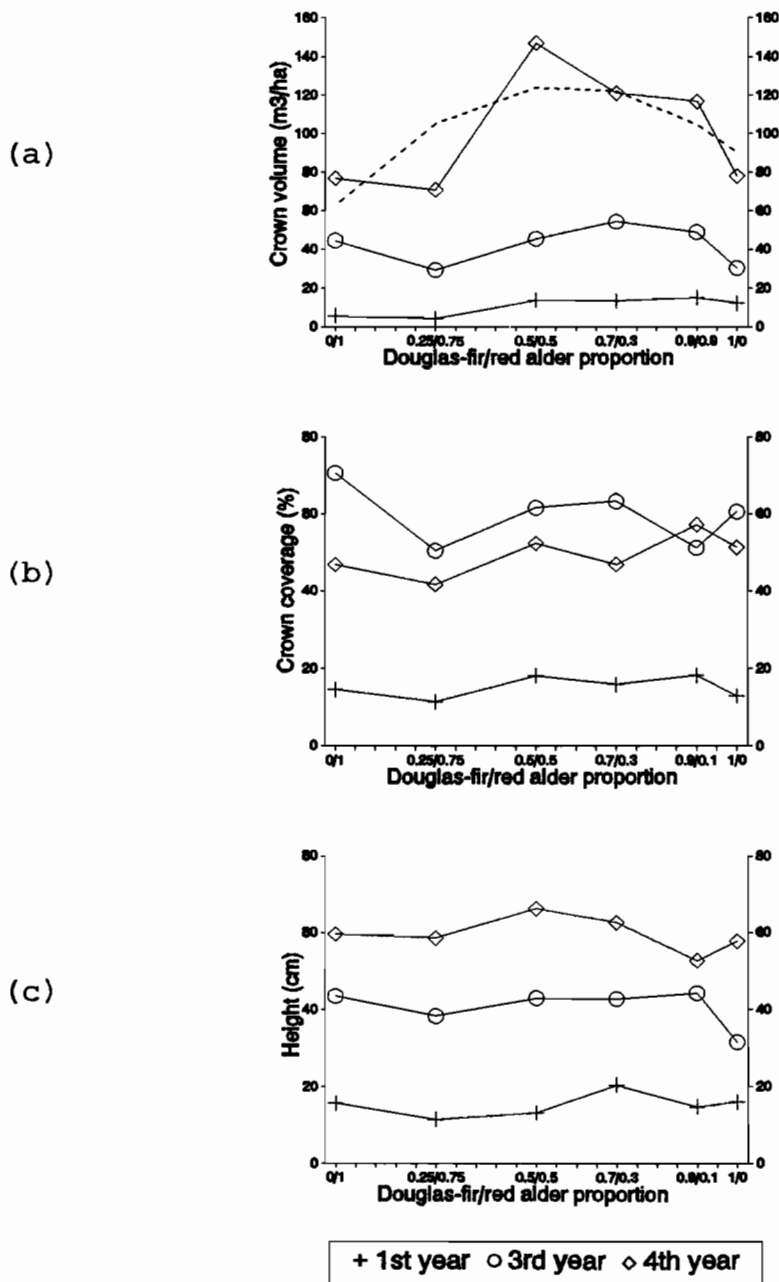
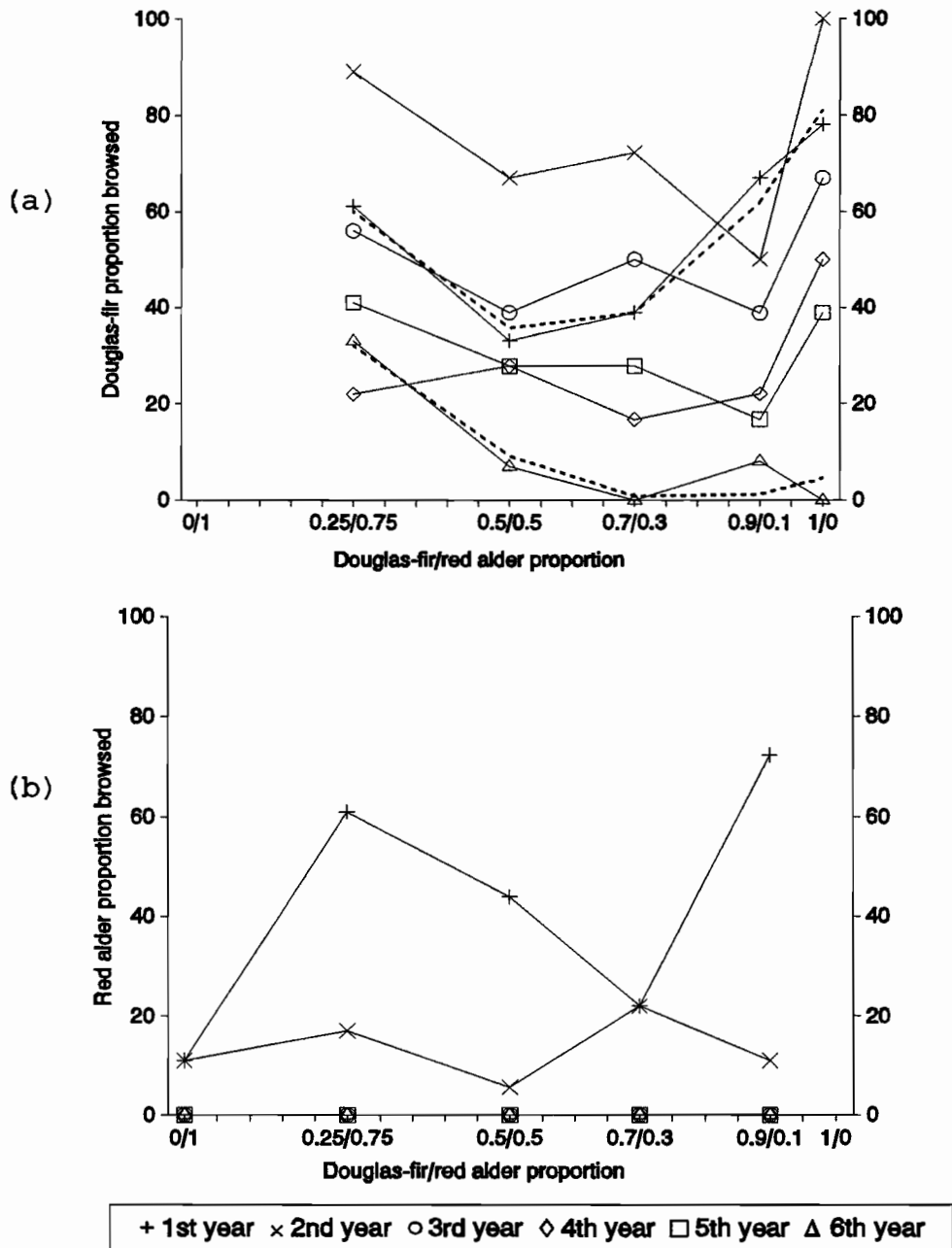


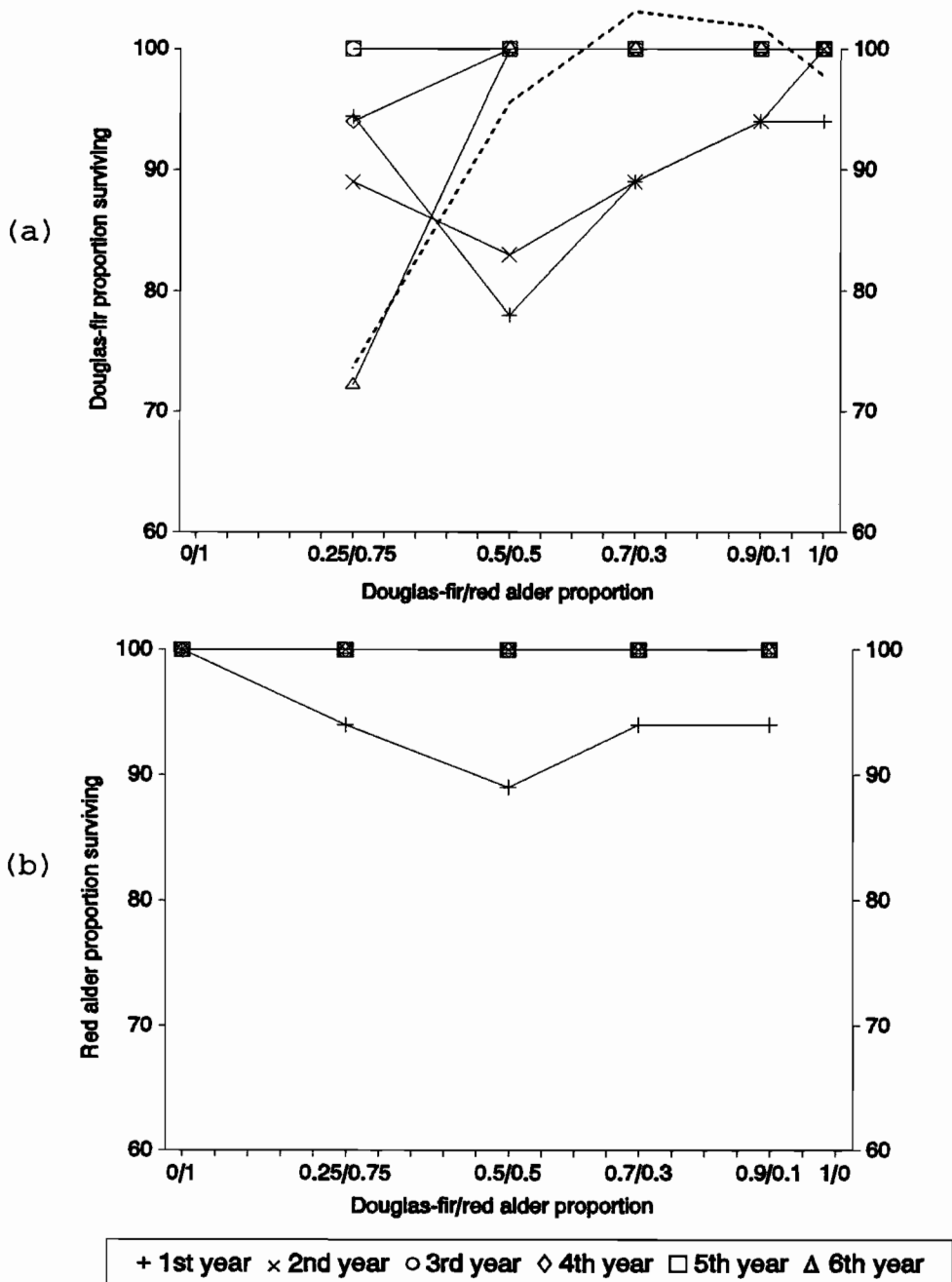
Figure 2-10. Proportion browsed of (a) Douglas-fir and (b) red alder saplings one to six years (1986-1991) after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.



browsed had significant quadratic relationships with red alder proportion for the first ( $p=0.04$ ,  $R^2=0.36$ ) and sixth years ( $p=0.005$ ,  $R^2=0.77$ ) (Figure 2-10a). In the first year, Douglas-fir saplings in the 0.0 red alder proportion had the highest proportion browsed (0.78), while saplings in the 0.5 red alder proportion had the lowest proportion browsed (0.33) (Figure 2-10a). In the sixth year, Douglas-fir saplings in the 0.75 red alder proportion had the highest proportions browsed (0.33), while the other four red alder proportions had similar proportion of browsed saplings (Figure 2-10a).

Proportion of red alder surviving did not vary significantly ( $p>0.05$ ) with red alder proportion during each of six years of the study (Figure 2-11b). In the sixth year, proportion of Douglas-fir surviving was quadratically related ( $p=0.003$ ,  $R^2=0.85$ ) to red alder proportion (Figure 2-11a). This significant response function resulted because of the reduced proportion of Douglas-fir surviving (0.72) in the 0.75 red alder proportion.

Figure 2-11. Proportion surviving of (a) Douglas-fir and (b) red alder saplings one to six years (1986-1991) after planting in a replacement series experiment in the Oregon Coast Range. A dotted line indicates a significant ( $p \leq 0.05$ ) response function for a given year.



#### D. Discussion and Conclusions

Red alder competition reduced the survival, growth, and yield of Douglas-fir. Results of this experiment showed that the highest proportions of red alder caused the most dramatic reductions in performance of Douglas-fir. However, at low proportions of red alder, there was some evidence that performance of Douglas-fir was better than observed for pure stands of Douglas-fir.

Total height of each species varied as significant linear functions with red alder proportion (Figure 2-2). For Douglas-fir, this relationship was negative, while for red alder was positive. There were also significant response functions in height increment of Douglas-fir during the second, fifth, and sixth years (Figure 2-4a). During the second year, Douglas-fir height increment increased with increasing red alder proportion. However, during the fifth and sixth years the slope of the response for height increment changed direction, such that it was decreasing with increasing red alder proportion. The second-year results suggest that Douglas-fir height increment is able to respond positively to initial crowding from red alder because of competition for light. Cole and Newton (1987) found a similar response for height of red alder growing at a range of densities. Height increment of red alder also responded positively to increases in its own



proportion during the fourth year of the study, when height growth was at its maximum (Figure 2-4a). These results suggest that the intensity of crowding among tree saplings must reach a critical amount before growth in height increases, and that when the intensity of crowding sufficiently exceeds this critical value, height growth begins to decline.

Conifer seedlings grow relatively slow at first. The first year after outplanting, most conifers experience planting shock that results from damage and stress caused during lifting, handling, and planting of the seedlings. This shock, combined with a limited root system, restricts first year height growth (Shepard et al. 1987). This may explain why no differences were found in Douglas-fir height in the first-year after planting.

Responses of absolute size and increment in basal diameter of Douglas-fir to red alder proportion varied from no relationship (years 1-3) to negative linear (year 4) to negative linear or quadratic with slope magnitude increasing with time (years 5 and 6) (Figure 2-3 and 2-5). These changes in Douglas-fir responses suggest that the intensity of red alder competition is increasing with time, and that saplings growing at high proportions of red alder are falling behind in their expected size development. Although absolute size and increment of red alder dbh was not significantly related to red alder proportion (Figure

2-6), in each of years 3-6 the smallest values were observed in the 0.1 red alder proportion. These results suggest that stem-diameter development is greater for stand-grown saplings than for open-grown saplings of red alder.

Stand variables (basal area, volume index, and predicted biomass) of each species increased with their own proportions, simply because these changes in stand composition reflected increases in a species density (Figure 2-7). The one notable difference was that Douglas-fir stand variables were quadratically related, while those for red alder were linearly related, to red alder proportion.

Responses of stand relative yields to red alder proportion, in general, indicate that red alder was the superior competitor when growing in mixture with Douglas-fir (Figure 2-8). The relative yields of red alder were significantly greater than the expected yields for each stand variable, while these for Douglas-fir did not differ from the expected yields. For volume index (Figure 2-8b), the relative yield total was less than 1 in mixture stands, indicating that the observed increases in alder relative yield did not compensate fully for decreases in relative yield of Douglas-fir. These responses in relative yield, in general, conform to a model of negative interference (Radosevich and Holt 1984). Red alder is a more aggressive

competitor than Douglas-fir for resources. One notable deviation from this model was the observation that relative yield of basal area for both species at the 0.1 red alder proportion exceeded their expected yields, with the result that the relative yield total was greater (but not significantly) than 1 (Figure 2-8a). This observation, although not conclusive, suggests that stand mixtures containing a low proportion of red alder may carry more basal area than pure stands of Douglas-fir.

For responses of understory vegetation, only crown volume of herbaceous species varied significantly with red alder proportion. In year 4, the highest values of crown volume occurred in the 0.5 red alder proportion, with lower values observed in the 0.0 and 1.0 proportions (Figure 2-9a). High proportion of red alder may have excluded herbaceous vegetation by reducing light availability to the understory. Low proportions of red alder generally supported a well-developed community of woody vegetation, which likewise may have excluded herbaceous vegetation. It is likely that herbaceous and woody competitors also interfered with development of Douglas-fir, because they formed a relatively homogenous canopy in the understory where Douglas-fir had been relegated as a result of alder competition.

Proportion browsed of Douglas-fir saplings was significantly related to red alder proportion in years 1

and 6 (Figure 2-10a). These relationships were quadratic, with high values of proportion browsed occurring at the 0.75 (both years) and 0.0 (year 1) red alder proportions. Although some evidence suggests that browsing may reduce height growth of Douglas-fir significantly as long as the terminal shoots remain within reach of the deer, other evidence suggests that after terminals grow out of reach, browsed trees tend to catch up with their unbrowsed counterparts (Strothmann and Douglass 1984). In this study, it appears that, at the 0.75 red alder proportion, a combination of red alder competition and animal damage contributed to reductions in sixth-year height increment of Douglas-fir (Figure 2-4a). In each year of the study, proportion browsed was generally lowest at intermediate proportions of red alder (Figure 2-10a). One explanation for these results is that, as long as the intensity of red alder competition does not severely limit height growth of Douglas-fir and therefore render them more vulnerable to animal damage, a low to intermediate proportion of red alder may reduce browsing on Douglas-fir simply by making these saplings less visible to deer.

Significant decreases in survival of Douglas-fir were not detected until year 6, and only for the highest red alder proportion (0.75) (Figure 2-11). In these stands, red alder had formed a closed canopy over the Douglas-fir, causing a high degree of overtopping shade. Although it is

likely that competition from red alder was the primary factor causing mortality of Douglas-fir, other contributing factors would include animal damage and competition from understory vegetation.

### III. Soil Nitrogen Accretion Under Red Alder: Influence on Foliar Nitrogen and Phosphorus of Young Douglas-fir

#### A. Introduction

##### 1. Nitrogen Cycle in Coastal Forests

The nitrogen content of soil is determined in part by climate through temperature and water supply on the activities of plants and microorganisms (Black 1968). Nitrogen that enters terrestrial ecosystems by fixation is an intersystem input from the atmosphere. This can be very important in certain situations, particularly in N-poor successional sites, such as in the postfire development of Douglas-fir forests of Oregon (Waring and Schlesinger 1985).

Red alder is the major hardwood species in coastal forests of the Pacific Northwest. Its abundant seedling regeneration on disturbed forest land and fast early growth make it an unwelcomed competitor of the highly valued Douglas-fir. However, its effects on the site may enhance Douglas-fir yield (Bormann and DeBell 1981). Elementary mineral cycling is faster in ecosystems dominated by red alder than by Douglas-fir --about three to five times

faster for uptake and six to eight times faster for return to the forest floor (Cole et al. 1978).

## 2. Rates of Nitrogen Fixation and Accretion Under Red Alder

Red alder is a nonleguminous, nitrogen-fixing woody plant and the major hardwood tree species in the Douglas-fir region of the Pacific Northwest (Tarrant et al. 1969). Nitrogen fixation by red alder typically accelerates N cycling in forest ecosystems even more than it increases N capital (Binkley et al. 1985). The generally faster cycling associated with deciduous trees has led to speculation that a deciduous component may increase nutrient turnover and thereby enhance productivity of conifer stands. The contribution of red alder to ecosystem production includes both the biomass of the red alder itself and many stimulatory effects of increased N availability on conifer growth (Binkley and Husted 1983).

Red alder fixes atmospheric nitrogen through its symbiosis with the root-nodule bacteria, Frankia spp. Annual rates of nitrogen accretion in naturally established stands of red alder have been estimated to be 85 kg/ha/year (Cole et al. in 1978), 100 kg/ha/year (Bormann and DeBell 1981), and 320 kg/ha/year (Newton et al. 1968).

Using a regression analysis of soil nitrogen content versus age, Bormann and DeBell (1981) estimated that nitrogen had accumulated at a nearly constant rate of about 35 kg/ha/year in mineral soil (0 to 20 cm depth) beneath a stand of red alder. They found that forest-floor N increased linearly from 10 to 40 years at a rate of 15 kg/ha/year, after an apparently rapid build-up in the first decade.

In a study of 27-year-old forest stands, Tarrant (1961) found that beneath a red alder-Douglas-fir mixture, total soil nitrogen was 65% greater than beneath a pure Douglas-fir stand. Even in the pure Douglas-fir stand, however, soil nitrogen content exceeded values established as indicators of low nitrogen status. In turn, the greater soil nitrogen supply beneath the mixed stand was reflected in results of analyses that showed Douglas-fir growing with alder had significantly more foliar nitrogen than did Douglas-fir growing alone. Conclusions from this study suggested that presence of red alder in this Douglas-fir plantation contributed to increased growth of dominant Douglas-fir, beginning at an age of 20 years.



### 3. Relationship of Foliar and Soil Nutrients for Trees

Nutrient concentrations in the foliage of forest tree species range widely in response to many factors including variability in soil nutrient availability that exists among sites. When nutrients are added to deficient soils, the relative growth rate in biomass of trees may increase, so that no increase in foliar nutrient concentration is observed. Instead, nutrients are distributed throughout a larger amount of biomass per tree. However, when factors such as light are limiting, nutrients may be taken up in excess of immediate metabolic requirements. This storage results in high concentrations in foliage (Waring and Schlesinger 1985).

Conifers appear to be particularly adapted to conditions of relatively low nutrient availability. In comparison with deciduous species, conifers have low photosynthetic rates and low foliar nutrient concentrations (Bockheim and Leide 1991).

Observed changes in trees, such as a greater abundance of dark green foliage and a greater increment in biomass, are often attributed to the nutritional effect of N accumulated in the soil. This additional N is beneficial in the Pacific Northwest, where tree nutrition and growth are typically N limited (Cole et al. 1978).

Brozek (1990) reported significant differences in biomass and nutrient concentration of 6-year-old seedlings of Douglas-fir growing for 4 years on sites formerly occupied by mature Douglas-fir or red alder. The Douglas-fir seedlings grown on the former red alder site showed increases of 65, 41, and 45% in biomass of current-year twigs, older twigs, and stems, respectively, over that of seedlings grown on the former Douglas-fir sites. The seedlings on the red alder site showed an increase in N and decreases in P, Ca, and Mg concentrations. There were also higher N/P and N/K ratios and lower availability of soil P.

In a study of nutrients in 5-year-old Douglas fir plantations under variable competition, nitrogen and phosphorus concentrations at high stand densities were lower than for those at low densities (Cole and Newton 1986). However, total nutrient content of foliage per hectare was greatest at high densities because of higher leaf area indices. In Cole and Newton's study, the nutrient analyses indicated that red alder had not yet contributed to increased nitrogen levels in either Douglas-fir foliage or soil.

Increased N availability from fixation by red and Sitka alder may have led to decreased fine root production by associated Douglas-fir so that a greater proportion of the total photosynthate was allocated to stem growth (Binkley, 1984).

#### 4. Scope, Objectives and Hypotheses

It is well documented that the presence of red alder can have a notable effect on the soil, nutrition, and growth of forest stands. The result of red alder's ability to fix nitrogen has frequently shown significant accretion of this nutrient in forest soils (Berg and Doerksen 1975, Cole et al. 1978, Tarrant et al. 1969, Zavitkovski and Newton 1967). This accretion can benefit red alder neighbors such as Douglas-fir, which is commonly found in association.

The effects of red alder on young Douglas-fir can vary depending on the proportion of the stand occupied by each species. Since nitrogen is one of the most important elements for tree growth, poor growth rates can result from nitrogen deficiency. Also, other factors such as interspecific and intraspecific competition for light and soil water can have important influences on growth.

Previous research on interactions between Douglas-fir and red alder has not attempted to link soil and plant responses. Identification of causal relationships is needed in order to ascertain the mechanisms of interactions between these two species. Therefore, the objectives for this study were to:

1. Identify differences in nitrogen and phosphorus concentrations in soil and in foliage of young Douglas-fir in the presence versus absence of red alder.

2. Describe relationships of nitrogen and phosphorus in foliage of young Douglas-fir versus that in soil collected adjacent to each sapling.

3. Determine if growth of young Douglas-fir is associated with levels of nitrogen and phosphorus in soil collected adjacent to each sapling.

This study tested the following hypotheses: (1) Soil nitrogen, phosphorus, carbon, and pH do not differ significantly between alder present and alder absent treatments; and (2) For a given amount of soil nitrogen, foliar nitrogen of Douglas-fir does not differ significantly between alder present and alder absent treatments.

## B. Methods

### 1. Site Description and Treatments

The experiment was conducted on the Cascade Head Experimental Forest near Otis, Oregon. The study site is located at T6S R10W S15 and S22 and has an elevation of 330 m above sea level. In the summer of 1985, the previous 120-year-old stand of Sitka spruce (Picea sitchensis) and western hemlock (Tsuga heterophylla) was clearcut harvested and the site was broadcast burned in the fall. The soil varies from very dark grayish brown loams, to silt loams. Slopes are between 0 to 50 percent. The site occurs within the Pacific Coast fog belt. The average minimum temperature is 20.2°C and the average maximum temperature is 20.9°C. Average annual precipitation is 2500 mm. The distribution of the high precipitation is between October and May, often in form of cloud condensation. Low precipitation occurs during June through September with only 3 to 4 weeks without rainfall.

The study was accomplished in an existing Douglas-fir/red alder replacement series experiment that was planted in March 1986. Vegetation plots in a replacement series have a fixed plant density but varying species proportion (Radosevich and Holt 1984). The size of each

plot was 0.073 ha (27 X 27 m), and the trees were planted on a 3- X 3-m spacing. Seedling mortality was replaced during each of the first three growing seasons. Each plot consisted of 81 saplings (9 X 9 rows), and the two outermost rows were designated as border rows, and therefore were not included in the tree measurements.

For this study the following species proportions (Douglas-fir/red alder) were used: 1.0/0.0, 0.5/0.5, and 0.0/1.0 (Figure 2-1). Each proportion was replicated three times in a randomized complete block design.

## 2. Vegetation and Soil Measurements

Measurements of soil nutrient concentrations (elemental kg/ha) were made to determine if they varied significantly depending on the presence or absence of red alder. Prior to collecting soil samples, a soil pit of 1-m depth was dug near study plots to determine the rooting depth and spatial distribution of red alder roots. Values of bulk density used to calculate kg/ha of each element were taken at the beginning of the study (1986) for 0-15, 15-30 and 60-90 cm depths (1.28, 0.44, and 0.63 g/cm<sup>3</sup> respectively).

Soil samples were collected during late March 1991 to coincide with the timing of baseline samples taken in 1986.

Three samples were taken in each treatment plot at each of three depths (depth 1=0-15, depth 2=15-30 and depth 3=60-90 cm) for a total of 81 samples. Sample points were located systematically in each plot in 1986. At each sample point the litter layer was removed to expose mineral soil. A Veihmeyer tube was pounded into the ground with which to extract soil samples. Each soil sample consisted of a 2-cm core, 15-30 cm in length. Soil samples were refrigerated immediately after collection, and processed for nutrient analyses as soon as possible.

The soil samples were analyzed for: "available" N (initial  $\text{NH}_4$ , initial  $\text{NO}_3$  and mineralizable  $\text{NH}_4$ ); total N,P,C; and pH. Two analyses were required to estimate available N. In the first analysis, initial concentration of  $\text{NH}_4$  and  $\text{NO}_3$  were measured by weighing 5-10 g of fresh soil, adding 2N KCl, placing the samples on a shaker for an hour, filtering the aqueous extract and analyzing for  $\text{NO}_3$  and  $\text{NH}_4$  analysis with a Alpkem Rapid Flow Analyzer 388. The other analysis was to determine mineralizable  $\text{NH}_4$ , which consisted of incubating 5-10 g soil sample at 40°C for one week, adding 4N KCl to bring the solution to 2N, and proceeding as in the first test.

The micro-Kjeldahl method (Nelson and Sommers 1972) was used to determine total N and P. This method consisted of combining dried and ground soil with accelerator and 10 ml concentrated  $\text{H}_2\text{SO}_4$ . The solution was gradually heated

and then maintained at 350°C until it turned clear. The sample was brought to a 75-ml volume with distilled water. An aliquot was submitted to the soils testing lab (Department of Forest Science, Oregon State University) for  $\text{NH}_4$  and  $\text{PO}_4^{-2}$  analysis with a Alpkem Rapid Flow Analyzer 388.

The Carlo-Erba NA 1500 Series 2 CNS Analyzer was used to determine total C. Samples of dry, ground soil, 0.3 g each, were wrapped in tin foil, placed in a crucible with Fe and Cu accelerator chips. The sample was heated to oxidize all carbon, and  $\text{CO}_2$  released from the process was measured.

For measurements of pH, 15 ml of distilled water were added to 15 g of fresh soil, the solution was stirred and another 15 ml of distilled water were added. The solution was stirred two more times at 30-minute intervals, and then pH was measured with a Coring Model 215 pH meter.

Douglas-fir foliar nitrogen was measured to determine if it varied significantly depending on the presence or absence of red alder. Two species proportions (Douglas-fir/red alder) were used in this experiment: 1.0/0.0 and 0.5/0.5. The experimental unit was an individual Douglas-fir tree. Foliage was sampled from three trees per plot, for a total of 18 saplings. Each sapling was located within 1 m of the point at which soil samples were collected. Each sapling was measured for basal stem



diameter (at 2 cm height), dbh (at 137 cm height), and height. The sampling was done in early March 1991 before initiation of shoot growth.

Samples were collected from each tree to represent three classes of foliage: class 1=current-year foliage from the top half of the crown; class 2=current-year foliage from the bottom half of the crown; and class 3=2+ year-old foliage. Each sample consisted of two subsamples that were pooled, one from the south side of the crown, and one from the north side of the crown. A portion of each sample was used to estimate specific leaf area ( $\text{cm}^2$  leaf area/g foliage dry weight).

The samples were refrigerated immediately after collection. Within 24 hours each sample was dried at  $70^\circ\text{C}$  to a constant weight. The dried needles were ground until they passed through a 40-mesh screen (Lavender 1970). Samples were analyzed for nitrogen and phosphorus by micro-kjeldahl techniques (Nelson and Sommers 1972).

In order to predict total above-ground and foliar biomass for saplings in the study, a total of 44 Douglas-fir were destructively sampled from 1987 to 1991. These saplings were selected to represent a range of sizes and species proportions from extra replacement series plots that were established adjacent to the study. Just prior to harvesting, each sapling was measured for basal stem diameter, dbh, height, and crown width.

Each tree was severed at groundline and returned to the laboratory where foliage and woody components were separated, dried at 70°C to a constant weight, and weighed. For twenty of the Douglas-fir, which were collected in 1991, foliage was separated into each of the three classes (described above) prior to drying.

### 3. Statistical Analysis

Analysis of variance was used to detect significant ( $\alpha=0.05$ ) differences in the soil variables (Table 3-1) among species proportions and depths. A split-plot experimental design was used with soil sample points within a treatment replication as main plots and depth within sample points as split plots. Orthogonal contrasts were used to make the following two comparisons of the soil variables: 1) average of depth 1 (0-15 cm) and depth 2 (15-30 cm) versus depth 3 (60-90 cm), and 2) depth 1 (0-15 cm) versus depth 2 (15-30 cm). If the treatment X depth or treatment X foliage class interactions were significant ( $p \leq 0.05$ ), least-squares treatment means within a given depth or foliage class were compared using a protected LSD test (Petersen 1985).

Table 3-1. Abbreviations and definitions of soil variables.

Variables	Units	Description
iniNH <sub>4</sub> -N1	kg/ha	Initial NH <sub>4</sub> -N at 0-15 cm depth
iniNH <sub>4</sub> -N2	kg/ha	Initial NH <sub>4</sub> -N at 15-30 cm depth
iniNH <sub>4</sub> -N3	kg/ha	Initial NH <sub>4</sub> -N at 60-90 cm depth
iniNO <sub>3</sub> -N1	kg/ha	Initial NO <sub>3</sub> -N at 0-15 cm depth
iniNO <sub>3</sub> -N2	kg/ha	Initial NO <sub>3</sub> -N at 15-30 cm depth
iniNO <sub>3</sub> -N3	kg/ha	Initial NO <sub>3</sub> -N at 60-90 cm depth
minNH <sub>4</sub> -N1	kg/ha	Mineralizable NH <sub>4</sub> -N at 0-15 cm depth
minNH <sub>4</sub> -N2	kg/ha	Mineralizable NH <sub>4</sub> -N at 15-30 cm depth
minNH <sub>4</sub> -N3	kg/ha	Mineralizable NH <sub>4</sub> -N at 60-90 cm depth
TN1	kg/ha	Total nitrogen at 0-15 cm depth
TN2	kg/ha	Total nitrogen at 15-30 cm depth
TN3	kg/ha	Total nitrogen at 60-90 cm depth
TP1	kg/ha	Total phosphorus at 0-15 cm depth
TP2	kg/ha	Total phosphorus at 15-30 cm depth
TP3	kg/ha	Total phosphorus at 60-90 cm depth
C1/N1	-----	Carbon/nitrogen ratio at 0-15 cm
C2/N2	-----	Carbon/nitrogen ratio at 15-30 cm
C3/N3	-----	Carbon/nitrogen ratio at 60-90 cm
Nindex-1	kg/ha	Available nitrogen index at 0-15 cm depth
Nindex-2	kg/ha	Available nitrogen index at 15-30 cm depth
Nindex-3	kg/ha	Available nitrogen index at 60-90 cm depth
NO <sub>3</sub> -N1	kg/ha	Nitrogen in NO <sub>3</sub> at 0-15 cm depth
NO <sub>3</sub> -N2	kg/ha	Nitrogen in NO <sub>3</sub> at 15-30 cm depth
NO <sub>3</sub> -N3	kg/ha	Nitrogen in NO <sub>3</sub> at 60-90 cm depth
PH1	-----	pH at 0-15 cm depth
PH2	-----	pH at 15-30 cm depth
PH3	-----	pH at 60-90 cm depth
DPH1	-----	pH accretion at 0-15 cm depth
DPH2	-----	pH accretion at 15-30 cm depth
DPH3	-----	pH accretion at 60-90 cm depth
DiniNH <sub>4</sub> -N1	kg/ha	Initial NH <sub>4</sub> -N accretion at 0-15 cm depth
DiniNH <sub>4</sub> -N2	kg/ha	Initial NH <sub>4</sub> -N accretion at 15-30 cm depth
DiniNH <sub>4</sub> -N3	kg/ha	Initial NH <sub>4</sub> -N accretion at 60-90 cm depth
DiniNO <sub>3</sub> -N1	kg/ha	Initial NO <sub>3</sub> -N accretion at 0-15 cm depth
DiniNO <sub>3</sub> -N2	kg/ha	Initial NO <sub>3</sub> -N accretion at 15-30 cm depth
DiniNO <sub>3</sub> -N3	kg/ha	Initial NO <sub>3</sub> -N accretion at 60-90 cm depth
DminNH <sub>4</sub> -N1	kg/ha	Mineralizable NH <sub>4</sub> -N accretion at 0-15 cm depth
DminNH <sub>4</sub> -N2	kg/ha	Mineralizable NH <sub>4</sub> -N accretion at 15-30 cm depth
DminNH <sub>4</sub> -N3	kg/ha	Mineralizable NH <sub>4</sub> -N accretion at 60-90 cm depth
DTN1	kg/ha	Total nitrogen accretion at 0-15 cm depth
DTN2	kg/ha	Total nitrogen accretion at 15-30 cm depth
DTN3	kg/ha	Total nitrogen accretion at 60-90 cm depth
DTP1	kg/ha	Total phosphorus accretion at 0-15 cm depth
DTP2	kg/ha	Total phosphorus accretion at 15-30 cm depth
DTP3	kg/ha	Total phosphorus accretion at 60-90 cm depth
DC1/N1	-----	Carbon/nitrogen ratio change at 0-15 cm
DC2/N2	-----	Carbon/nitrogen ratio change at 15-30 cm
DC3/N3	-----	Carbon/nitrogen ratio change at 60-90 cm
DNindex-1	kg/ha	Available nitrogen index accretion at 0-15 cm
DNindex-2	kg/ha	Available nitrogen index accretion at 15-30 cm
DNindex-3	kg/ha	Available nitrogen index accretion at 60-90 cm
DNO <sub>3</sub> -N1	kg/ha	NO <sub>3</sub> -N accretion at 0-15 cm depth
DNO <sub>3</sub> -N2	kg/ha	NO <sub>3</sub> -N accretion at 15-30 cm depth
DNO <sub>3</sub> -N3	kg/ha	NO <sub>3</sub> -N accretion at 60-90 cm depth

Multiple regression models were developed to enable predictions of biomass of needles per Douglas-fir foliar class and for entire trees (Table 3-2). The following model forms were tested and one was selected for each dependent variable:

$$B = b_0 + b_1 (\text{overtop}) + b_{11} (\text{volindx}) + b_{12} (\text{overtop})(\text{volindx})$$

$$\text{Log } B = b_0 + b_1 (\text{overtop}) + b_{11} (\text{volindx}) + b_{12} (\text{overtop})(\text{log volindx})$$

$$\text{Log } B = b_0 + b_1 (\text{overtop}) + b_{11} (\text{log volindx}) + b_{12} (\text{overtop})(\text{log volindx})$$

where B is the biomass of wood or needles per foliar class or total wood or needles per tree, and  $b_0$ ,  $b_1$ ,  $b_{11}$  and  $b_{12}$  are regression coefficients, overtop is an indicator variable of presence (1) versus absence (0) of red alder, and volindx is stem volume index, a commonly used predictor of tree biomass (Zavitkovski and Stevens 1972, DeBell et al. 1989, Shainski and Radosevich 1992), which was calculated as height X (stem diameter)<sup>2</sup>. The best model to describe the data was chosen on the basis of the highest adjusted R<sup>2</sup> (from regressions of predicted B versus observed B) and the lowest mean-squared error.

Biomass per foliage class was predicted for each of the 18 Douglas-fir saplings with the biomass equations (Table 3-2). These equations were used to calculate, for each foliage class, the variables listed in Table 3-3.

Analysis of variance was used to detect significant

Table 3-2. Regression coefficients for predicting biomass (g) components of Douglas-fir. Values reported for  $S_{y.x}$  and adjusted  $R^2$  were calculated using untransformed dependent variables.

Dependent <sup>1</sup> variable	Eq. <sup>2</sup> #	$b_0$	Regression Coefficients				$S_{y.x}$	Adj. $R^2$	n
			$b_{01}$	$b_1$	$b_{11}$				
Totfol	2	4.727	-6.276E-1	8.133E-1	----	43.977	.942	44	
Totwood	2	5.385	----	9.073E-1	----	52.925	.988	44	
Ndltop	2	7.384E-1	----	2.567E-1	----	1.452	.162	20	
Ndlbot	1	4.023	-7.410	3.864	----	3.916	.940	20	
Ndl2yr	1	3.071	-4.049	1.196	1.838	2.571	.791	20	
Woodtop	1	1.391	----	6.166E-1	----	1.046	.805	20	
Woodbot	1	8.637	-3.161	2.163	----	1.994	.946	20	
Wood2yr	2	2.944	----	8.850E-1	----	6.665	.977	20	

<sup>1</sup>Variables description:

Totfol	Total foliage biomass
Totwood	Total wood biomass
Ndltop	Current needles biomass from the top half of the crown
Ndlbottom	Current needles biomass from the bottom half of the crown
Ndl2yr	2+ year-old needles biomass from the entire tree

<sup>2</sup>Equations:

1.  $Y = b_0 + b_{01} * \text{overtop} + b_1 * \text{volindx1} + b_{11} * \text{overtop} * \log \text{volindx1}$   
 Weighted least squares were used to estimate parameters for model 1.  
 2.  $\log(Y) = b_0 + b_{01} * \text{overtop} + b_1 * \log \text{volindx1} + b_{11} * \text{overtop} * \log \text{volindx1}$

Where

$\text{volindx1}$	$= (\text{basal diameter (dm)})^2 * \text{height (dm)}$ ,
$\text{volindx2}$	$= (\text{dbh (dm)})^2 * \text{height (dm)}$ , and
$\text{overtop}$	$= 1$ if Douglas-fir proportion $\leq 0.5$ , else
$\text{overtop}$	$= 0$

Table 3-3. Abbreviations and definitions of variables of Douglas-fir sapling size and foliar nutrient and biomass content.

Variable	Units	Description
BD	mm	Basal diameter measured at 2 cm above ground.
DBH	mm	Diameter at breast height measured at 137 cm above ground.
		HT cm Total
		height of the seedlings.
LA1	m <sup>2</sup>	Leaf area for the top 1-year-old foliage
LA2	m <sup>2</sup>	Leaf area for the bottom 1-year-old foliage
LA3	m <sup>2</sup>	Leaf area for the 2+ year-old foliage
N/LA1	g/m <sup>2</sup>	N per leaf area of the top 1-year-old foliage
N/LA2	g/m <sup>2</sup>	N per leaf area of the bottom 1-year-old foliage
N/LA3	g/m <sup>2</sup>	N per leaf area of the 2+ year-old foliage
P/LA1	g/m <sup>2</sup>	P per leaf area of the top 1-year-old foliage
P/LA2	g/m <sup>2</sup>	P per leaf area of the bottom 1-year-old foliage
P/LA3	g/m <sup>2</sup>	P per leaf area of the 2+ year-old foliage
Biomass1	g	Biomass of the top 1-year-old foliage
Biomass2	g	Biomass of the bottom 1-year-old foliage
Biomass3	g	Biomass of the 2+ year-old foliage
N1	g	N in the top 1-year-old foliage
N2	g	N in the bottom 1-year-old foliage
N3	g	N in the 2+ year-old foliage
P1	g	P in the top 1-year-old foliage
P2	g	P in the bottom 1-year-old foliage
P3	g	P in the 2+ year-old foliage
%N1	%	N percent in the top 1-year-old foliage
%N2	%	N percent in the bottom 1-year-old foliage
%N3	%	N percent in the 2+ year-old foliage
%P1	%	P percent in the top 1-year-old foliage
%P2	%	P percent in the bottom 1-year-old foliage
%P3	%	P percent in the 2+ year-old foliage
SLA1	cm <sup>2</sup> /g	Specific leaf area in the top 1-year-old foliage
SLA2	cm <sup>2</sup> /g	Specific leaf area in the bottom 1-year-old foliage
SLA3	cm <sup>2</sup> /g	Specific leaf area in the 2+ year-old foliage
TBiomass	g	Total biomass per sapling
TotalN	g	Total nitrogen per sapling
TotalP	g	Total phosphorus per sapling
TLA	m <sup>2</sup>	Total leaf area per sapling
TN/LA	g/m <sup>2</sup>	Total nitrogen per leaf area per sapling
TP/LA	g/m <sup>2</sup>	Total phosphorus per leaf area per sapling

( $\alpha=0.05$ ) differences among species proportions and foliage classes). A split plot experimental design was used with trees within a treatment replication as main plots and foliar classes within trees as split plots. Orthogonal contrasts were used to test for treatment differences in: 1) average of class 1 (top current-year foliage) and class 2 (bottom current-year foliage) versus class 3 (2+ year-old foliage), and 2) class 1 (top current-year foliage) versus class 2 (bottom current-year foliage).

Current amount and six-year change (1986-1991) in soil nitrogen, phosphorus, carbon (converted to elemental kg/ha), and pH were calculated for each depth. For depth 3 (60-90 cm), current amount and six-year change in soil nitrogen, phosphorus, carbon and pH were calculated and then divided by two in order to adjust the sample volume to make it comparable to depths 1 and 2.

Relationships of foliar nutrient content and growth of individual Douglas-fir versus current and six-year change (1986-1991) in the soil variables were tested with correlation and regression analyses (SAS 1988). Indicator variables were specified in order to estimate a full regression model which contained separate slopes and intercepts for each of the two species proportions. The extra sum-of-squares approach was used to reduce the full model to those variables that were significant ( $\alpha=0.05$ ) (Neter et al. 1989).

## C. Results

### 1. Soil Nitrogen, Phosphorus, Carbon, and pH

Observations for the soil pit revealed that nodules of red alder were particularly abundant in the top 10 cm of soil, lateral roots of diameter < 5 mm permeated the soil well below the maximum depth of the soil pit (1 m), and clay subsoil was detected at 50 to 70 cm depth.

Differences in soil nutrients among species proportions were found only for mineralizable  $\text{NH}_4\text{-N}$  at the 15-30 cm depth in year 6 (Table 3-4). In pure stands of Douglas-fir, mineralizable  $\text{NH}_4\text{-N}$  (73.14 kg/ha) was significantly ( $p \leq 0.05$ ) higher than in mixed stands of Douglas-fir and alder (52.79 kg/ha) and than in pure stands of red alder (51.07 kg/ha) (Figure 3-1a). Average mineralizable  $\text{NH}_4\text{-N}$  at the 60-90 cm depth (44.69 kg/ha) was significantly ( $p = 0.02$ ) lower than that for the average of the 0-15 and 15-30 cm depth (57.67 kg/ha).

Available N did not differ significantly ( $p > 0.05$ ) among the species proportions in year 6; however, the magnitude of responses was similar to that observed for mineralizable  $\text{NH}_4$ . Available N at the 60-90 cm depth (43.34 kg/ha) was significantly lower ( $p = 0.001$ ) than the



Table 3-4. Responses of 1986 and 1991 soil nutrient content (kg/ha) to soil depth and Douglas-fir/red alder species proportion. See Table 3-1 for definitions of the soil variables.

Soil Variable	Species Proportion (Douglas-fir/red alder)					
	1.0/0.0		0.5/0.5		0.0/1.0	
	1986	1991	1986	1991	1986	1991
iniNH <sub>4</sub> -N1	2.21	3.33	1.53	3.41	2.10	4.96
iniNH <sub>4</sub> -N2	3.40	6.64	10.18	3.68	7.33	4.39
iniNH <sub>4</sub> -N3	18.08	3.74	7.86	4.67	146.95	6.35
minNH <sub>4</sub> -N1	159.29	69.05	952.51	49.84	85.18	50.15
minNH <sub>4</sub> -N2	593.64	73.14*	130.60	52.79	6064.45	51.07
minNH <sub>4</sub> -N3	2131.53	33.96 <sup>1</sup>	2123.38	50.20 <sup>1</sup>	630.53	49.92 <sup>1</sup>
iniNO <sub>3</sub> -N1	----	2.38	18.99	3.64	6.31	6.95
iniNO <sub>3</sub> -N2	----	3.27	15.28	3.29	2.70	5.43
iniNO <sub>3</sub> -N3	20.12	1.48	35.54	2.86	23.98	6.37
Nindex-1	----	68.10	172.65	50.07	72.30	52.14
Nindex-2	----	69.77	228.79	52.40	47.46	52.10
Nindex-3	1451.11	31.70 <sup>1</sup>	354.88	48.39 <sup>1</sup>	212.49	49.93 <sup>1</sup>
TN1	2847.46	4864.20	2915.29	4510.00	2035.15	4565.00
TN2	4596.90 <sup>2</sup>	5242.65	3358.22 <sup>2</sup>	4792.20	2904.41 <sup>2</sup>	4148.55
TN3	8213.27 <sup>1</sup>	3577.49	9338.18 <sup>1</sup>	5161.31	8995.58 <sup>1</sup>	5214.68
TP1	1210.95	1426.33	1019.63	1094.87	1061.72	1055.27
TP2	1496.36	1957.20	1063.65	1555.05	1112.86	1563.45
TP3	3685.07 <sup>1</sup>	2631.89 <sup>1</sup>	3236.81 <sup>1</sup>	2505.95 <sup>1</sup>	2700.40 <sup>1</sup>	3060.93 <sup>1</sup>
TC1	60909.42	92901.60	59483.60	99440.73	51851.07	106410.33
TC2	86655.45	96799.50	81476.85	98694.75	66137.40	87163.65
TC3	179476.20 <sup>1</sup>	60503.47	165181.20 <sup>1</sup>	92927.10	193314.41 <sup>1</sup>	110144.28
C/N1	19.84	18.69	19.62	21.98	23.89	21.88
C/N2	18.58	18.40	22.05	20.21	22.65	20.25
C/N3	22.37	16.30 <sup>1</sup>	18.24	17.61 <sup>1</sup>	20.41	19.76 <sup>1</sup>
NO <sub>3</sub> -N1	----	2812.31	6108.05	3296.74	4621.88	4138.03
NO <sub>3</sub> -N2	----	4055.09 <sup>2</sup>	8943.63	3917.19 <sup>2</sup>	6353.93	5291.46 <sup>2</sup>
NO <sub>3</sub> -N3	19119.02	5177.87 <sup>1</sup>	18764.32	5724.15 <sup>1</sup>	15321.41	9143.01 <sup>1</sup>
pH1	5.00	5.01	4.88	4.96	4.99	4.74
pH2	4.84	4.98	4.88	5.18	5.15	4.99
pH3	4.75	5.29	5.03	5.16	4.83	5.05

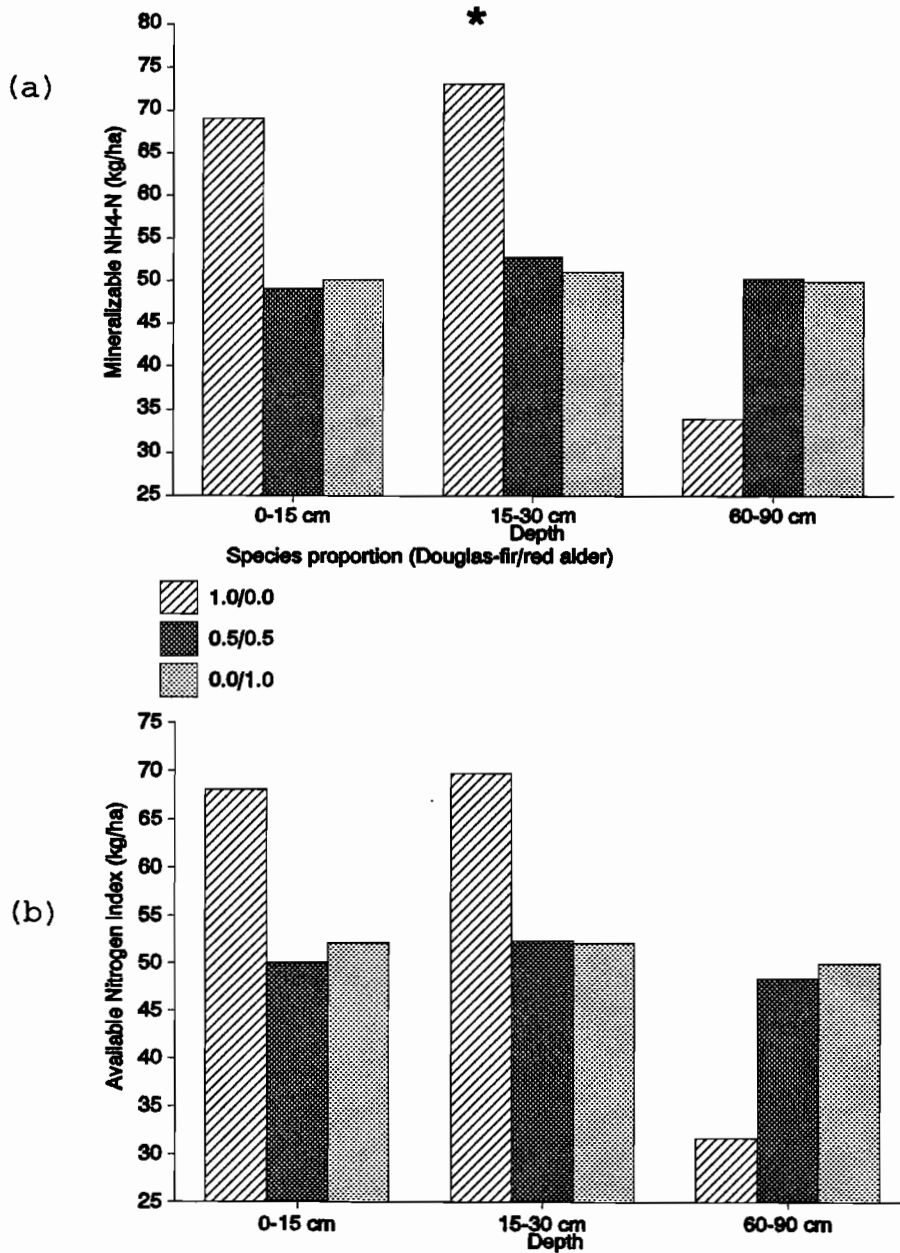
\*Significant ( $p \leq 0.05$ ) species proportions.

<sup>1</sup>Significant ( $p \leq 0.05$ ) differences between the average of depth 1 (0-15 cm) and depth 2 (15-30 cm) versus depth 3 (60-90 cm).

<sup>2</sup>Significant ( $p \leq 0.05$ ) differences between depth 1 (0-15 cm) and depth 2 (15-30 cm).

---- Missing data.

Figure 3-1. Responses of 1991 (a) mineralizable NH<sub>4</sub>-N and (b) available N index (kg/ha) to soil depth and Douglas-fir/red alder species proportion. Significant differences among species proportions are indicated with an asterisk (\*). Differences among depths are described in the text.



average available N at the 0-15 and 15-30 cm depths (57.43 kg/ha) (Figure 3-1b).

Although total N in the first and sixth year did not vary significantly ( $p > 0.05$ ) among species proportions, there were significant differences in the orthogonal contrasts in 1986. Independent of species proportion, total N at 60-90 cm depth (8849 kg/ha) was significantly ( $p = 0.0001$ ) greater than that for the average of the 0-15 and 15-30 cm depths (3109.57 kg/ha) (Figure 3-2a). Total N at the 0-15 cm depth (2599.3 kg/ha) was also significantly ( $p = 0.02$ ) different from the 15-30 cm depth (3619.84 kg/ha).

In both the first and the sixth years, total C did not vary significantly ( $p > 0.05$ ) among species proportions; however, it did vary by depth. In 1986, total C was significantly ( $p = 0.001$ ) greater at 60-90 cm depth (179323.94 kg/ha) than for the average of the 0-15 and 15-30 cm depths (67752.30 kg/ha) (Figure 3-2b). Such differences among depths were not detected in the sixth-year data.

No significant differences ( $p \leq 0.05$ ) were found among red alder proportions for total P; however, in 1986, total P at 60-90 cm depth (3207.43 kg/ha) was significantly higher ( $p = 0.0001$ ) than that for the average of 0-15 and 15-30 cm depths (1163.53 kg/ha) (Figure 3-3a). In the sixth year, a significant difference ( $p = 0.001$ ) was also found for total P between the 60-90 cm depth (2732.92 kg/ha) and the

Figure 3-2. Responses of 1986 (a) total nitrogen and (b) total carbon (kg/ha) to soil depth and Douglas-fir/red alder species proportion. Differences among depths are described in the text.

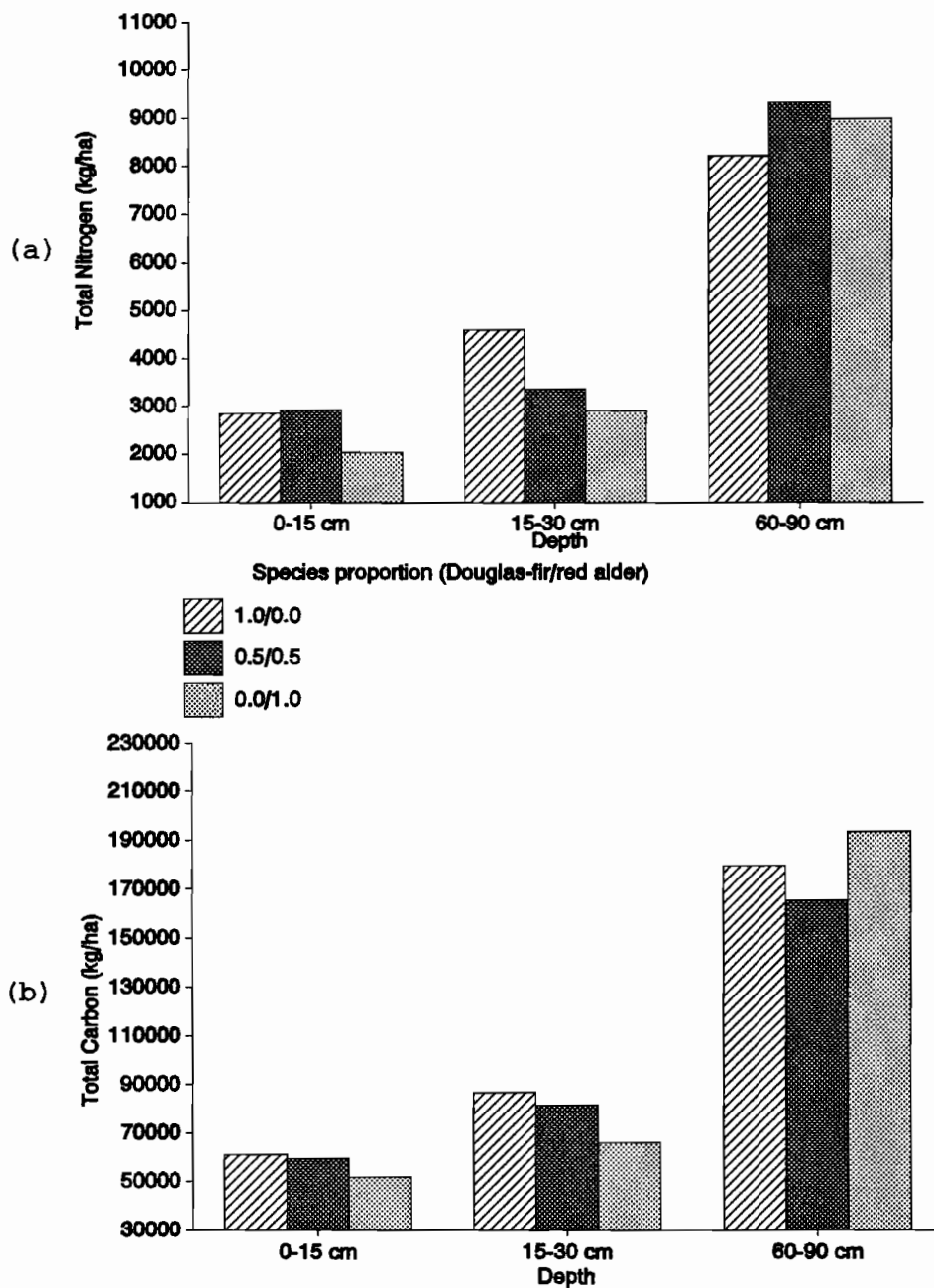
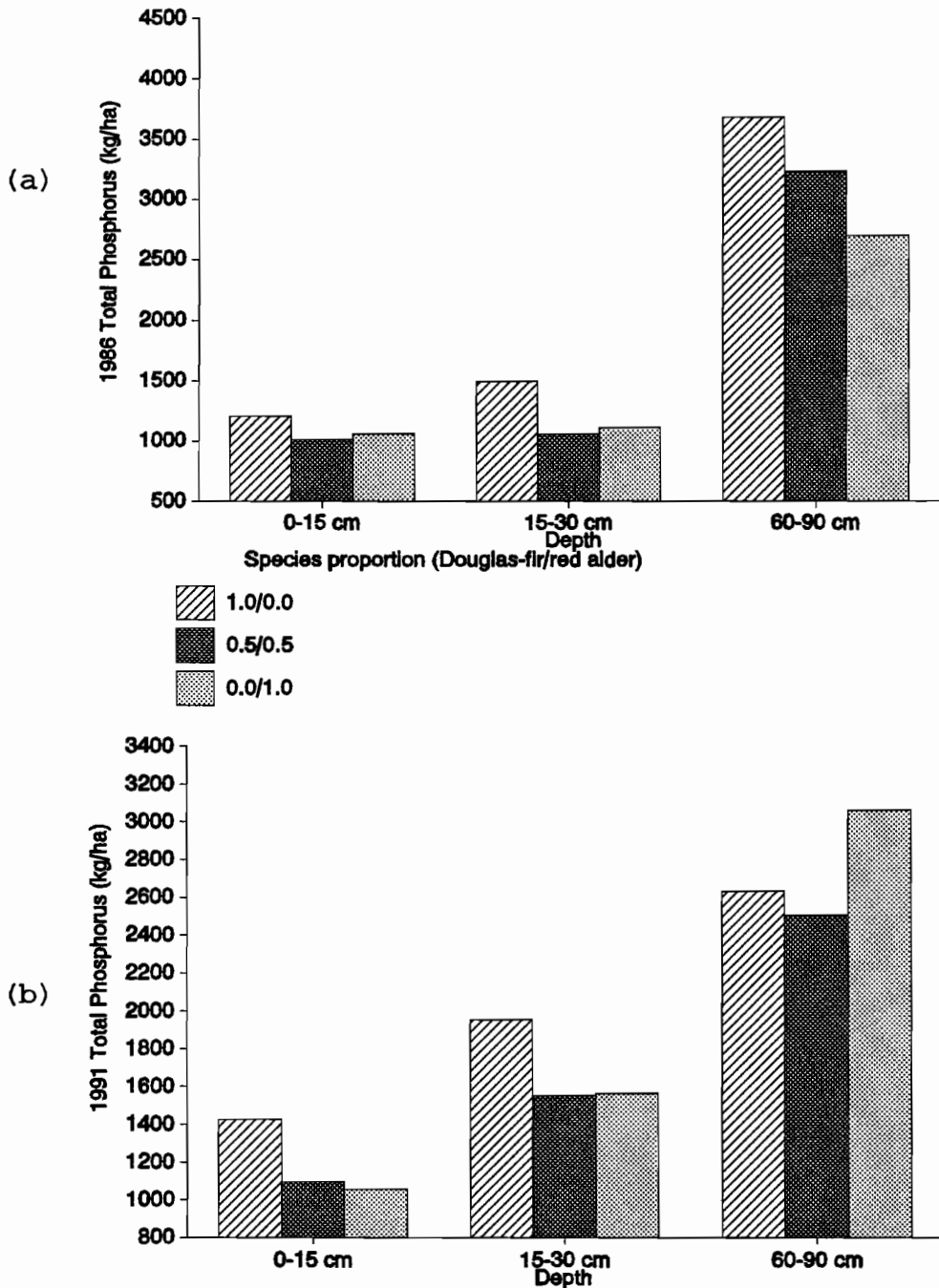


Figure 3-3. Responses of (a) 1986 and (b) 1991 total phosphorus (kg/ha) to soil depth and Douglas-fir/red alder species proportion. Differences among depths are described in the text.



average of the 0-15 and 15-30 cm depths (1442.03 kg/ha) (Figure 3-3b).

The ratio of total carbon to total nitrogen (C/N) did not vary significantly ( $p>0.05$ ) among species proportions for either 1986 or 1991 data. However, in year 6 the C/N ratio at the 60-90 cm depth (17.89) was significantly ( $p=0.004$ ) less than that for the 0-15 and 15-30 cm depths (20.24) (Figure 3-4a).

Soil content of  $\text{NO}_3\text{-N}$  did not differ significantly ( $p>0.05$ ) among species proportions.  $\text{NO}_3\text{-N}$  at the 60-90 cm depth (6681.68 kg/ha) was significantly higher ( $p=0.0001$ ) than the mean of the 0-15 cm and 15-30 cm depths (3918.47 kg/ha). At the 0-15 cm depth,  $\text{NO}_3\text{-N}$  percent (3415.69 kg/ha) was significantly ( $p=0.05$ ) lower than that at the 15-30 cm depth (4421.25 kg/ha) (Figure 3-4b).

The average change in total N (1986-91) for the 0-15 and 15-30 cm depths (1577.53 kg/ha) was significantly higher ( $p=0.001$ ) than that at the 60-90 cm depth (-4197.85 kg/ha) (Table 3-5). The average change in total C differed significantly ( $p=0.001$ ) between the 60-90 cm depth (-91465.65 kg/ha) and the average of the 0-15 and 15-30 cm depths (29149.46 kg/ha) (Table 3-5).

Figure 3-4. Responses of 1991 (a) carbon/nitrogen ratio and (b) NO<sub>3</sub>-N (kg/ha) to soil depth and Douglas-fir/red alder species proportion. Differences among depths are described in the text.

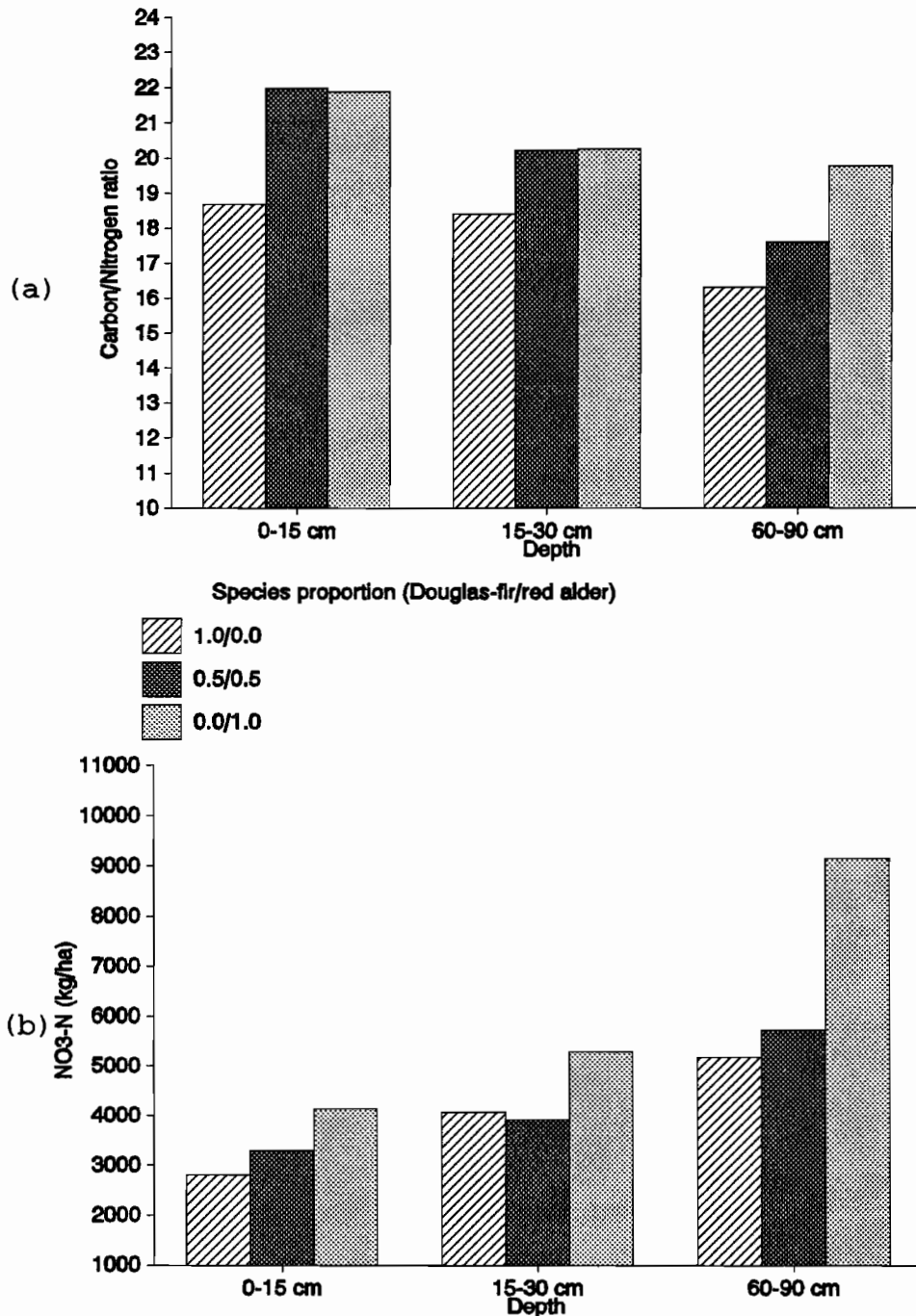


Table 3-5. Responses of the 1986-91 change in soil variables (kg/ha) to soil depth and Douglas-fir/red alder species proportion. See Table 3-1 for definitions of the soil variables.

Soil Variable	Species Proportion (Douglas-fir/red alder)		
	1.0/0.0	0.5/0.5	0.0/1.0
DiniNH <sub>4</sub> -N1	1.04	1.88	2.86
DiniNH <sub>4</sub> -N2	3.24	-6.51	-2.94
DiniNH <sub>4</sub> -N3	-14.20	-3.19	-140.60
DiniNO <sub>3</sub> -N1	-----	-12.85	0.94
DiniNO <sub>3</sub> -N2	-----	-9.10	2.71
DiniNO <sub>3</sub> -N3	-17.51	-29.67	-15.99
DminNH <sub>4</sub> -N1	-91.35	-902.67	-35.04
DminNH <sub>4</sub> -N2	-520.50	-77.81	-6013.38
DminNH <sub>4</sub> -N3	-2099.09	-20.73.18	-580.62
DNindex-1	-----	-100.65	-26.74
DNindex-2	-----	-155.94	8.68
DNindex-3	-690.52	-302.90	-138.71
DTN1	2016.74	1594.71	2529.85
DTN2	645.75	1433.99	1244.15
DTN3	-4635.79 <sup>1</sup>	-4176.86 <sup>1</sup>	-3780.91 <sup>1</sup>
DTP1	215.38	75.24	-6.45
DTP2	460.85	491.40	434.60
DTP3	-1053.18	-730.87	360.52
DTC1	31992.18	39957.13	54559.27
DTC2	10144.05	17217.90	21026.25
DTC3	-118972.73 <sup>1</sup>	-72254.10 <sup>1</sup>	-83170.13 <sup>1</sup>
DC/N1	-1.15	2.36	-2.01
DC/N2	-1.18	-1.84	-2.41
DC/N3	-6.07	-0.63	-0.65
DNO <sub>3</sub> -N1	-----	-940.47	301.70
DNO <sub>3</sub> -N2	-----	-2947.46	62.95
DNO <sub>3</sub> -N3	-10426.79	-10299.21	-7177.89
DpH1	0.01	0.07	-0.28
DpH2	0.14	0.37	-0.20
DpH3	0.55	0.11	0.19

<sup>1</sup>Significant ( $p \leq 0.05$ ) differences between the average of depth 1 (0-15 cm) and depth 2 (15-30) versus depth 3 (60-90 cm).

----- Missing data.



## 2. Douglas-fir Foliar Nitrogen and Phosphorus

Analysis of variance for Douglas-fir foliar nitrogen (%) revealed a significant ( $p=0.008$ ) interaction between foliar class and species proportion (Table 3-6). For top current-year foliage, Douglas-fir N in pure Douglas-fir stands (1.59%) was significantly greater ( $p=0.02$ ) than that for trees in mixed Douglas-fir/red alder stands (1.45%) (Table 3-6). For 2+ year-old foliage, foliar N of trees in pure stands of Douglas-fir (1.34%) was significantly lower ( $p=0.02$ ) than that for trees in mixed stands (1.48%). In current-year foliage, foliar N (1.57%) was significantly greater ( $p=0.0004$ ) than that for 2+ year-old foliage (1.41%) (Table 3-6). Foliar N in the top current-year foliage (1.52%) was significantly ( $p=0.02$ ) lower than that in the bottom current-year foliage (1.62%).

Foliar P did not vary significantly ( $p=0.144$ ) among species proportions; however, foliar P was significantly ( $p=0.017$ ) greater in current-year foliage (0.21%) than in 2+ year-old foliage (0.19%) (Table 3-6).

Specific leaf area (SLA) did not differ significantly ( $p=0.13$ ) between species proportions; however, mean SLA of 2+ year-old foliage (73.15  $\text{cm}^2/\text{g}$ ) was significantly less ( $p=0.001$ ) than the overall mean for current-year foliage (80.90) (Table 3-6). Mean SLA for current-year foliage was

Table 3-6. Responses of Douglas-fir foliar nutrient means to foliar class and Douglas-fir/red alder species proportion. See Table 3-3 for definitions of the foliar nutrient and biomass variables.

Foliage Variable	Species Proportion (Douglas-fir/red alder)	
	1.0/0.0	0.5/0.5
%N1*	1.588	1.454
%N2	1.644 <sup>2</sup>	1.586 <sup>2</sup>
%N3*	1.335 <sup>1</sup>	1.476 <sup>1</sup>
%P1	0.250	0.166
%P2	0.245	0.165
%P3	0.215 <sup>1</sup>	0.159 <sup>1</sup>
N1	0.055	0.039
N2	0.313	0.052
N3	0.080	0.062
P1	0.008	0.004
P2	0.046	0.005
P3	0.012	0.007
Biomass1	3.515	2.677
Biomass2	19.782	3.357
Biomass3	6.190	4.316
SLA1	80.177	90.026
SLA2	72.152 <sup>2</sup>	81.242 <sup>2</sup>
SLA3	71.098 <sup>1</sup>	75.200 <sup>1</sup>
N/LA1*	1.994	1.624
N/LA2*	2.280 <sup>2</sup>	1.953 <sup>2</sup>
N/LA3	1.888	1.972
P/LA1*	0.314	0.185
P/LA2*	0.340 <sup>2</sup>	0.203 <sup>2</sup>
P/LA3*	0.297	0.213
LA1	0.028	0.024
LA2	0.138	0.027
LA3	0.042	0.033
TBiomass	29.488	10.350
TotalN	0.448	0.152
TotalP	0.066	0.016
TLA	0.208	0.084
TN/LA	6.162	5.549
TP/LA	0.952	0.602

\* Significant ( $p \leq 0.05$ ) differences between species proportions.

<sup>1</sup> Significant ( $p \leq 0.05$ ) differences for foliar class 1 (top 1-year-old foliage) and foliar class 2 (bottom 1-year-old foliage) versus foliar class 3 (2+ year-old foliage).

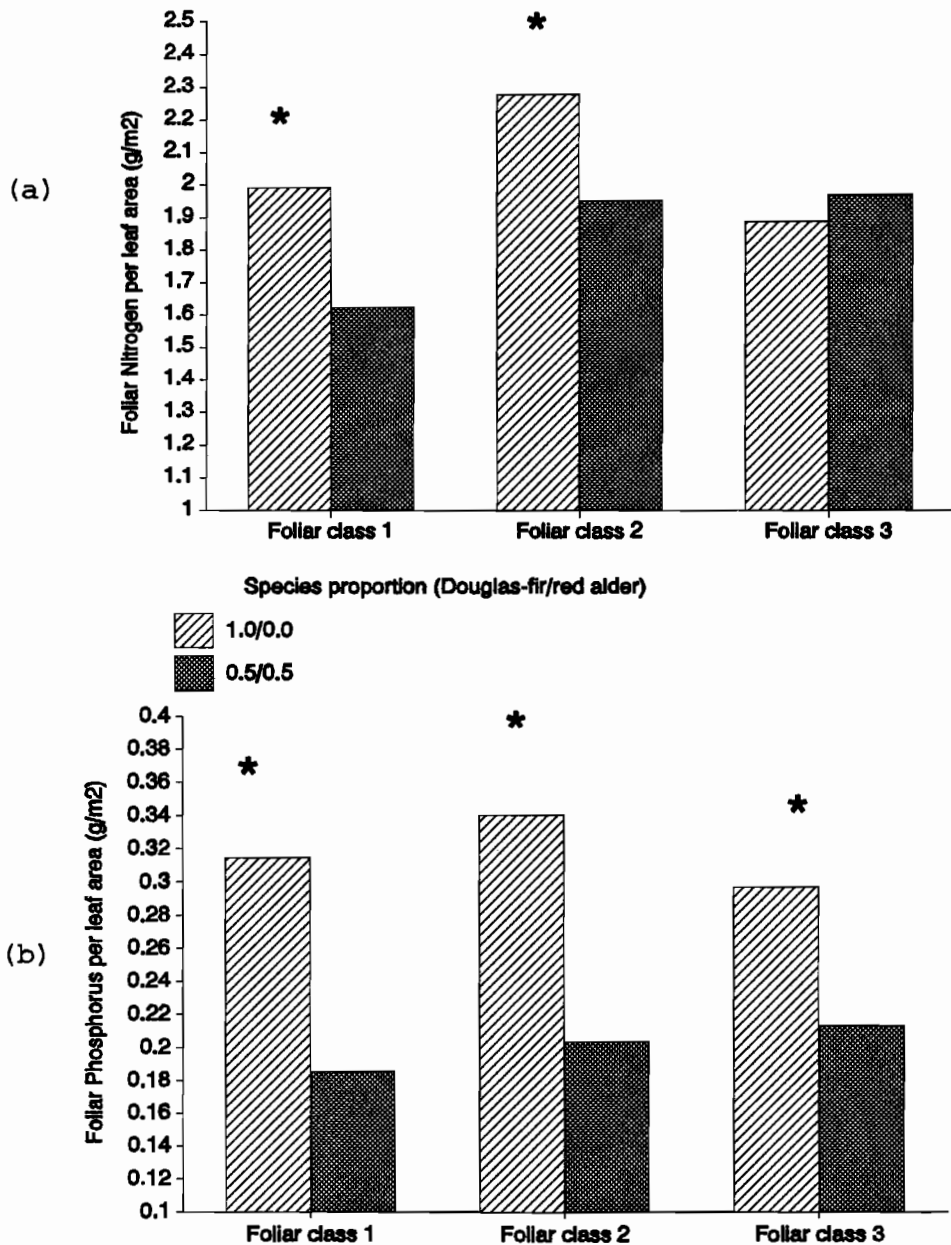
<sup>2</sup> Significant ( $p \leq 0.05$ ) differences between foliar class 1 (top 1-year-old foliage) versus foliar class 2 (bottom 1-year-old foliage).

significantly ( $p=0.0002$ ) greater in the top ( $85.10 \text{ cm}^2/\text{g}$ ) than in the bottom ( $76.70 \text{ cm}^2/\text{g}$ ) half of the crown.

Nitrogen per leaf area in top current-year foliage was significantly higher ( $p=0.01$ ) in pure stands of Douglas-fir ( $1.99 \text{ g/m}^2$ ) than in mixed stands ( $1.62 \text{ g/m}^2$ ) (Table 3-6, Figure 3-5). Nitrogen per leaf area in the bottom current-year foliage was significantly higher in pure stands of Douglas-fir ( $2.28 \text{ g/m}^2$ ) than that in mixed stands ( $1.95 \text{ g/m}^2$ ). The overall mean of N per leaf area in current-year foliage was significantly ( $p=0.001$ ) lower in top ( $1.96 \text{ g/m}^2$ ) than in the bottom ( $12.12 \text{ g/m}^2$ ) half of the crown (Figure 3-5a).

Mean values of phosphorus per leaf area ( $\text{g/m}^2$ ) in the top current-year foliage, bottom current-year foliage, and 2+ year-old foliage ( $0.31$ ,  $0.34$  and  $0.30 \text{ g/m}^2$ , respectively) were significantly higher in pure Douglas-fir stands than those ( $0.18$ ,  $0.20$  and  $0.21 \text{ g/m}^2$ , respectively) in mixed stands. Mean phosphorus per leaf area of current-year foliage was significantly lower ( $p=0.02$ ) in the top ( $0.25 \text{ g/m}^2$ ) than in the bottom ( $0.27 \text{ g/m}^2$ ) half of the crown (Figure 3-5b).

Figure 3-5. Responses of Douglas-fir foliar (a) nitrogen and (b) phosphorus per leaf area ( $\text{g}/\text{m}^2$ ) to foliar class and Douglas-fir/red alder species proportion. Significant ( $p \leq 0.05$ ) differences between species proportions are indicated with an asterisk (\*). Differences among foliar classes are described in the text.



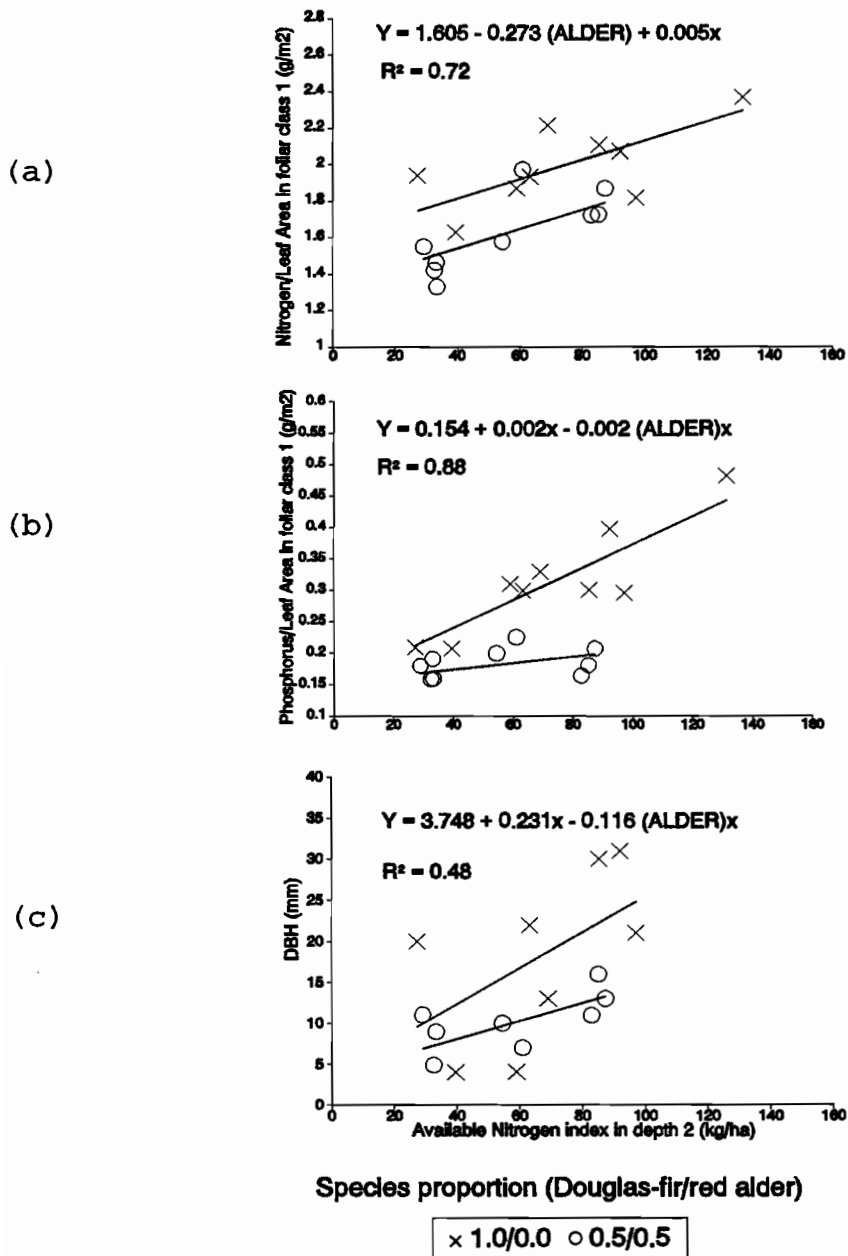
### 3. Relationships of Foliar and Soil Nitrogen and Phosphorus for Douglas-fir

Correlation analyses revealed several significant ( $p \leq 0.05$ ) linear relationships between the Douglas-fir and soil nutrient variables (described below). All of the correlation coefficients for these analyses are given in Appendix 1.

The regression analysis of top current-year foliar N ( $\text{g/m}^2$ ) versus available N at the 15-30 cm soil depth ( $R^2=0.72$ ) revealed a significant difference ( $p=0.0001$ ) in intercepts between pure Douglas-fir stands and mixed stands (Figure 3-6a). No difference was found between slopes. These results indicate that for a given level of available N, the N content per leaf area is greater for pure Douglas-fir stands than for mixed stands.

The regression analysis of top current-year foliar P ( $\text{g/m}^2$ ) versus available N at the 15-30 cm soil depth ( $R^2=0.88$ ) revealed a significant difference ( $p=0.0001$ ) in slopes between pure Douglas-fir stands and mixed stands (Figure 3-6b). The regression slope differed significantly ( $p=0.0001$ ) from zero only for saplings in pure Douglas-fir stands. These results indicate that with increasing levels of available N, foliar P of Douglas-fir increases for saplings in pure stands but does not change for saplings in mixed stands.

Figure 3-6. Relationships of (a) N and (b) P content per leaf area ( $\text{g}/\text{m}^2$ ) of current-year Douglas-fir foliage, and (c) Douglas-fir DBH to available soil N at 15-30 cm depth. The  $R^2$  represents the full model for both species proportions. In the regression equations, ALDER=1 and 0 for 0.5/0.5 and 1.0/0.0 species proportions, respectively.



The regression analysis of Douglas-fir DBH versus available N at 15-30 cm soil depth ( $R^2=0.48$ ) revealed a significant difference ( $p=0.009$ ) in slopes between pure Douglas-fir stands and mixed stands (Figure 3-6c). These results indicate that with increasing levels of available N, dbh of Douglas-fir increases at a greater rate for saplings in pure stands than for those in mixed stands.

#### D. Discussion and Conclusions

Contrary to expectations, availability of soil nitrogen (1991) as mineralizable  $\text{NH}_4$  at the 15-30 cm depth was greater in the absence than in the presence of red alder (Figure 3-1a). Although statistical differences among species proportions were detected only for this variable, the magnitude of differences among species proportions were similar at the 0-15 cm depth (Figure 3-1a) and for the index of available nitrogen (Figure 3-1b). One explanation for these results is that the more open conditions associated with absence of red alder contributed to increased rates and duration of nitrogen mineralization.

For the 5-year period of measurement (March 1986-91), the change in soil variables did not differ significantly among species proportions (Table 3-5). These results indicate that presence of red alder did not cause a net accretion of nitrogen or influence the pH or content of carbon and phosphorus of soils. Cole and Newton (1986) also found no significant effects on soil nitrogen and phosphorus from the five-year presence of red alder in a Douglas-fir plantation.

Soil characteristics varied significantly among depths. In 1986, each of total nitrogen, phosphorus, and carbon, and  $\text{NO}_3$  content were significantly higher at the 60-90 cm depth versus the average of the 0-15 and 15-30 cm



depths (Table 3-4). Available nitrogen as  $\text{NH}_4$  did not vary significantly with depth. In forest soils, cation exchange sites are usually adequate to retain soil ammonium, and if this compound is particularly abundant, nitrifying bacteria usually oxidize it to nitrate that then leaches to lower depths (Binkley 1986). This may explain the increase with depth that was observed for nitrate and total nitrogen. In general, forest soils are very tight with respect to nitrogen cycling, and leaching typically removes less than 1% of the N cycled annually. Exceptions occur only for soils with very high rates of N mineralization, such as those occupied by red alder which may lose over 50 kg/ha of nitrogen annually to stream water (Binkley 1986).

The average change (1986-91) in total nitrogen and carbon was significantly greater for the average of the 0-15 and 15-30 cm depths versus that for the 60-90 cm depth (Table 3-5). This change was positive for the 0-15 and 15-30 cm depths and negative for the 60-90 cm depths. In 1991, the ratio of carbon to nitrogen (C/N) was significantly lower at the 60-90 depth versus the average of the 0-15 and 15-30 cm depths (Table 3-4). Since this study was established within a year after 120-year-old trees were clearcut harvested and the site was broadcast burned, the high values of total carbon and nitrogen that were measured at the 60-90 cm depth in 1986 may reflect the high content of root biomass at this depth, most of which

had subsequently decomposed by 1991. The higher C/N ratio measured in 1991 for the top two layers versus the lower layer may have resulted because disturbances associated with harvesting and broadcast burning may have increased the carbon content in top layers of the soil, and its decomposition and incorporation into the soil was well underway by year 6.

Douglas-fir foliage had higher contents of nitrogen and phosphorus (expressed as g/m<sup>2</sup>) in the absence than in the presence of red alder (Table 3-6, Figure 3-5). These differences were observed in current-year foliage for nitrogen and in both current year and 2+ year-old foliage for phosphorus. Large, vigorous saplings growing in the absence of overtopping red alder probably have greater access to limited supplies of available nitrogen and phosphorus than the smaller, suppressed saplings growing under red alder.

Specific leaf area (SLA) of Douglas-fir foliage was higher in the top versus bottom half of the crown (current-year foliage), and in current-year versus 2+ year-old foliage (Table 3-6). Typically, shade foliage of Douglas-fir has a higher SLA than sun foliage, because it is thinner and has fewer layers of palisade parenchyma for a given mass of foliage (Berg and Doerksen 1975). However, SLA differences among foliar classes observed in the present study may be more indicative of degree of maturity

rather than degree of shading of foliage. It is likely that current-year foliage in the top half of the crown is composed of late-season and somewhat younger, lammas growth, while that in the bottom half is composed of mature foliage which developed throughout the growing season from a single flush of shoot growth.

Nitrogen and phosphorus content ( $\text{g/m}^2$ ) of current-year foliage and dbh of Douglas-fir each were significantly related to available soil nitrogen at the 15-30 cm depth (Figure 3-6). For nitrogen content, this relationship indicated that, for any level of available soil nitrogen, foliar N of Douglas-fir was  $0.27 \text{ g/m}^2$  higher for saplings growing in the absence versus presence of red alder (Figure 3-6a). Foliar P and dbh of Douglas-fir increased at a faster rate with increasing levels of available soil nitrogen for saplings growing in the absence versus presence of red alder (Figure 3-6b,c). From these results, it is possible to infer that both foliar nutrient content and growth of Douglas-fir saplings are linked to availability of soil nitrogen. These linkages probably exist because large, vigorous saplings growing in the absence of red alder have a faster transpiration stream (e.g., passive uptake of nitrogen), a more extensive root system (e.g., active uptake of phosphorus), and greater rates and duration of cambial growth than the smaller, suppressed saplings growing under red alder.

#### IV. CONCLUSIONS AND SILVICULTURAL IMPLICATIONS

Results of this study are similar to those found by Shainski and Radosevich (1992) in an addition-series in which density and species proportion were varied independently. Using high-density plantings, they found that red alder was the dominant competitor and overtopped the Douglas-fir by the second year of the study. Competition for light was mediated by density effects on the leaf area index (LAI) of each species. For example, increasing alder LAI reduced the light reaching the understory Douglas-fir. In contrast, increasing Douglas-fir LAI in the presence of overtopping alder increased the light availability to understory conifers, due to Douglas-fir's suppression of alder LAI. The result was that understory Douglas-fir were able to increase their growth by exerting a competitive influence on overstory red alder. Availability of soil moisture also declined with increasing stand density, resulting in increasingly negative leaf water potentials for each species. Growth rates concurrently declined as plant water stress increased.

Similar to the present research, Cole and Newton (1986, 1987) found that red alder competition became more pronounced with time because of its compounding, suppressive effects on morphology and growth of Douglas-fir. After the first year, growth of red alder exceeded

that of Douglas-fir, so that differences in height were accentuated with time. Increased competition for light resulted in progressively greater growth reductions with increasing age of the stand. Alder did not enhance conifer growth under the observed conditions nor increase soil or conifer foliar nitrogen.

In the present study, reductions in the survival and growth of Douglas-fir from red alder competition did not become statistically significant until the sixth and fourth years after planting, respectively. Therefore, silviculturists can afford to wait several years after establishment of conifer plantations prior to conducting competition release treatments. Unfortunately, the best control of red alder from manual cutting is for saplings that are at least five years old (DeBell and Turpin 1989), and Douglas-fir should be released from red alder before survival and growth reductions become significant.

By the sixth year after planting, red alder had not yet caused a net accretion in total or available nitrogen. In the meantime, competition had become severe depending on the relative proportion of alder. Lower proportions of red alder in the stand will delay the onset of their competitive effects on associated Douglas-fir.

It appears that alder competition for light, which limits carbon allocation of Douglas-fir to roots (Chan 1984), resulted in limited root growth and reduced foliar

nutrition of Douglas-fir. Alder may also limit mineralization of soil nitrogen by reducing fluctuations in air and soil temperature through the moderating influence of its closed canopy. Early in development, pure stands of Douglas-fir are more open than those mixed with or dominated by red alder, and thus, they appear to have higher rates of nitrogen mineralization. The result is that Douglas-fir in pure stands are more able to absorb and allocate nitrogen to their foliage, resulting in higher levels of foliar nutrition. The enhanced nutrition of the tree (both nitrogen and phosphorus) contributes to better growth.

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## VI. APPENDIX

Appendix 1.

Table A-1. Correlation coefficients for 1991 Douglas-fir foliar and soil nutrients. See Tables 3-1 and 3-3 for definitions of the soil and foliar nutrient variables.

Table A-1.

Tree foliar Variables	Soil Nutrient Parameters																	
	iniNH <sub>4</sub> -N			iniNH <sub>4</sub> -N			iniNO <sub>3</sub> -N			iniNO <sub>3</sub> -N			minNH <sub>4</sub> -N					
	1	n	2	1	n	2	1	n	2	1	n	2	1	n	2			
BD	0.066	18	0.426	18	-0.122	18	-0.392	18	-0.289	18	-0.372	18	0.380	18	0.256	18	-0.139	18
DBH	0.010	16	0.456	16	0.245	16	-0.193	16	-0.006	16	-0.131	16	0.535*16	16	0.648*16	16	0.074	16
HT	0.128	18	0.430	18	0.154	18	-0.134	18	-0.180	18	-0.122	18	0.403	18	0.259	18	0.033	18
LA1	0.347	18	0.380	18	-0.172	18	-0.225	18	-0.343	18	-0.356	18	0.269	18	0.026	18	-0.118	18
LA2	0.115	18	0.530*18	18	-0.078	18	-0.350	18	-0.265	18	-0.265	18	0.394	18	0.293	18	-0.089	18
LA3	0.108	18	0.525*18	18	-0.035	18	-0.275	18	-0.277	18	-0.285	18	0.305	18	0.237	18	0.029	18
N/LA1	-0.271	18	0.246	18	-0.154	18	0.068	18	0.437	18	0.148	18	0.546*18	18	0.717*18	18	-0.356	18
N/LA2	0.067	18	0.350	18	-0.338	18	-0.108	18	0.115	18	0.006	18	0.306	18	0.438	18	-0.302	18
N/LA3	-0.197	18	-0.002	18	0.109	18	0.198	18	0.057	18	0.502*	18	-0.128	18	-0.223	18	0.245	18
P/LA1	-0.192	18	0.093	18	-0.027	18	-0.088	18	0.344	18	-0.025	18	0.509*18	18	0.682*18	18	-0.282	18
P/LA2	-0.020	18	0.205	18	-0.188	18	-0.162	18	0.218	18	-0.136	18	0.475*18	18	0.632*18	18	0.324	18
P/LA3	-0.211	18	-0.051	18	-0.111	18	0.003	18	0.346	18	0.098	18	0.333	18	0.431	18	-0.255	18
Biomass1	0.085	18	0.436	18	-0.056	18	-0.349	18	-0.282	18	-0.349	18	0.407	18	0.265	18	-0.107	18
Biomass2	0.112	18	0.532*18	18	-0.056	18	-0.356	18	-0.260	18	-0.258	18	0.411	18	0.314	18	-0.090	18
Biomass3	0.080	18	0.500*18	18	-0.025	18	-0.298	18	-0.280	18	-0.289	18	0.331	18	0.257	18	-0.002	18
N1	0.110	18	0.465	18	-0.203	18	-0.173	18	-0.065	18	-0.201	18	0.507*18	18	0.398	18	-0.257	18
N2	0.155	18	0.586*18	18	-0.110	18	-0.355	18	-0.264	18	-0.271	18	0.407	18	0.321	18	-0.110	18
N3	0.079	18	0.514*18	18	-0.050	18	-0.266	18	-0.266	18	-0.278	18	0.320	18	0.241	18	0.031	18
P1	0.024	18	0.317	18	-0.047	18	-0.226	18	0.051	18	-0.196	18	0.577*18	18	0.554*18	18	-0.227	18
P2	0.142	18	0.570*18	18	-0.039	18	-0.360	18	-0.244	18	-0.246	18	0.433	18	0.360	18	-0.076	18
P3	0.088	18	0.500*18	18	0.003	18	-0.347	18	-0.321	18	-0.270	18	0.323	18	0.216	18	0.025	18
%N1	0.007	18	0.067	18	-0.277	18	0.482*	18	0.616*	18	0.470*	18	0.316	18	0.409	18	-0.354	18
%N2	-0.004	18	0.168	18	-0.271	18	0.046	18	0.169	18	0.231	18	-0.004	18	0.158	18	0.031	18
%N3	-0.220	18	-0.087	18	0.073	18	0.279	18	0.199	18	0.456	18	-0.271	18	-0.205	18	0.384	18
%P1	-0.080	18	0.017	18	-0.111	18	0.054	18	0.424	18	0.063	18	0.442	18	0.589*18	18	-0.308	18
%P2	-0.038	18	0.151	18	-0.210	18	-0.115	18	0.272	18	-0.082	18	0.409	18	0.597*18	18	-0.297	18
%P3	-0.205	18	-0.074	18	-0.156	18	0.031	18	0.390	18	0.066	18	0.243	18	0.441	18	-0.243	18
SpLA1	0.474*18	18	-0.225	18	-0.096	18	0.369	18	0.001	18	0.201	18	-0.385	18	-0.521*18	18	0.045	18
SpLA2	-0.117	18	-0.292	18	0.144	18	0.194	18	0.023	18	0.272	18	-0.484*18	18	-0.464	18	0.481*18	18
spLA3	-0.036	18	-0.117	18	-0.062	18	0.101	18	0.210	18	-0.045	18	-0.184	18	0.062	18	0.127	18
TBiomass	0.106	18	0.531*18	18	-0.051	18	-0.350	18	-0.270	18	-0.273	18	0.401	18	0.306	18	-0.073	18
TotalN	0.143	18	0.581*18	18	-0.105	18	-0.339	18	-0.262	18	-0.275	18	0.405	18	0.317	18	-0.093	18
TotalP	0.129	18	0.557*18	18	-0.033	18	-0.360	18	-0.247	18	-0.254	18	0.433	18	0.354	18	-0.069	18
TLA	0.125	18	0.537*18	18	-0.075	18	-0.338	18	-0.277	18	-0.279	18	0.380	18	0.279	18	-0.067	18
TN/LA	-0.182	18	0.286	18	-0.192	18	0.062	18	0.294	18	0.276	18	0.365	18	0.475	18	-0.222	18
TP/LA	-0.148	18	0.092	18	-0.116	18	-0.090	18	0.321	18	-0.026	18	0.470*18	18	0.624*18	18	-0.319	18

\* Significant at p≤0.05.



Table A-1. (Continued).

Tree foliar Variables	Soil Nutrient Parameters																	
	TN1	n	TN2	n	TN3	n	TP1	n	TP2	n	TP3	n	TC1	n	TC2	n	TC3	n
BD	-0.128	18	0.059	18	-0.445	18	-0.110	18	-0.137	18	-0.244	18	-0.161	18	0.085	18	-0.356	18
DBH	-0.303	16	-0.214	16	-0.172	16	-0.026	16	-0.036	16	-0.120	16	-0.045	16	0.320	16	-0.082	16
HT	0.051	18	0.139	18	-0.260	18	-0.150	18	-0.168	18	-0.212	18	0.123	18	0.282	18	-0.114	18
LA1	-0.142	18	-0.064	18	-0.456	18	-0.155	18	-0.175	18	-0.252	18	-0.083	18	0.032	18	-0.343	18
LA2	-0.145	18	0.049	18	-0.430	18	-0.146	18	-0.171	18	-0.278	18	-0.136	18	0.116	18	-0.339	18
LA3	-0.186	18	0.030	18	-0.312	18	-0.237	18	-0.254	18	-0.298	18	-0.099	18	0.184	18	-0.206	18
N/LA1	0.257	18	0.551*	18	-0.131	18	0.338	18	0.328	18	0.182	18	-0.081	18	0.356	18	-0.141	18
N/LA2	0.293	18	0.374	18	-0.352	18	0.193	18	0.166	18	-0.028	18	0.010	18	0.208	18	-0.369	18
N/LA3	0.287	18	0.143	18	0.148	18	0.058	18	0.045	18	0.052	18	0.257	18	0.264	18	0.210	18
P/LA1	0.227	18	0.424	18	-0.049	18	0.402	18	0.386	18	0.260	18	-0.049	18	0.195	18	-0.112	18
P/LA2	0.176	18	0.358	18	-0.220	18	0.325	18	0.306	18	0.145	18	-0.079	18	0.136	18	-0.284	18
P/LA3	-0.028	18	0.130	18	0.028	18	0.429	18	0.406	18	0.342	18	-0.245	18	-0.073	18	-0.105	18
Biomass1	-0.078	18	0.081	18	-0.420	18	-0.127	18	-0.154	18	-0.245	18	-0.082	18	0.140	18	-0.310	18
Biomass2	0.117	18	0.071	18	-0.422	18	-0.138	18	-0.164	18	-0.275	18	-0.108	18	0.136	18	-0.332	18
Biomass3	-0.154	18	0.059	18	-0.338	18	-0.220	18	-0.241	18	-0.292	18	-0.078	18	0.200	18	-0.231	18
N1	0.021	18	0.237	18	-0.429	18	0.040	18	0.018	18	-0.124	18	-0.109	18	0.218	18	-0.339	18
N2	-0.135	18	0.064	18	-0.452	18	-0.154	18	-0.177	18	-0.300	18	-0.133	18	0.128	18	-0.365	18
N3	-0.154	18	0.064	18	-0.313	18	-0.231	18	-0.249	18	-0.293	18	-0.071	18	0.226	18	-0.208	18
P1	0.133	18	0.318	18	-0.264	18	0.247	18	0.220	18	0.071	18	-0.045	18	0.208	18	-0.236	18
P2	-0.073	18	0.110	18	-0.397	18	-0.108	18	-0.133	18	-0.258	18	-0.066	18	0.173	18	-0.311	18
P3	-0.202	18	-0.017	18	-0.343	18	-0.204	18	-0.232	18	-0.288	18	-0.117	18	0.122	18	-0.246	18
%N1	0.283	18	0.439	18	0.022	18	0.482*	18	0.491*	18	0.366	18	-0.049	18	0.235	18	-0.023	18
%N2	0.174	18	0.137	18	-0.030	18	0.202	18	0.189	18	0.095	18	-0.034	18	0.014	18	-0.105	18
%N3	0.160	18	0.056	18	0.395	18	-0.010	18	0.012	18	0.082	18	0.180	18	0.162	18	0.372	18
%P1	0.227	18	0.384	18	0.000	18	0.509*	18	0.498*	18	0.369	18	-0.073	18	0.127	18	-0.091	18
%P2	0.133	18	0.299	18	-0.132	18	0.379	18	0.363	18	0.220	18	-0.128	18	0.060	18	-0.232	18
%P3	-0.061	18	0.117	18	0.075	18	0.366	18	0.360	18	0.314	18	-0.262	18	-0.096	18	-0.082	18
SpLA1	-0.065	18	-0.300	18	0.114	18	-0.023	18	-0.002	18	0.053	18	0.076	18	-0.244	18	0.081	18
SpLA2	-0.252	18	-0.415	18	0.487*	18	-0.071	18	-0.044	18	0.127	18	-0.090	18	-0.326	18	0.416	18
spLA3	-0.183	18	-0.112	18	0.296	18	-0.064	18	-0.018	18	0.054	18	-0.137	18	-0.160	18	0.177	18
TBiomass	-0.126	18	0.070	18	-0.412	18	-0.158	18	-0.184	18	-0.283	18	-0.102	18	0.153	18	-0.315	18
TotalN	-0.135	18	0.073	18	-0.436	18	-0.162	18	-0.186	18	-0.298	18	-0.124	18	0.153	18	-0.344	18
TotalP	-0.087	18	0.102	18	-0.339	18	-0.108	18	-0.134	18	-0.251	18	-0.076	18	0.170	18	-0.303	18
TLA	-0.158	18	0.042	18	-0.416	18	-0.170	18	-0.194	18	-0.289	18	-0.130	18	0.130	18	-0.319	18
TN/LA	0.379	18	0.507*	18	-0.172	18	0.282	18	0.259	18	0.099	18	0.066	18	0.380	18	-0.160	18
TP/LA	0.137	18	0.328	18	-0.089	18	0.409	18	0.389	18	0.262	18	-0.129	18	0.096	18	-0.180	18

\* Significant at  $p \leq 0.05$ .

Table A-1. (Continued).

Tree foliar Variables	Soil Nutrient Parameters																	
	C1/N		C2/N		C3/N		Nindex		Nindex		NO <sub>3</sub> -N		NO <sub>3</sub> -N		NO <sub>3</sub> -N			
	1	n	2	n	3	n	1	n	2	n	3	n	1	n	2	n	3	n
DB	-0.176	18	0.052	18	-0.043	18	0.321	18	0.114	18	-0.181	18	-0.286	18	-0.267	18	-0.258	18
DBH	-0.120	16	0.218	16	0.168	16	0.497*16		0.541*16		0.027	16	0.036	16	-0.034	16	-0.048	16
HT	0.082	18	0.373	18	0.265	18	0.360	18	0.126	18	0.001	18	-0.168	18	-0.260	18	-0.175	18
LA1	0.011	18	0.185	18	0.012	18	0.193	18	-0.113	18	-0.152	18	-0.414	18	-0.346	18	-0.310	18
LA2	-0.104	18	0.164	18	-0.036	18	0.333	18	0.124	18	-0.120	18	-0.267	18	-0.308	18	-0.191	18
LA3	0.026	18	0.365	18	0.139	18	0.255	18	0.068	18	-0.008	18	-0.216	18	-0.339	18	-0.200	18
N/LA1	-0.568*18		-0.290	18	-0.181	18	0.572*18		0.704*18		-0.321	18	0.386	18	0.305	18	0.352	18
N/LA2	-0.441	18	-0.228	18	-0.283	18	0.277	18	0.359	18	-0.270	18	-0.082	18	-0.056	18	0.022	18
N/LA3	-0.023	18	0.304	18	0.313	18	-0.079	18	-0.222	18	0.306	18	0.106	18	-0.045	18	0.222	18
P/LA1	-0.431	18	-0.364	18	-0.226	18	0.510*18		0.703*18		-0.284	18	0.257	18	0.344	18	0.184	18
P/LA2	-0.392	18	-0.352	18	-0.337	18	0.447	18	0.608*18		-0.359	18	0.068	18	0.174	18	0.056	18
P/LA3	-0.439	18	-0.473*18		-0.457	18	0.351	18	0.487*18		-0.232	18	0.338	18	0.381	18	0.354	18
Biomass1	-0.110	18	0.138	18	0.043	18	0.349	18	0.121	18	-0.152	18	-0.276	18	-0.278	18	-0.270	18
Biomass2	-0.088	18	0.178	18	-0.023	18	0.349	18	0.146	18	-0.121	18	-0.264	18	-0.304	18	-0.200	18
Biomass3	0.017	18	0.344	18	0.126	18	0.281	18	0.094	18	-0.040	18	-0.207	18	-0.331	18	-0.212	18
N1	-0.292	18	0.013	18	-0.061	18	0.460	18	0.269	18	-0.267	18	-0.143	18	-0.140	18	-0.072	18
N2	-0.105	18	0.176	18	-0.055	18	0.339	18	0.137	18	-0.138	18	-0.290	18	-0.331	18	-0.200	18
N3	0.026	18	0.391	18	0.127	18	0.274	18	0.075	18	-0.003	18	-0.187	18	-0.328	18	-0.193	18
P1	-0.307	18	-0.127	18	-0.077	18	0.534*18		0.481*18		-0.251	18	-0.066	18	0.050	18	-0.538	18
P2	-0.057	18	0.217	18	0.013	18	0.366	18	0.183	18	-0.108	18	-0.285	18	-0.308	18	-0.204	18
P3	0.007	18	0.302	18	0.080	18	0.267	18	0.049	18	-0.014	18	-0.255	18	-0.350	18	-0.212	18
%N1	-0.493*18		-0.325	18	-0.225	18	0.353	18	0.457	18	-0.262	18	0.414	18	0.410	18	0.583*18	
%N2	-0.352	18	-0.227	18	-0.276	18	0.002	18	0.130	18	0.090	18	-0.176	18	-0.006	18	0.188	18
%N3	0.044	18	0.270	18	0.164	18	-0.207	18	-0.166	18	0.442	18	0.255	18	0.119	18	0.324	18
%P1	-0.454	18	-0.437	18	-0.289	18	0.444	18	0.637*18		-0.290	18	0.262	18	0.411	18	0.270	18
%P2	-0.414	18	-0.416	18	-0.400	18	0.390	18	0.593*18		-0.290	18	0.106	18	0.224	18	0.129	18
%P3	-0.402	18	-0.481	18	-0.508	18	0.266	18	0.509*18		-0.220	18	0.379	18	0.409	18	0.366	18
SpLA1	0.316	18	0.071	18	-0.050	18	-0.399	18	-0.469*18		0.082	18	-0.145	18	-0.033	18	0.047	18
SpLA2	0.212	18	0.039	18	0.069	18	-0.435	18	-0.389	18	0.507*18		0.082	18	0.055	18	0.205	18
spLA3	0.057	18	-0.111	18	-0.238	18	-0.164	18	0.116	18	0.127	18	0.210	18	0.226	18	0.160	18
TBiomass	-0.068	18	0.215	18	0.012	18	0.340	18	0.136	18	-0.107	18	-0.257	18	-0.314	18	-0.207	18
TotalN	-0.091	18	0.213	18	-0.023	18	0.340	18	0.135	18	-0.122	18	-0.272	18	-0.330	18	-0.198	18
TotalP	-0.061	18	0.218	18	0.020	18	0.368	18	0.181	18	-0.102	18	-0.275	18	-0.303	18	-0.202	18
TLA	-0.074	18	0.212	18	0.002	18	0.319	18	0.106	18	-0.100	18	-0.269	18	-0.324	18	-0.202	18
TN/LA	-0.499*18		-0.131	18	-0.099	18	0.384	18	0.432	18	-0.165	18	0.196	18	0.108	18	0.274	18
TP/LA	-0.448	18	-0.420	18	-0.359	18	0.467	18	0.641*18		-0.312	18	0.232	18	0.316	18	0.206	18

\* Significant at  $p \leq 0.05$ .

Table A-1. (Continued).

Tree foliar Variables	Soil Nutrient Parameters																									
	DiniNH <sub>4</sub> -N			DiniNH <sub>4</sub> -N			DiniNO <sub>3</sub> -N			DiniNO <sub>3</sub> -N																
	1	n		2	n		3	n		1	n		2	n		3	n									
BD	-0.146	16		0.386	18		-0.459	16		0.123	3		-0.170	3		0.541	6		0.163	16		-0.349	18		-0.006	16
DBH	-0.134	14		0.497*	16		-0.458	14		-0.080	3		-0.372	3		0.157	5		-0.264	14		-0.151	16		-0.032	14
HT	0.026	16		0.466	18		-0.294	16		0.729	3		0.493	3		0.037	6		0.201	16		-0.223	18		0.071	16
LA1	0.175	16		0.339	18		-0.330	16		0.740	3		0.508	3		0.580	6		0.156	16		-0.250	18		0.092	16
LA2	-0.099	16		0.446	18		-0.530*	16		0.310	3		0.014	3		0.480	6		0.162	16		-0.315	18		-0.041	16
LA3	-0.062	16		0.437	18		-0.474	16		0.385	3		0.094	3		0.141	6		0.148	16		-0.154	18		-0.074	16
N/LA1	-0.378	16		0.507*	18		-0.171	16		-0.700	3		-0.457	3		-0.204	6		0.318	16		-0.262	18		0.032	16
N/LA2	-0.024	16		0.502*	18		0.324	16		-0.701	3		-0.458	3		-0.224	6		0.396	16		-0.181	18		-0.301	16
N/LA3	-0.062	16		0.182	18		0.002	16		-0.447	3		-0.162	3		-0.599	6		0.282	16		-0.041	18		0.030	16
P/LA1	-0.317	16		0.309	18		-0.065	16		-0.843	3		-0.645	3		0.177	6		0.233	16		0.006	18		-0.020	16
P/LA2	-0.192	16		0.323	18		-0.155	16		-0.877	3		-0.696	3		0.193	6		0.194	16		-0.016	18		-0.084	16
P/LA3	-0.274	16		0.166	18		0.055	16		-0.620	3		-0.359	3		0.009	6		0.139	16		-0.054	18		-0.013	16
Biomass1	-0.101	16		0.418	18		-0.424	16		0.234	3		-0.065	3		0.463	6		0.177	16		-0.333	18		0.014	16
Biomass2	-0.103	16		0.443	18		-0.521*	16		0.225	3		-0.074	3		0.455	6		0.158	16		-0.291	18		-0.028	16
Biomass3	-0.083	16		0.433	18		-0.448	16		0.225	3		-0.074	3		0.068	6		0.155	16		-0.176	18		-0.300	16
N1	-0.090	16		0.539*	18		-0.414	16		0.727	3		0.491	3		0.685	6		0.283	16		-0.350	18		0.079	16
N2	-0.070	16		0.467	18		-0.579*	16		0.225	3		-0.074	3		0.477	6		0.158	16		-0.296	18		-0.073	16
N3	-0.084	16		0.446	18		-0.472	16		0.343	3		0.050	3		0.057	6		0.169	16		-0.173	18		-0.061	16
P1	-0.190	16		0.435	18		-0.263	16		-0.983	3		-0.993	3		0.546	6		0.258	16		-0.100	18		0.058	16
P2	-0.094	16		0.447	18		-0.531*	16		0.104	3		-0.196	3		0.467	6		0.148	16		-0.186	18		-0.037	16
P3	-0.090	16		0.422	18		-0.470	16		0.147	3		-0.153	3		0.099	6		0.148	16		-0.209	18		-0.055	16
%N1	-0.013	16		0.370	18		0.085	16		-0.035	3		0.262	3		-0.115	6		0.295	16		-0.060	18		0.182	16
%N2	-0.052	16		0.299	18		-0.133	16		-0.255	3		0.043	3		-0.175	6		0.240	16		-0.023	18		-0.471	16
%N3	-0.120	16		0.008	18		-0.013	16		0.780	3		0.931	3		-0.343	6		0.170	16		0.155	18		-0.245	16
%P1	-0.195	16		0.262	18		0.027	16		-0.424	3		-0.136	3		0.227	6		0.244	16		0.098	18		0.023	16
%P2	-0.209	16		0.270	18		-0.103	16		-0.681	3		-0.433	3		0.203	6		0.157	16		0.042	18		-0.158	16
%P3	-0.264	16		0.094	18		0.052	16		-0.444	3		-0.158	3		0.073	6		0.085	16		0.019	18		-0.120	16
SpLA1	0.585*	16		-0.296	18		0.279	16		0.389	3		0.645	3		0.144	6		-0.116	16		0.274	18		0.146	16
SpLA2	-0.064	16		-0.392	18		0.253	16		0.870	3		0.977	3		0.156	6		-0.278	16		0.235	18		-0.210	16
spLA3	-0.082	16		-0.235	18		0.112	16		0.901	3		0.732	3		0.441	6		-0.175	16		0.248	18		-0.338	16
TBiomass	-0.100	16		0.448	18		-0.510*	16		0.226	3		-0.074	3		0.369	6		0.161	16		-0.273	18		0.027	16
TotalN	-0.075	16		0.478*	18		-0.566*	16		0.291	3		-0.006	3		0.404	6		0.169	16		-0.283	18		-0.066	16
TotalP	-0.101	16		0.453	18		-0.517*	16		0.098	3		-0.201	3		0.456	6		0.157	16		-0.190	18		-0.036	16
TLA	-0.083	16		0.452	18		-0.524*	16		0.368	3		0.076	3		0.418	6		0.163	16		-0.286	18		-0.044	16
TN/LA	-0.222	16		0.560*	18		-0.223	16		-0.609	3		-0.346	3		-0.618	6		0.444	16		-0.232	18		-0.105	16
TP/LA	-0.267	16		0.286	18		-0.059	16		-0.767	3		-0.542	3		0.124	6		0.195	16		-0.022	18		-0.040	16

\* Significant at  $p \leq 0.05$ .

Table A-1. (Continued).

Tree foliar Variables	Soil Nutrient Parameters																	
	DC1/N		DC2/N		DC3/N		DNindex		DNindex		DNindex		DNO <sub>3</sub> -N		DNO <sub>3</sub> -N		DNO <sub>3</sub> -N	
	1	n	2	n	3	n	1	n	2	n	3	n	1	n	2	n	3	n
BD	-0.470*	18	0.116	18	-0.549*	18	0.478	3	-0.026	3	0.360	6	0.029	3	0.152	3	-0.670	6
DBH	-0.428	16	-0.023	16	-0.510*	16	0.284	3	-0.234	3	-0.401	5	-0.180	3	-0.058	3	-0.515	5
HT	-0.223	18	0.129	18	-0.429	18	0.926	3	0.614	3	0.750	6	0.656	3	0.744	3	-0.331	6
LA1	-0.359	18	0.193	18	-0.468*	18	0.932	3	0.627	3	0.732	6	0.667	3	0.755	3	-0.405	6
LA2	-0.504*	18	0.103	18	-0.586*	18	0.631	3	0.158	3	0.440	6	0.212	3	0.331	3	-0.579	6
LA3	-0.397	18	0.160	18	-0.572*	18	0.691	3	0.237	3	0.547	6	0.290	3	0.505	3	-0.629	6
N/LA1	0.240	18	0.139	18	-0.106	18	-0.910	3	-0.581	3	-0.943*	6	-0.625	3	-0.716	3	0.346	6
N/LA2	-0.026	18	0.040	18	-0.043	18	-0.910	3	-0.582	3	-0.439	6	-0.625	3	-0.717	3	0.392	6
N/LA3	0.035	18	-0.220	18	0.359	18	-0.739	3	-0.303	3	0.564	6	-0.355	3	-0.467	3	0.302	6
P/LA1	-0.294	18	0.151	18	-0.097	18	-0.980	3	-0.749	3	-0.858*	6	-0.784	3	-0.854	3	0.164	6
P/LA2	-0.278	18	0.186	18	-0.161	18	-0.991	3	-0.792	3	-0.781	6	-0.824	3	-0.888	3	0.142	6
P/LA3	-0.384	18	0.131	18	-0.029	18	-0.860	3	-0.490	3	-0.835*	6	-0.537	3	-0.637	3	0.349	6
Biomass1	-0.408	18	0.132	18	-0.549*	18	0.568	3	0.080	3	-0.513	6	0.134	3	0.256	3	0.687	6
Biomass2	-0.502*	18	0.095	18	-0.579*	18	0.560	3	0.071	3	0.428	6	0.125	3	0.246	3	-0.581	6
Biomass3	-0.408	18	0.150	18	-0.556*	18	0.560	3	0.071	3	0.545	6	0.125	3	0.246	3	-0.698	6
N1	-0.417	18	0.212	18	-0.443	18	0.925	3	0.612	3	0.472	6	0.654	3	0.742	3	-0.367	6
N2	-0.493*	18	0.094	18	-0.608*	18	0.560	3	0.071	3	0.442	6	0.126	3	0.247	3	-0.589	6
N3	-0.420	18	0.142	18	-0.562*	18	0.658	3	0.193	3	0.535	6	0.247	3	0.364	3	-0.626	6
P1	-0.459	18	0.220	18	-0.321	18	-0.851	3	-0.999*	3	-0.353	6	-0.996	3	-0.979	3	-0.102	6
P2	-0.510*	18	0.112	18	-0.559*	18	0.454	3	-0.052	3	0.432	6	0.002	3	0.126	3	-0.510	6
P3	-0.481*	18	0.112	18	-0.574*	18	0.493	3	-0.008	3	-0.650	6	0.046	3	0.169	3	-0.713	6
%N1	-0.056	18	0.211	18	0.291	18	-0.393	3	0.120	3	-0.430	6	0.065	3	-0.056	3	0.869*	6
%N2	0.124	18	0.119	18	0.238	18	-0.586	3	-0.102	3	-0.293	6	-0.156	3	-0.277	3	0.738	6
%N3	0.088	18	-0.189	18	0.329	18	0.504	3	-0.868	3	0.210	6	0.840	3	0.766	3	0.462	6
%P1	-0.265	18	0.198	18	0.052	18	-0.721	3	-0.278	3	-0.758	6	-0.330	3	-0.444	3	0.307	6
%P2	-0.263	18	0.239	18	-0.078	18	-0.898	3	-0.558	3	-0.784	6	-0.603	3	-0.697	3	0.225	6
%P3	-0.304	18	0.132	18	-0.033	18	-0.736	3	-0.299	3	-0.921*	6	-0.351	3	-0.464	3	0.309	6
SpLA1	0.285	18	-0.028	18	0.346	18	0.032	3	0.528	3	0.575	6	0.480	3	0.369	3	0.701	6
SpLA2	0.211	18	0.106	18	0.344	18	0.634	3	0.936	3	0.279	6	0.915	3	0.859	3	0.675	6
spLA3	0.062	18	0.058	18	-0.039	18	0.997*	3	0.823	3	-0.699	6	0.853	3	0.911	3	0.112	6
TBiomass	-0.487*	18	0.110	18	-0.584*	18	0.561	3	0.071	3	0.502	6	0.126	3	0.247	3	-0.668	6
TotalN	-0.488*	18	0.110	18	-0.607*	18	0.615	3	0.138	3	0.525	6	0.192	3	0.312	3	-0.659	6
TotalP	-0.515*	18	0.121	18	-0.563*	18	0.449	3	-0.058	3	0.446	6	-0.003	3	0.120	3	-0.577	6
TLA	-0.489*	18	0.121	18	-0.594*	18	0.678	3	0.219	3	0.532	6	0.272	3	-0.389	3	-0.628	6
TN/LA	-0.118	18	0.001	18	0.069	18	-0.853	3	-0.478	3	-0.279	6	-0.525	3	-0.626	3	0.563	6
TP/LA	-0.337	18	0.168	18	-0.104	18	-0.946	3	-0.658	3	-0.840*	6	-0.699	3	-0.781	3	0.227	6

\* Significant at  $p \leq 0.05$ .

Table A-1. (Continued).

Tree foliar Variables	Soil Nutrient Parameters											
	DTN1 n	DTN2 n	DTN3 n	DTP1 n	DTP2 n	DTP3 n	DTC1 n	DTC2 n	DTC3 n			
BD	0.014 18	-0.042 18	0.102 18	0.019 18	-0.149 18	0.158 18	-0.195 18	0.017 18	-0.312 18			
DBH	-0.227 16	-0.041 16	-0.014 16	-0.206 16	-0.255 16	-0.142 16	-0.364 16	-0.045 16	-0.366 16			
HT	-0.019 18	0.069 18	0.222 18	-0.068 18	-0.151 18	0.348 18	-0.091 18	0.100 18	-0.137 18			
LA1	0.142 18	0.023 18	0.300 18	0.165 18	-0.041 18	0.421 18	-0.006 18	-0.118 18	-0.109 18			
LA2	-0.083 18	-0.080 18	0.092 18	-0.137 18	-0.222 18	0.162 18	-0.251 18	-0.018 18	-0.308 18			
LA3	-0.029 18	0.150 18	0.236 18	-0.114 18	-0.162 18	0.274 18	-0.167 18	0.171 18	-0.233 18			
N/LA1	-0.105 18	0.093 18	0.015 18	-0.134 18	0.034 18	-0.259 18	-0.280 18	0.092 18	0.011 18			
N/LA2	0.160 18	0.124 18	-0.006 18	-0.032 18	0.072 18	-0.020 18	0.030 18	0.110 18	0.059 18			
N/LA3	0.006 18	-0.131 18	-0.303 18	-0.112 18	0.117 18	0.424 18	0.097 18	-0.201 18	0.095 18			
P/LA1	-0.103 18	0.056 18	-0.027 18	-0.044 18	0.050 18	-0.476*18	-0.262 18	0.098 18	-0.071 18			
P/LA2	-0.018 18	0.109 18	0.046 18	-0.032 18	0.051 18	-0.397 18	-0.193 18	0.157 18	-0.043 18			
P/LA3	-0.350 18	-0.193 18	-0.169 18	-0.155 18	0.096 18	-0.547*18	-0.422 18	-0.120 18	-0.082 18			
Biomass1	0.026 18	-0.005 18	0.142 18	0.020 18	-0.149 18	0.216 18	-0.158 18	0.050 18	-0.290 18			
Biomass2	-0.081 18	-0.069 18	0.084 18	-0.149 18	-0.226 18	0.152 18	-0.248 18	-0.014 18	-0.311 18			
Biomass3	-0.032 18	0.136 18	0.190 18	-0.111 18	-0.158 18	0.254 18	-0.174 18	0.149 18	-0.258 18			
N1	0.053 18	0.058 18	0.233 18	0.046 18	-0.028 18	0.220 18	-0.163 18	0.126 18	-0.101 18			
N2	-0.068 18	-0.058 18	0.100 18	-0.160 18	-0.230 18	0.161 18	-0.242 18	-0.004 18	-0.307 18			
N3	-0.019 18	0.152 18	0.202 18	-0.132 18	-0.160 18	0.284 18	-0.157 18	0.165 18	-0.249 18			
P1	-0.007 18	0.058 18	0.138 18	0.062 18	0.036 18	-0.092 18	-0.223 18	0.142 18	-0.119 18			
P2	-0.061 18	-0.013 18	0.111 18	-0.158 18	-0.203 18	0.143 18	-0.234 18	0.042 18	-0.278 18			
P3	-0.117 18	0.006 18	0.122 18	-0.158 18	-0.194 18	0.220 18	-0.249 18	0.041 18	-0.308 18			
%N1	-0.025 18	0.103 18	0.196 18	0.019 18	0.302 18	-0.032 18	-0.092 18	0.148 18	0.479*18			
%N2	0.104 18	0.111 18	0.091 18	-0.028 18	0.178 18	0.046 18	0.105 18	0.150 18	0.338 18			
%N3	0.029 18	-0.026 18	-0.134 18	-0.208 18	-0.018 18	0.188 18	0.162 18	-0.060 18	0.177 18			
%P1	-0.073 18	0.056 18	0.033 18	0.047 18	0.192 18	-0.439 18	-0.212 18	0.126 18	0.097 18			
%P2	-0.052 18	0.104 18	0.072 18	-0.029 18	0.108 18	-0.452 18	-0.201 18	0.181 18	0.043 18			
%P3	-0.307 18	-0.119 18	-0.122 18	-0.192 18	0.031 18	-0.650*18	-0.361 18	-0.050 18	-0.053 18			
SpLA1	0.122 18	-0.026 18	0.172 18	0.154 18	0.180 18	0.277 18	0.294 18	0.003 18	0.404 18			
SpLA2	-0.096 18	-0.021 18	0.182 18	0.002 18	0.091 18	0.103 18	0.092 18	0.052 18	0.363 18			
spLA3	-0.020 18	0.116 18	0.197 18	-0.151 18	-0.177 18	-0.391 18	0.034 18	0.198 18	0.110 18			
TBiomass	-0.068 18	-0.024 18	0.111 18	-0.136 18	-0.212 18	0.180 18	-0.233 18	0.024 18	-0.304 18			
TotalN	-0.055 18	-0.015 18	0.127 18	-0.150 18	-0.214 18	0.190 18	-0.229 18	0.033 18	-0.295 18			
TotalP	-0.070 18	-0.006 18	0.118 18	-0.150 18	-0.192 18	0.147 18	-0.242 18	0.049 18	-0.282 18			
T/LA	-0.065 18	-0.028 18	0.133 18	-0.124 18	-0.208 18	0.200 18	-0.230 18	0.027 18	-0.292 18			
TN/LA	0.025 18	0.053 18	-0.116 18	-0.126 18	0.097 18	0.030 18	-0.087 18	0.018 18	0.071 18			
TP/LA	-0.162 18	-0.005 18	-0.050 18	-0.080 18	0.069 18	-0.502*18	-0.308 18	0.052 18	-0.069 18			

\* Significant at  $p \leq 0.05$ .

Table A-1. (Continued).

Tree Foliar Variables	Soil Nutrient Parameters											
	PH1	n	PH2	n	PH3	n	DPH1	n	DPH2	n	DPH3	n
BD	0.091	18	-0.059	18	0.164	18	0.217	16	0.217	14	-0.100	15
DBH	0.520*	16	0.065	16	0.252	16	0.587*	14	0.154	12	-0.155	13
HT	0.095	18	0.136	18	0.100	18	0.285	16	0.293	14	-0.265	15
LA1	-0.110	18	0.007	18	-0.062	18	-0.000	16	0.202	14	-0.253	15
LA2	0.184	18	0.053	18	0.110	18	0.338	16	0.304	14	-0.146	15
LA3	0.180	18	0.266	18	0.086	18	0.369	16	0.383	14	-0.352	15
N/LA1	0.381	18	-0.350	18	0.566*	18	0.288	16	-0.296	14	0.411	15
N/LA2	-0.127	18	-0.627*	18	0.271	18	-0.228	16	-0.513	14	0.350	15
N/LA3	-0.214	18	-0.133	18	-0.289	18	-0.190	16	0.223	14	0.069	15
P/LA1	0.471	18	-0.313	18	0.386	18	0.338	16	-0.508	14	0.245	15
P/LA2	0.324	18	-0.357	18	0.335	18	0.202	16	-0.568*	14	0.206	15
P/LA3	0.658*	18	0.018	18	0.292	18	0.601*	16	-0.290	14	0.349	15
Biomass1	0.071	18	-0.010	18	0.167	18	0.234	16	0.245	14	-0.149	15
Biomass2	0.188	18	0.041	18	0.104	18	0.343	16	0.284	14	-0.167	15
Biomass3	0.199	18	0.246	18	0.103	18	0.398	16	0.372	14	-0.340	15
N1	0.086	18	-0.187	18	0.242	18	0.143	16	0.021	14	0.015	15
N2	0.152	18	0.020	18	0.109	18	0.302	16	0.274	14	-0.151	15
N3	0.186	18	0.252	18	0.102	18	0.387	16	0.390	14	-0.330	15
P1	0.270	18	-0.252	18	0.197	18	0.248	16	-0.299	14	-0.035	15
P2	0.178	18	0.017	18	0.043	18	0.310	16	0.203	14	-0.249	15
P3	0.233	18	0.265	18	0.049	18	0.449	16	0.398	14	-0.321	15
%N1	0.160	18	-0.405	18	0.212	18	-0.077	16	-0.603*	14	0.484	15
%N2	-0.144	18	-0.461	18	0.065	18	-0.310	16	-0.518	14	0.354	15
%N3	-0.075	18	-0.093	18	-0.188	18	-0.190	16	-0.085	14	0.187	15
%P1	0.409	18	-0.359	18	0.253	18	0.199	16	-0.679*	14	0.269	15
%P2	0.370	18	-0.316	18	0.299	18	0.206	16	-0.634*	14	0.244	15
%P3	0.676*	18	0.019	18	0.342	18	0.535*	16	-0.311	14	0.388	15
SpLA1	-0.363	18	0.044	18	-0.499*	18	-0.457	16	-0.133	14	-0.144	15
SpLA2	-0.014	18	0.350	18	-0.302	18	-0.075	16	0.135	14	-0.096	15
spLA3	0.245	18	0.078	18	0.152	18	-0.045	16	0.152	14	0.163	15
TBiomass	0.189	18	0.084	18	0.108	18	0.356	16	0.304	14	-0.207	15
TotalN	0.159	18	0.055	18	0.116	18	0.317	16	0.287	14	-0.180	15
TotalP	0.198	18	0.465	18	0.054	18	0.340	16	0.216	14	-0.257	15
TLA	0.177	18	0.099	18	0.101	18	0.340	16	0.323	14	-0.198	15
TN/LA	0.046	18	-0.521*	18	0.294	18	-0.017	16	-0.336	14	0.416	15
TP/LA	0.511*	18	-0.238	18	0.361	18	0.400	16	-0.489	14	0.283	15

\* Significant at  $p \leq 0.05$ .