AN ABSTRACT OF THE THESIS OF

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Title: Stand Development after 20-years of Growth in Douglas-fir and Red Alder Mixtures

Abstract approved:

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This study examines the long-term role of interference on stand development of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and red alder (*Alnus rubra* Bong.) planted mixtures in the Central Cascades of Oregon, USA. The two species are common associates in naturally regenerated and planted conifer stands in the Pacific Northwest. Due to red alder's rapid height growth, Douglas-fir is often impeded when in the presence of red alder. However, because of red alder's ability to fix nitrogen and increase soil nutrient cycling rates Douglas-fir development can potentially be enhanced when in red alder presence.

The relationship between current stand structure, tree mortality, tree size and varying mixtures of species proportions were examined in this study. Treatments included four proportions of red alder either planted simultaneously with the Douglas-fir or delayed 5-years after initial Douglas-fir planting. The objectives of this study were to determine if species mixtures were capable of a greater yield when compared to monocultures and then to determine which form of interference was taking place within and between species.

A long-term replacement series study was established in 1986 to understand the role of interference on two commercially valuable species. Six treatments of each planting time were created with the following proportions (Douglas-fir/red alder, respectively): 1.0/0.0, 0.9/0.1, 0.7/0.3, 0.5/0.5, 0.25/0.75, 0.0/1.0. Each treatment was replicated three times in a randomized complete-block design. Measurement of diameter at breast height (cm) of each stem, total height (m), and number of live/dead stems were determined in 1988-1991, 1993, 1995, 1998 and 2007.

Yields of both the 0.5/0.5 simultaneous and delayed treatment mixtures were notably higher than the monocultures. Per-tree basal area, height, and survival decreased for both the Douglas-fir and red alder as the relative density (proportion) of red alder increased in the simultaneously planted mixtures. In the delayed mixtures, Douglas-fir per-tree basal area, height, and survival increased as red alder density increased. Red alder development indicated only minor decreases in survival as its density increased in the delayed treatment mixtures.

Competition was the dominant mechanism of stand development for all treatments. In the simultaneously planted treatments the Douglas-fir was driven most by interspecific competition, while red alder development exhibited trends for intraspecific competition. In the delayed planted treatments both species experienced intraspecific competition, although this effect was minor for red alder. These results support the competitive effects of red alder on Douglas-fir and itself when seedlings are established at the same time. The delayed treatments however, showed the importance of density on individual tree development over time.

Stand Development after 20-years of Growth in Douglas-fir and Red Alder Mixtures

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APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Brennan T. Garrelts, Author

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CHAPTER ONE

INTRODUCTION

Sustainable forest management

Sustainable forest management has become an important goal for forestry. Currently, there are commitments by federal agency and private land owners to restore, enhance and sustain a full range of forest values: economic, social and ecological. In essence, sustainable forest management is defined as: *The practice of managing forest resources to meet the long-term forest product needs of humans while maintaining the biodiversity of forested landscapes*. Both forest managers and the public are interested in ways to meet this definition and the goals set forth by it.

Researchers have demonstrated that increasing the diversity of tree species in planted stands is one way to support ecological diversity. Previous research indicates that compared to monoculture stands of conifer species, mixed stands of conifers and hardwood species are capable of increasing biodiversity through: available soil fertility (Rothe et al. 2002; Binkley 2003), nutrient cycles, tree production, understory flora richness, and total ecosystem production (Binkely 2003; Radosevich et al. 2006). While these mixtures are capable of ecological gains, economic gains can also be achieved when both planted species are commercially valuable.

Two species that naturally grow together in the central Cascade Mountains of Oregon are Douglas-fir (P*seudotsuga menziesii* var. *menziesii* [Mirb.] Franco) and red alder (*Alnus rubra* Bong.). Both species are commercially valued in Pacific Northwest log markets. There are many previous studies that focus on the associations of these two species (Newton et al. 1968; Hibbs et al. 1989; Puettmann et al. 1992; Knowe and Hibbs 1996; Radosevich et al. 2006) because of their high individual ecological and economic value. In addition, the species have also been closely examined because intra- and inter-specific interference strongly drives their size and allometry (Cole and Newton 1986, 1987; Shainsky and Radosevich 1991; Knowe and Hibbs 1996; D'amato 2002).

Interference

Interference is the general term for the interaction among and between species of plant populations that influences the growth and/or development of its neighbor (Radosevich et al. 2007). Total plant density, species proportion, and the spatial relationships within mixed species systems are significant factors which contribute to interference and individual plant development (Radosevich et al. 2007). Understanding the mechanisms of interference that alter plant development enhances the ability to create mixed species systems capable of enhanced diversity, yield and efficiency.

Mixed crops of plant species are capable of several different forms of interspecific interference, including: neutralism, competition, mutualism, commensalism, amensalism, and parasitism (Burkholder 1952). In the case of Douglas-fir and red alder mixtures, two forms of inter- and intra-specific interference are most likely: competition and facilitation. Both beneficial and detrimental processes may occur concurrently, so the observed outcome in tree growth reflects their net influence (Goldberg 1990; Shainsky and Rose 1995). The level of competition depends on the effectiveness of each species in competing for resources; the responsiveness of each species to resource supply and the effects of species proportions in the mixtures on the two preceding factors (Jolliffe et al. 1984). By examining current structure and development over time of species mixtures it is possible to discern which forms of interference are dominating species development (Goldberg 1990). Unfortunately, the understanding of the nature of such interactions in long-term mixed crop studies is both limited and conflicting.

One way to examine interference among plants species is to study changes in physiological and morphological growth responses associated with the differences in the environment, and then assess those changes relative to the correlations between the proportion and/or density of neighbors (Shainsky and Radosevich 1992). Investigating the current physiological growth and development of plants reveal the effects of immediate growing conditions, while examining the size and morphology of a group of individuals exhibits their earlier developmental conditions (Giordano and Hibbs 1993). One way to establish a pattern of interference of past growing conditions is to measure plant dimensions over time intervals and relate those measurements to resource proportion/density (Giordano and Hibbs 1993). The presence of two plant species within an essential resource space increases the complexity of the interaction (Clement et al. 1929; Harper 1961, 1977). Additionally, the complexity of inter- and intra-specific interference increases as the density of the two species increases (Jolliffe et al. 1984).

Finally there are several ways to quantify interference in stands of trees. In general, tree height and mortality are capable indicators of stand structure and development over time. However, while these variables are important to determining the interference processes occurring in these mixtures, previous research of long-term neighborhood competition demonstrates that diameter development may be better determinant of interference (Wagner and Radosevich 1998, Knowe 1991), such as per-tree or total stand basal area.

Douglas-fir/red alder mixtures

In natural mixed stands of red alder and Douglas-fir, red alder is generally the dominant competitor, capable of rapid establishment and substantial early height growth. The early height growth of red alder exceeds all Pacific Northwest species except black cottonwood (*Populus trichocarpa*) and balsam popular (*P.balsamifera*) (Newton and Cole 1994). In a controlled density experiment, Shainsky (1988) found that once red alder achieved crown closure, understory solar radiation was constant across all densities, indicating that red alder was superior in its ability to occupy (capture) available above-ground resources. In addition, red alder is also highly competitive below-ground because its roots systems are capable of greater soil exploitation than Douglas-fir (Giordano and Hibbs 1993).

Douglas-fir is also a capable competitor in its own right. If allowed to grow in an open environment it is capable of attaining heights greater than red alder after only 25 years (Newton et al. 1968) and has greater photosynthetic material (Cole and

Newton 1986). Given appropriate planting densities, Douglas-fir stand basal area can be greater than red alder after 25 years (Cole and Newton 1986). When planted in mixtures, the sustained height growth and greater total height of Douglas-fir will eventually allow the species to attain co-dominate and eventual dominate canopy positions (Cole and Newton 1987) in mixed stands.

The early development of Douglas-fir and red alder in mixed stands is highly dependent upon levels of interference. The rapid above- and below-ground development of red alder causes an increased level of competition for resources for Douglas-fir. The greater ability of Douglas-fir to endure lower moisture and light conditions than red alder increases its ability to become the dominant canopy layer once red alder growth stagnates; usually between ages 25 and 40 (Newton et al. 1968; Miller and Murray 1978).

The significant amount of interest in Douglas-fir/red alder mixtures arises from red alder's symbiotic relationship with the nitrogen fixing bacteria, *Frankia spp*. *Frankia spp*. is a bacteria residing in nodules on the root tips of certain tree and shrub species, that fixes atmospheric nitrogen, turning inorganic N_2 into available organic ammonia (NH_3) for plant consumption (Gordon and Weaver 1983). Annual rates of nitrogen accretion in natural stands of red alder range from 85 (Cole et al. 1978), 100 (Bormann and DeBell 1981) to 320 kg/ha/year (Newton et al. 1968). Research indicates that enhanced conifer growth, in the presence of red alder, only occurs where soil nitrogen levels are limiting (Binkley 1982). Furthermore, intense competition during early development for light and moisture can nullify any gross positive effects of enhanced soil nitrogen for conifer growth, demonstrating only the negative net effect from competition (Shainsky and Radosevich 1992). Therefore, if nitrogen is limiting Douglas-fir growth then any nitrogen that the red alder contributes will help diminish the competition effect of the red alder on the Douglas-fir, otherwise if nitrogen is not limiting Douglas-fir growth or red alder is not capable to fixing enough nitrogen for conifer use the presence of red alder would not be expected to enhance growth.

Motivation and objectives

Although the interference between young Douglas-fir and red alder has been extensively studied (Tarrant 1961; Miller and Murray 1978; Binkley 2003; Shainsky and Radosevich 1991, 1992; Puettmann et al. 1992; Radosevich et al. 2006), many of these studies conflict. Shainsky and Radosevich (1992) show that density dependent relationships of seedling stem volume exist between Douglas-fir and red alder and that competition for resources is the dominant process influencing growth. Research by Tarrant (1961), Binkley (1983) and Miller et al. (1993) demonstrate that the nitrogen fixing ability of red alder enhances the growth of Douglas-fir on sites with low soil fertility. While the strong affect that both inter- and intra-specific competition has on young individuals of Douglas-fir and red alder has been well documented (Weiner and Thomas 1986; Radosevich et al. 2007), little is known about the long-term relationship between interference and stand development. In addition, examination of a 20-year-old mixed stand in an established experiment can provide forest managers with information about the mid- stages of development of species mixtures and the role that interference plays between these two economically and ecologically valuable species. More carefully designed, long-term experiments are needed to further enhance the knowledge base of the interactions between these two species. Examining the stand development after 20-years, as well as the development over time of the mixed stands will further the understanding of tree species interference and stand development of mixed species.

The goals of this study are to:

1) Determine which species mixtures are capable of over- and under-yielding relative to a monoculture treatment of each species.

2) Document the interference process after 20-years of species mixture development.

3) Determine at which age interference processes begin to influence the per-tree development of each species.

These goals are designed to help achieve the overall objective:

- To determine how relative proportions of two tree species in a mixture, one capable of facilitation and competition and another only competition, affect individual tree and stand development.

References

Binkley, D., 1982. Nitrogen fixation and net primary production in a young Sitka alder stand. Canadian Journal of Botany 60, 281-284.

Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Canadian Journal of Forest Research 33, 2274-2279.

Bormann, B.T., DeBell, D.S., 1981. Nitrogen content and other soil properties related to age or red alder stands. Soil Science Society of America Journal 45(2), 428-432.

Burkholder, P.R., 1952. Cooperation and conflict among primitive organisms. American Scientist 40, 601-631.

Clements, F.E., Weaver, J.E., Hanson, H.C., 1929. Plant competition. Carnegie institute of Washington, Washington, D.C. *In.* Jolliffe, P.A., Nimjas, A.N., and Reuneckles, V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology. 21: 227-243.

Cole, D.W., Gessel, S.P. and Turner, J. 1978. Utilization and management of alder: comparative mineral cycling in red alder and Douglas-fir. USDA Forest Service General Technical Report PNW-70.

Cole, E.C., Newton, M., 1986. Fifth year responses of Douglas-fir to crowding and non-coniferous competition. Canadian Journal of Forest Research 16, 727-737.

Cole, E.C., Newton, M., 1987. Nutrient moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. Canadian Journal of Forest Research 17, 181-186.

Goldberg, D.E., 1990. Components of resource competition in plant communities. In: J.B.Grace, Tilman, D. (Eds.), Prospectives in plant competition Academic Press, New York, pp. 27-40.

Gordon, J.C., Wheeler, C.T., 1983. Biological nitrogen fixation in forest ecosystems: foundations and applications. Dr. W. Junk Publishers, Boston.

Grotta, A.T., Gartner, B.L., Radosevich, S.R., 2004. Influence of species proportion and timing of establishment on stem quality in mixed red alder- Douglas-fir plantations. Canadian Journal of Forest Research 34, 863-870.

Harper, J.L., 1961. Approaches to the study of plant competition. In, Symposia of the Society for Experimental Biology, pp. 1-39. *In* Jolliffe, P.A., Nimjas, A.N., and Reuneckles, V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology. 21: 227-243.

Jolliffe, P.A., Nimjas, A.N., Reuneckles, V.C., 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology 21, 227-243.

Miller, R.E., Murray, M.D., 1978. The effects of red alder on the growth of Douglas-fir. In: Briggs, D.G., DeBell, D.S., Atkinson, W.A. (Eds.), Utilization and Management of Alder. USDA Forest Service: General Technical Report PNW-70.

Miller, R.E., Reukema, D.L., Max, T.A., 1993. Size of Douglas-fir trees in relation to distance from a mixed alder-Douglas-fir stand. Canadian Journal of Forest Research 23, 2413-2418.

Newton, M., Cole, E.C., 1994. Stand development and successional implication: Pure and Mixed Stands. In: Hibbs, D.E., DeBell, D.S., Tarrant, R.F. (Eds.), The Biology and Management of Red Alder. Oregon State University Press, Corvallis.

Newton, M., El Hassan, B.A., Zavitkovski, J., 1968. Role of red alder in western Oregon forest succession. In: Trappe, J.M. (Ed.), Biology of alder. USDA Forest Service: General Technical Report PNW-70, Portland, Oregon.

Puettmann, K.J., Hibbs, D.E., Hann, D.W., 1992. The dynamics of mixed stands of Alnus rubra and Pseudotsuga menziesii: extension of size-density analysis to species mixtures. Journal of Ecology 36, 769-782.

Radosevich, S.R., Hibbs, D.E., Ghersa, C.M., 2006. Effects of species mixtures on growth and stand development of Douglas-fir and Red Alder. Canadian Journal of Forest Research 36.

Roth, A., Cormack, K.J., Sigrid, S.C., Makineci, E., Son, Y., 2002. Soil carbon and nitrogen changes under Douglas-fir with and without red alder. Soil Science Society of America Journal 66, 1955-1988.

Shainsky, L.J., Radosevich, S.R., 1991. Analysis of yield-density relationships in experimental stands of Douglas-fir and red alder seedlings. Forest Science 37, 574-592.

Shainsky, L.J., Radosevich, S.R., 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology 73 30-45.

Shainsky, L.J., Rose, C.L., 1995. Effects of competition on the foliar chemistry of young Douglas-fir in monoculture and mixed stands with young red alder. Canadian Journal of Forest Research 25, 1969-1973.

Stubblefield, G., Oliver, C.D., 1978. Silvicultural implications of the reconstruction of mixed alder/conifer stands. In: Briggs, D.G., DeBell, D.S., Atkinson, W.A. (Eds.), Utilization and Management of alder. USDA Forest Service, pp. 307-320.

Tarrant, R.F., 1961. Stand development and soil fertility in a Douglas-fir/red alder plantation. Forest Science 7, 238-246.

CHAPTER TWO

METHODS

Study site

This study was conducted from data gathered at the H.J. Andrews (HJA) Experimental Forest (122º 10' W, 44º 14' N) on the west-central slope of the Cascade Mountain Range in western Oregon in a Douglas-fir height potential site III classification zone. It is located in the *Tsuga heterophylla* vegetation zone (Franklin and Dryness 1971), characterized by a wet, mild, maritime climate. Annual precipitation averages 230 cm with 94% occurring between September and May. Mean annual minimum temperature is -8.5 C and mean annual maximum temperature is 26.9 C. Typical winter snowpack is variable, occasionally accumulating over 1m. (Radosevich et al. 2006). Elevations at the study site range from 500 to 800m above sea level. The soil fertility of the study site is considered moderate; characterized by deep, well-drained gravelly loam over a cobbly silt loam C horizon formed from basic igneous rock and volcanic ash (Rothe et al. 2003, Radosevich et al. 2006).

Experimental design

The experiment was conducted as a randomized complete block, modified replacement series design. In this design, total tree density in every treatment is constant, while proportions of the two species vary. The replacement series experiment is used to determine the yields of mixtures (treatments) by comparing them to monoculture yields (controls). There are two systematic variations among the 8 treatments in this experiment (Figure 2.1):

1. a subset of treatments where both species were planted at the same time (simultaneous planting) (treatments 2, 4, 6, 10)
2. a subset of treatments where red alder was planted five years after the initial Douglas-fir were planted (1992) (delayed planting) (treatments 3, 5, 7, 11)

The experimental site has three (3) blocks, containing one replication of the 8 treatments and 3 controls (Douglas-fir monoculture, simultaneous red alder and delayed red alder monocultures) in $27m^2$ plots (0.073ha) (Figures 2.1 and 2.2). Tree seedlings were planted on a 3m grid, where each plot consisted of 81 total trees (9x9 rows). The treatments were labeled 2-7, 10-11 and the controls 1, 12, 13. Location of both treatments and controls were randomly assigned within each of the three blocks. Natural mortality over the past 20 years has resulted in a mix of spatial conditions throughout the treatments.

This study was created and implemented using a previous experiment designed by Radosevich and Hibbs (Radosevich et al. 2006). In the spring and summer of 1985, the experimental site was clearcut of old-growth *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (western hemlock). Following the clearcut harvest, the site was broadcast burned in the fall of 1985. In the spring of 1986, seedlings were planted according to the density, spacing, species proportions and timing listed in Table 2.1. The site was initially planted with 1-0 Douglas-fir nursery stock seedlings according to the treatments listed in Table 2.1 and Figure 2.1. Because of a mistake in planting (Radosevich et al. 2006), the 1-0 red alder nursery stock seedlings were not planted until the spring of 1987. Tree seedlings of either species that died were replanted only in the first year of the experiment (1988).

Table 2.1: Treatment definitions for Douglas-fir and red alder planting (DF=Douglas-fir, RA=red alder).

MIXED TREATMENT	PROPORTION DF	PROPORTION RA	RA PLANTING	CONTROL TREATMENT	PROPORTION DF	PROPORTION RA	RA PLANTING
2	0.9	0.1	SIMULTANEOUS	1	1.0	0.0	----------------
3	0.9	0.1	5 YR DELAYED	12	0.0	1.0	SIMULTANEOUS
4	0.7	0.3	SIMULTANEOUS	13	0.0	1.0	5YR DELAYED
5	0.7	0.3	5 YR DELAYED				
6	0.5	0.5	SIMULTANEOUS				
7	0.5	0.5	5 YR DELAYED				
10	0.25	0.75	SIMULTANEOUS				
11	0.25	0.75	5 YR DEALYED				

Figure 2.1: Initial species treatment plots with nested measurement sub-plots.

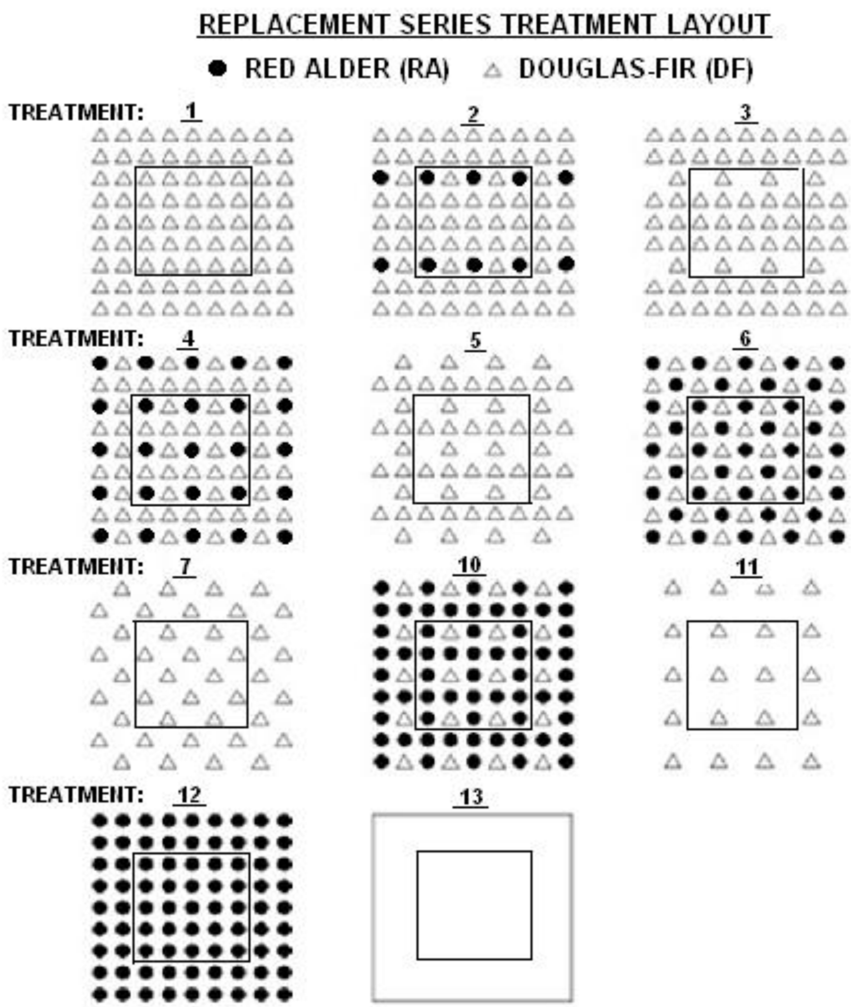
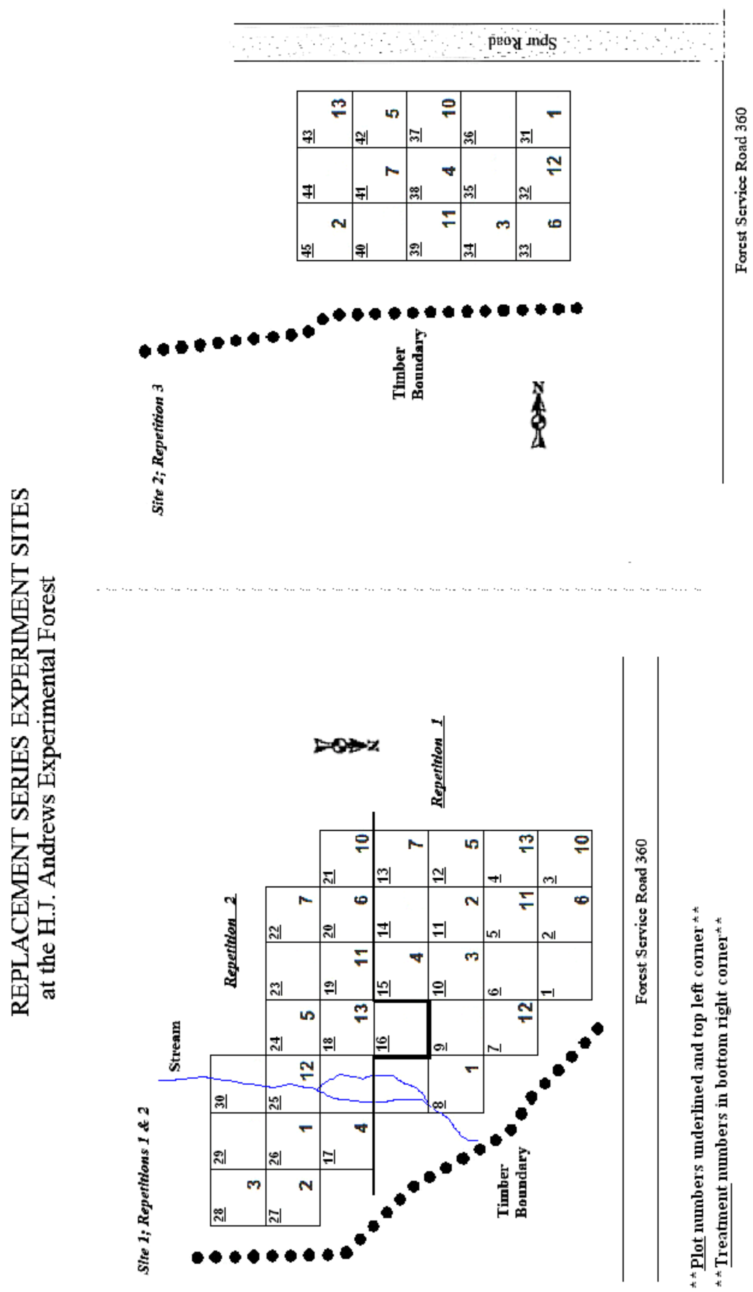


Figure 2.2: Replacement series experimental site and layout. Plots without treatment numbers were not used for analysis in this study



Data collection

In each plot only the centermost 25 trees were measured. Thus, each measurement plot was surrounded by two buffer rows, thereby reducing any confounding edge effects. Simultaneous planted treatments were measured at the beginning of the growing season in 1988, 1989, 1990, 1991, 1993, 1995, 1998, and 2007. Delayed planted treatments were measured in 1995, 1998, and 2007. Stem diameters were collected 2cm from the ground during the early years of development (simultaneous treatments: 1988, 1989, 1991, delayed treatments 1995, 1998) and then measured at breast height during later stand age. Stem diameter of each measurement tree was recorded (millimeters) and basal area was determined using the formula:

$$BA = r^2 * \pi \qquad \text{EQU 2.1}$$

For trees with multiple stems, basal area was computed for the tree's dominant stems and then summed as the total basal area for one individual. Basal area was chosen as the response variable because of its sensitivity to inter- and intra-specific interference (Tappeiner II, et al. 2007).

Biological and statistical significance

A priori, I was interested in determining the biologically significant trends of growth of the two species. Also, due to the high degree of variability observed during data collection, it was concluded that an α=0.05 probably would be too restrictive to determined effects. Given this, an α=0.1 was used to determine statistically significant results, and p-values greater than but close to a value 0.1 are considered statistically valid. The biological trends of the results are discussed, with support drawn from statistical inferences.

Data analysis

Research Question 1: Does species proportion affect over- and under-yielding?

Relative land output (RLO) was used to examine the relative productivity of the treatment mixtures versus a monoculture. Relative land output assesses the mixed stand (treatment) productivity when equivalent amounts of land are allocated to monoculture stands (controls) (Radosevich et al 2006, Jolliffe 2008). RLO was calculated using the following formula:

$$RLO = \frac{total\ treatment\ basal\ area}{(x)BADF_c + (1-x)BARA_c} \qquad \text{EQU 2.2}$$

Where (x) = equivalent proportion of Douglas-fir in the monoculture (control 1)

$BADF_c$ = the total basal area of Douglas-fir in the monoculture treatment (1)

(1-x) = equivalent proportion of red alder in the monoculture (control 12 or 13)

$BARA_c$ = the total basal area of red alder in the monoculture control treatments (12 or 13)

The interpretation of RLO uses the value 1.0 as an index value of the monoculture yield. If the treatment mixtures have a RLO of 1.0, there is no difference in yield between the treatment mixture and the monoculture. However, if the RLO value of the treatment mixture is above or below the index value of 1.0, then the treatment mixture is either over-yielding or under-yielding relative to the monoculture treatments.

Analysis of RLO was separated into simultaneous planting- and delayed planting- treatments and analyzed separately. A logarithm transformation of basal area was performed to satisfy assumptions of constant variance. Assumptions of normality and constant variance were checked and found to be appropriate. An analysis of variance (ANOVA) (α=0.1) using a MIXED procedure to test the null hypothesis (H_0) that the RLO values of the treatments did not vary from 1.0, the monoculture index value. An LSMEANS was also computed to tests the null hypothesis that there was no difference among treatments. The analysis was completed in SAS v.9.1 (SAS Institute, Inc. 2003) using the following model:

$$Y_{ij} = \mu + \beta_i + t_j + \varepsilon_{ij} \qquad \text{EQU 2.3}$$

Where Y_{ij} is the logarithm basal area of the j^{th} treatment divided by the weighted average of the given species in the control treatments

μ is the overall mean

β_i is the effect of the i^{th} block (1, 2, 3) ~ $N(0, \sigma^2_\beta)$

t_j is the effect of the j^{th} treatment

ε_{ij} is the random error that represents variability among treatments within blocks ~ $N(0, \sigma^2_\varepsilon)$

Once the analysis was completed and RLO estimates and appropriate confidence intervals generated, all values were back-transformed and described in the results and discussion sections of this thesis.

Research Question 2: Has 20 years of interference affected the current development of each species?

Mean height, the ratio of current live versus originally planted stems, and basal area for data collected in 2007 was sorted and analyzed by planting definition and species (Table 2.1).

Analysis of these response variables were completed separately by species and planting definition (Table 2.1). The assumptions of constant variance and normality were assessed for each response variable. A logarithm transformation of basal area was completed in order to satisfy the assumptions of constant variance. An analysis of variance (ANOVA) (α=0.1) was run using a 'mixed' procedure for each response variable to test the null hypothesis (H_0) that the each treatment response did not vary from zero. The following model was used for all response variables:

$$Y_{ij} = \mu + \beta_i + t_j + \varepsilon_{ij} \qquad \text{EQU 2.4}$$

Where Y_{ij} is the response variable of the j^{th} treatment

μ is the overall mean

β_i is the effect of the i^{th} block (1, 2, 3) ~ $N(0, \sigma^2_\beta)$

t_j is the effect of the j^{th} treatment

ε_{ij} is the random error that represents variability among treatments within blocks ~ $N(0, \sigma^2_\varepsilon)$

Estimates of each response variable per treatment were generated using ‘lsmeans’. These estimates were then sorted according to the proportion of red alder in the treatment and a ‘regression’ procedure was used to determine if the response variables changed significantly (α=0.1). The analysis was completed in SAS v.9.1 (SAS Institute, Inc. 2003) using the following models:

μ{mean height|red alder density}= $\beta_0 + \beta_1$red alder density EQU 2.5

μ{survival proportion|red alder density}= $\beta_0 + \beta_1$red alder density EQU 2.6

μ{log(per-tree basal area)|red alder density}= $\beta_0 + \beta_1$red alder density EQU 2.7

Research Question 3: When does interference begin to affect individual tree growth over time in treatment mixtures?

In this analysis, per-tree mean basal area was computed for each species occurring within each treatment by year to assess how the species in each treatment developed over time. The analysis was separated into two categories and two sub-categories:

1a) simultaneously planted treatments of Douglas-fir,

1b) delayed planted treatments of Douglas-fir,

2a) simultaneous planted treatments of red alder,

2b) delayed planted treatments of red alder.

Analysis of the above categories was preformed separately, but in the same manner.

Prior to model selection, a logarithm transformation was preformed on basal area to correct for the assumption of constant variance. Both the assumptions of constant variance and normality then were found to be appropriate for all categories. The Akaike Information Criterion (AICc) was used to determine the best covariance structure for repeated measures of the same treatments over multiple years. An autoregressive(1) covariance structure was determined to be the best model. In this covariance structure, the greater the interval between two sampled years the smaller the correlation. For example, the covariance between years 1988 and 1991 is smaller than the covariance between years 1988 and 1998.

The null hypothesis (H_0), which states that mean basal area per tree for each species is not different among treatments and years, was tested using a mixed procedure (α=0.1) with a autoregressive(1) covariance adjustment in SAS v.9.1 (SAS Institute, Inc. 2003). The following model was used to complete the analysis:

$$Y_{ijkl} = \mu + \beta_i + t_j + \varepsilon_{ij} + y_k + ty_{ik} + \varepsilon_{ijkl} \qquad \text{EQU 2.8}$$

Where Y_{ijk} is the logarithm of the mean basal area of the species/treatment in the j^{th} treatment in the i^{th} block and the k^{th} year

μ is the overall mean of log basal area of the Douglas-fir

β_i is the effect of the i^{th} block (1, 2, 3) ~ $N(0, \sigma^2_\beta)$

t_j is the effect of the j^{th} treatment (1-7, 10, 11)

ε_{ij} is the random error term that represents variability among treatments within blocks ~ $N(0, \sigma^2_\varepsilon)$

y_k is the effect of each k^{th} year (1988, ’89, ’90, ’91, ’93, ’95, ’98, and 2007)

ty_{ik} is the interaction effect of treatment j within year k, ty_{ik} ~ $N(0, \sigma^2_t)$ k=1988, 1989,...,n_i

ε_{ijkl} is the random error term represents variability between blocks among treatments and years and $\varepsilon_{\underline{ijkl}}$~$N(0, \sigma^2\ )$ and

$$\varepsilon_{ijkl} \sim MVN(\underline{0}, \sigma^2) \text{ and } \sigma^2 \begin{bmatrix} 1 & p & p^2 & p^3 & p^4 & p^5 & p^6 & p^7 \\ p & 1 & p & p^2 & p^3 & p^4 & p^5 & p^6 \\ p^2 & p & 1 & p & p^2 & p^3 & p^4 & p^5 \\ p^3 & p^2 & p & 1 & p & p^2 & p^3 & p^4 \\ p^4 & p^3 & p^2 & p & 1 & p & p^2 & p^3 \\ p^5 & p^4 & p^3 & p^2 & p & 1 & p & p^2 \\ p^6 & p^5 & p^4 & p^3 & p^2 & p & 1 & p \\ p^7 & p^6 & p^5 & p^4 & p^3 & p^2 & p & 1 \end{bmatrix} \text{ represents}$$

autoregressive(1) covariance structure among treatments and years.

Once the analyses were completed and mean basal area estimates and appropriate confidence intervals were generated all values were back-transformed to the original scale for the results and discussion sections.

References

Franklin, J.F., Dryness, C.T., 1971. A checklist of vascular plants on the H.J. Andrews experimental forest. USDA Forest Service PNW-RN-138.

Jolliffe, P.A., 2008. Personal communication.

Jolliffe, P.A., Nimjas, A.N., Reuneckles, V.C., 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology 21, 227-243.

Radosevich, S.R., Hibbs, D.E., Ghersa, C.M., 2006. Effects of species mixtures on growth and stand development of Douglas-fir and Red Alder. Canadian Journal of Forest Research 36, 769-782.

Roth, A., Jörg, E., Hibbs, D.E., 2003. Do admixed broadleaves improve foliar nutrient status of conifer tree crops. Forest Ecology and Management 172, 328-329.

Tappeiner, J.C., Maguire, D.A., Harrington, T.B., 2007. Silviculture and ecology of western U.S. Forests. Oregon State University Press, Corvallis, Oregon.

CHAPTER THREE

RESULTS

Relative land output

Research Question 1: Does species proportion affect over- and under-yielding?

Simultaneous treatments

After 20-years of growth and stand development, the relative land output (RLO) estimates of the simultaneously planted treatments were not significantly different ($p>0.1$) from the monoculture control index of 1.0 ($F_{3,6} = 1.08$, $p=0.4273$). Treatment 6 (0.5DF / 0.5RA respectively) had the largest estimated RLO of the simultaneous treatments, and second largest or all treatments (Figure 3.3), 1.30 (90% RLO confidence limits of 0.94 and 1.79). Treatment 4 (0.7DF / 0.3RA) had the second largest estimated RLO within simultaneous treatments, 1.23 (90% confidence limits 0.89, 1.70). Treatment 2 (0.9DF / 0.1RA) followed with an estimated RLO of 1.09 (90% confidence limits 0.79, 1.51). Finally, treatment 10 (0.25DF / 0.75RA) had the smallest estimated RLO in the simultaneous treatments, 0.88 (90% confidence limits 0.64, 1.22) (Figure 3.3). These results are also listed in Table 3.1a.

Delayed treatments

Unlike the simultaneous planting treatments, the delayed planted treatments were statistically different ($p<0.1$) from the monoculture index ($F_{3,6} = 3.37$, $p=0.096$)

(Figure 3.2). Treatment 7 (0.5DF / 0.5RA) had the greatest RLO of both simultaneous and delayed treatments, 1.37 (90% confidence intervals 1.07, 1.74) (Figure 3.3). Treatment 11 (0.25DF / 0.75RA) had the second largest RLO for the delayed planted treatments, 1.23 (90% confidence limits 0.96, 1.57). Followed by treatment 5 (0.7DF / 0.3RA), with an RLO of 1.07 (90% confidence limits 0.84, 1.37). Finally, treatment 3 (0.9DF / 0.1RA) had the lowest estimated value among the delayed treatments (Figure 3.3) with an RLO of 0.88 (90% confidence limits 0.69, 1.13). These results are also presented in Table 3.1b.

It can be concluded that the delayed treatment 7 (0.5DF / 0.5RA) ($p=0.05$) was the only planted treatment mixture that produced an estimated RLO value sizably greater than the monoculture index. Overall, both the simultaneous and delayed treatments suggest trends of increasing RLO estimated values as the relative density of red alder increases in the mixtures from 0.1 to 0.5. RLO estimates decrease when the proportion of red alder increases from 0.5 to 0.75 for both treatment types as well.

Table 3.1a/b: Relative land output values of treatment mixtures.

Test that RLO is not equal to monoculture control index of 1.0. RLO and corresponding confidence bounds have been back transformed from the logarithm scale. (CNTL=monoculture control, SL=simultaneous treatment, DL=delayed treatments, DF=Douglas-fir, RA=red alder)

1a: simultaneously planted treatments

Treatment	Planting Proportion (DF / RA)	RLO	Contribution of DF/ RA to RLO (%)	SE	DF	T value	Pr > T	Lower 90% Bound	Upper 90% Bound
1 - CNTL	1.0 / 0.0	1.00	100 / 0	-	-	-	-	-	-
2 - SL	0.9 / 0.1	1.09	68 / 32	0.17	6	0.52	0.62	0.79	1.51
4 - SL	0.7 / 0.3	1.23	63 / 37	0.17	6	1.24	0.26	0.89	1.70
6 - SL	0.5 / 0.5	1.30	47 / 53	0.17	6	1.58	0.17	0.94	1.79
10 - SL	0.25 / 0.75	0.88	48 / 52	0.17	6	-0.77	0.47	0.64	1.22
12 - CNTL	0.0 / 1.0	1.00	0 / 100	-	-	-	-	-	-

1b: delayed planted treatments

Treatment	Planting Proportion (DF / RA)	RLO	Contribution of DF / RA to RLO (%)	SE	DF	T value	Pr > T	Lower 90% Bound	Upper 90% Bound
1 - CNTL	1.0 / 0.0	1.00	100 / 0	-	-	-	-	-	-
3 - DL	0.9 / 0.1	0.88	91 / 9	0.13	6	-1.00	0.36	0.69	1.13
5 - DL	0.7 / 0.3	1.07	83 / 17	0.13	6	0.56	0.59	0.84	1.37
7 - DL	0.5 / 0.5	1.37	66 / 34	0.13	6	2.49	0.05	1.07	1.74
11 - DL	0.25 / 0.75	1.23	74 / 26	0.13	6	1.62	0.16	0.96	1.57
13 - CNTL	0.0 / 1.0	1.00	0 / 100	-	-	-	-	-	-

Figure 3.1: Relative land output of simultaneous treatments.

(90% confidence intervals, DF= Douglas-fir, RA= red alder, TRMT= treatment, CNTL= monoculture control)

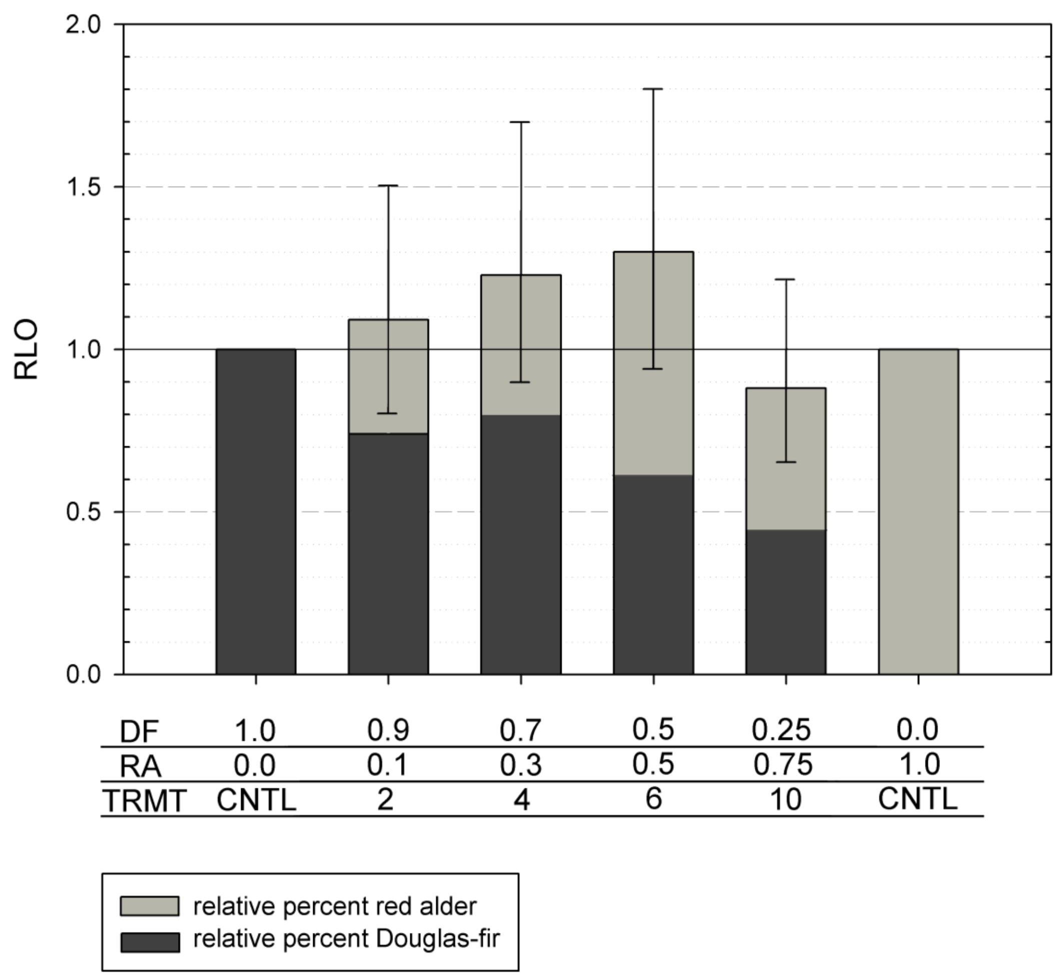


Figure 3.2: Relative land output of delayed treatments.

(90% confidence intervals, DF=Douglas-fir, RA=red alder, TRMT=treatment, CNTL=monoculture control)

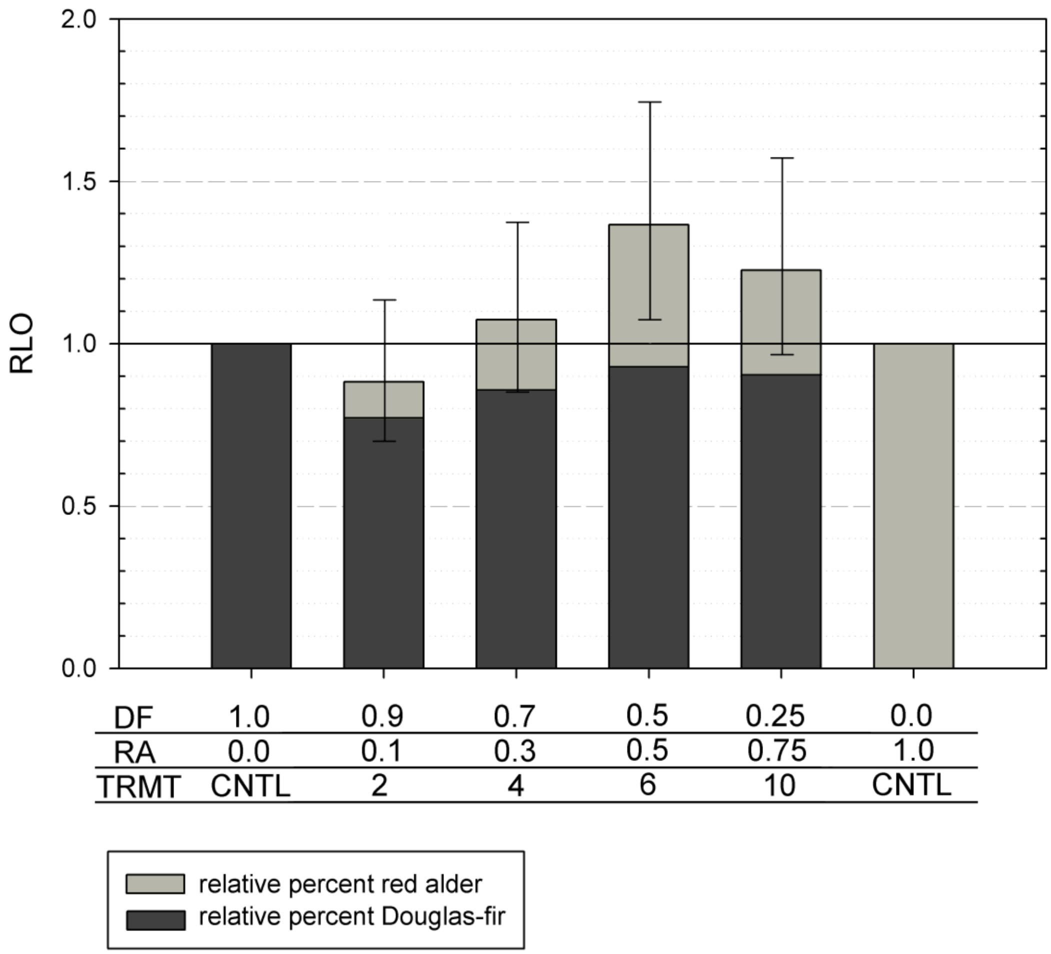
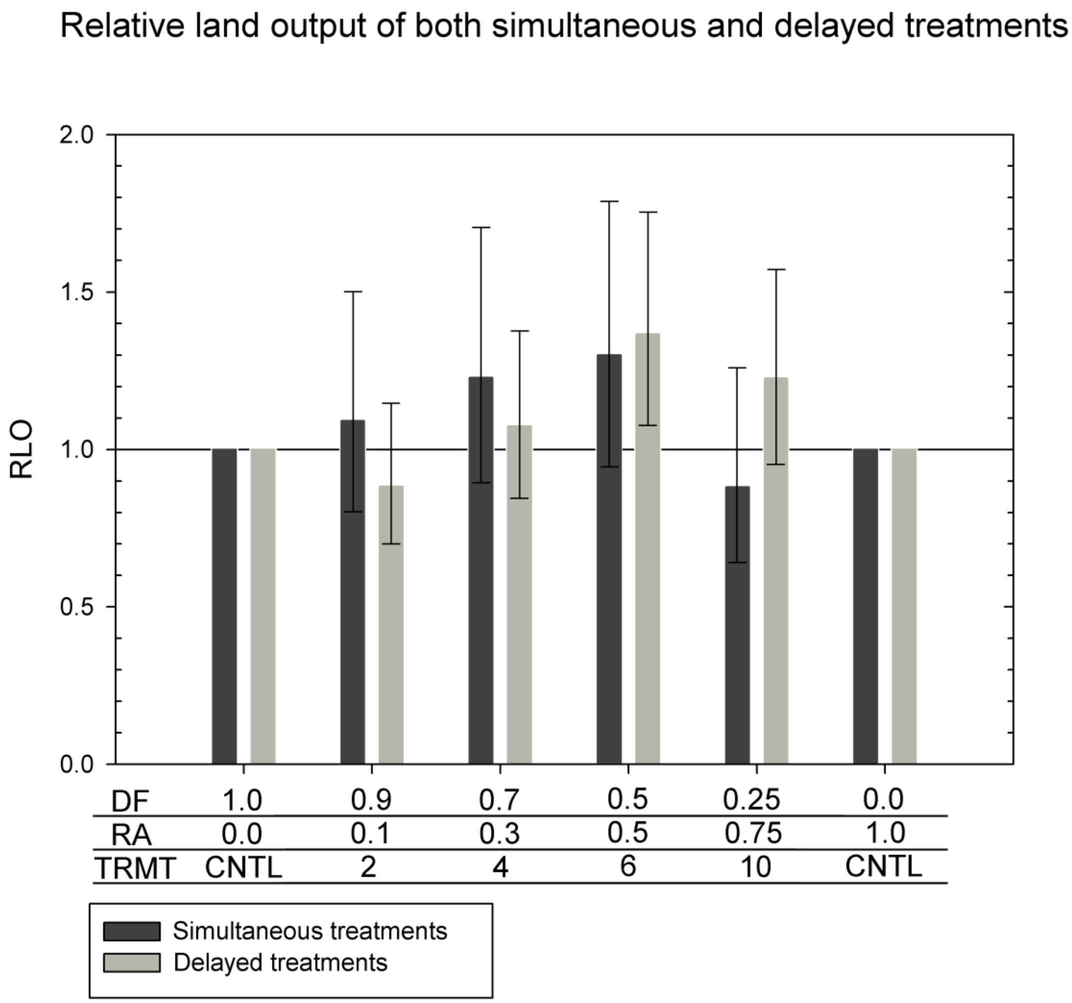


Figure 3.3: Relative land output of simultaneously planted treatments and delayed planted treatments. (DF= Douglas-fir, RA= red alder, TRMT= treatment, CNTL= monoculture control)



Mixture development at age 20

Research Question 2: Has 20 years of interference affected the current development of each species?

Twenty-years of growth have resulted in varied degrees of species development across the treatment mixtures. The influences of inter- and intra-specific interference occurring within the mixtures are distinguishable by examining the development of each species over the entire gradient of treatment mixtures. The results of per-tree basal area, survival, and mean height are discussed.

Table 3.2: Stand development values of treatment mixtures in 2007.

(DBH= diameter at breast height, CNTL=monoculture control, SL=simultaneous treatment, DL=delayed treatments)

Treatment	Per-tree DBH (cm^2)		Per-tree Height (m)		Per-tree Surviorship (#alive / #planted)	
	DF	RA	DF	RA	DF	RA
1 - CNTL	204.6		13.3		92.0%	
2 - SL	184.9	254.7	12.6	12.0	89.5%	83.3%
3 - DL	212.7	65.4	13.0	8.6	77.2%	61.1%
4 - SL	212.7	317.3	13.4	13.1	95.8%	66.7%
5 - DL	229.5	101.0	13.5	10.9	85.4%	55.6%
6 - SL	181.3	236.7	11.8	11.8	83.3%	82.1%
7 - DL	246.7	148.1	12.7	11.2	83.3%	56.4%
10 - SL	117.3	167.7	9.8	10.7	77.8%	56.1%
11 - DL	314.2	51.4	12.4	8.0	83.3%	35.1%
12 - CNTL		223.9		13.8		57.3%
13 - CNTL		79.0		8.7		30.7%

Simultaneous treatments

A regression analysis of median per-tree basal area of both Douglas-fir and red alder on the proportion of red alder in the treatment mixture demonstrates a important decrease in basal area of Douglas-fir as the density of red alder increases in the mixture ($p=0.109$, $r^2=0.630$) (Table Figure 3.4). The regression for the red alder indicates a less pronounced relationship between basal area and density of red alder in mixture ($p=0.263$, $r^2=0.385$). This demonstrates that red alder basal area does not statistically correlate with increases in its own density (Figure 3.4).

The regression analysis for mean height of Douglas-fir on increasing relative density of red alder in the mixture demonstrates a strong relationship in decreasing height as relative density of red alder increases ($p=0.054$, $r^2=0.759$). The mean height of red alder does not demonstrate a change as its own density increased in mixtures ($p=0.776$, $r^2=0.031$) (Figure 3.5).

A regression analysis of proportion of survived to planted trees for Douglas-fir indicated a negative slope as red alder density increased ($p=0.101$, $r^2=0.645$). The red alder proportion of survival indicated a significant decrease in survival as the proportion of red alder increased in the mixtures ($p=0.037$, $r^2=0.813$) (Figure 3.6).

Delayed treatments

A regression analysis of median per-tree basal area of Douglas-fir indicates significant increasing basal area as density of red alder increases in treatment mixtures ($p=0.020$, $r^2=0.833$). A regression analysis of red alder basal area development does not change as its own density increases ($p=0.825$, $r^2=0.019$) (Figure 3.7).

Mean height of both Douglas-fir and red alder indicate suggestive trends of decreases in height as red alder density increases. Regression analysis of both species indicates a negative slope, ($p=0.116$, $r^2=0.616$ and $p=0.119$, $r^2=0.585$) for Douglas-fir and red alder respectively (Figure 3.8).

The percent survival of Douglas-fir demonstrates no change in treatment mixtures as red alder density increases ($p=0.247$, $r^2=0.567$). A regression analysis of red alder percent survival demonstrates a significant negative relationship between the percent survival and an increase in its own density ($p=0.037$, $r^2=0.813$) (Figure 3.9).

Figure 3.4: Median per-tree basal area development at age 20 of Douglas-fir and red alder in simultaneous treatments across increasing densities of red alder (90% confidence intervals).

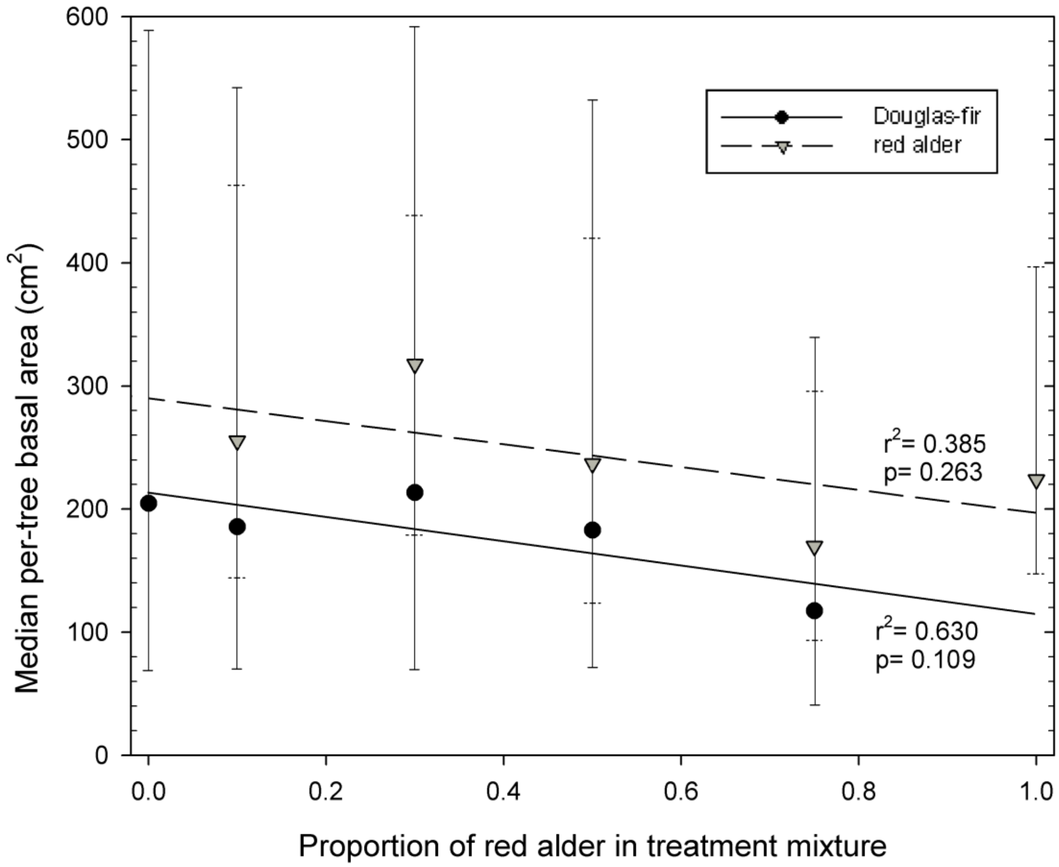


Figure 3.5: Mean height development at age 20 of Douglas-fir and red alder in simultaneous treatments across increasing densities of red alder (90% confidence intervals).

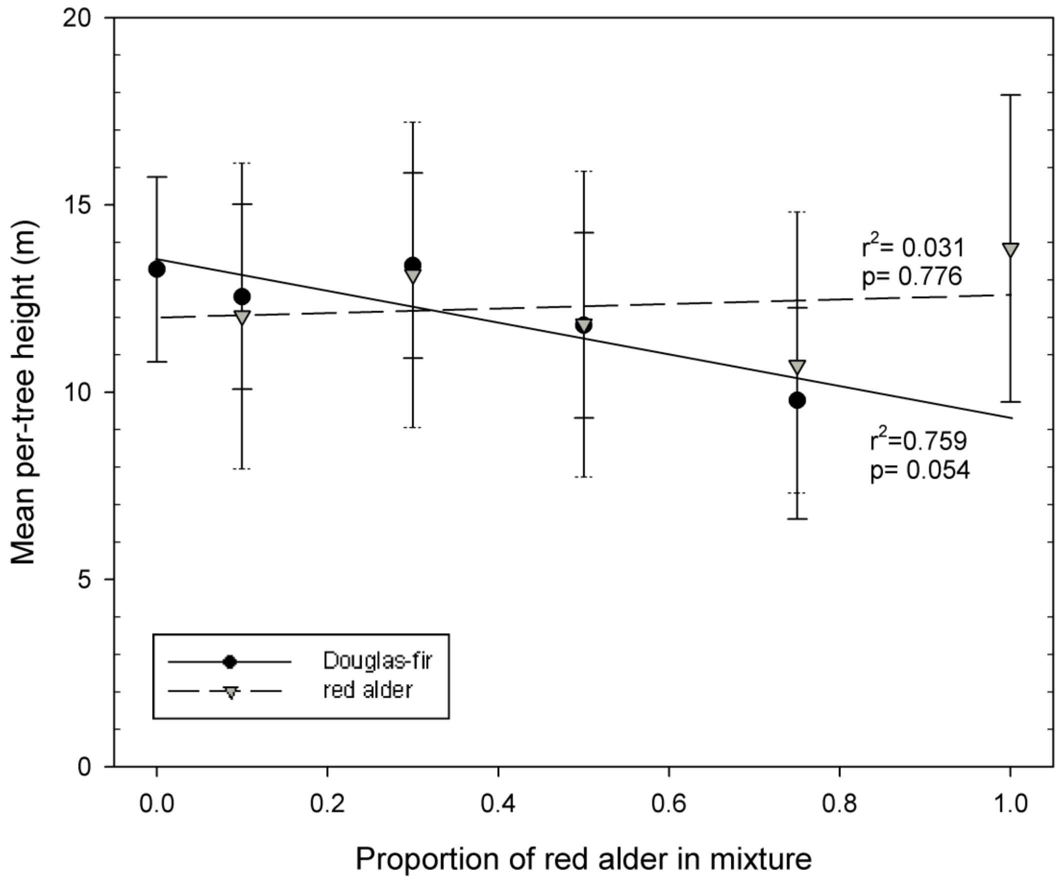


Figure 3.6: Proportion of surviving trees since planting at age 20 of Douglas-fir and red alder in simultaneous treatments across increasing densities of red alder (90% confidence intervals).

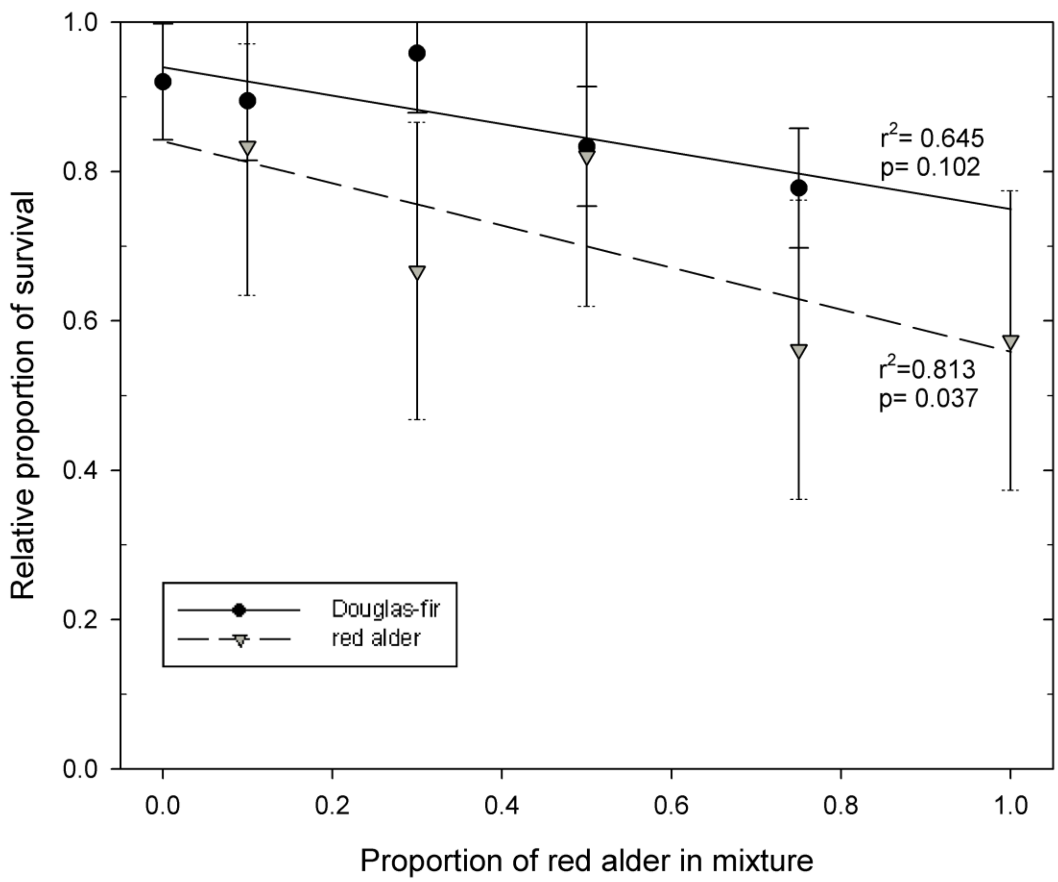


Figure 3.7: Median per-tree basal area development at age 20 of Douglas-fir and 15 of red alder in delayed treatments across increasing densities of red alder (90% confidence intervals).

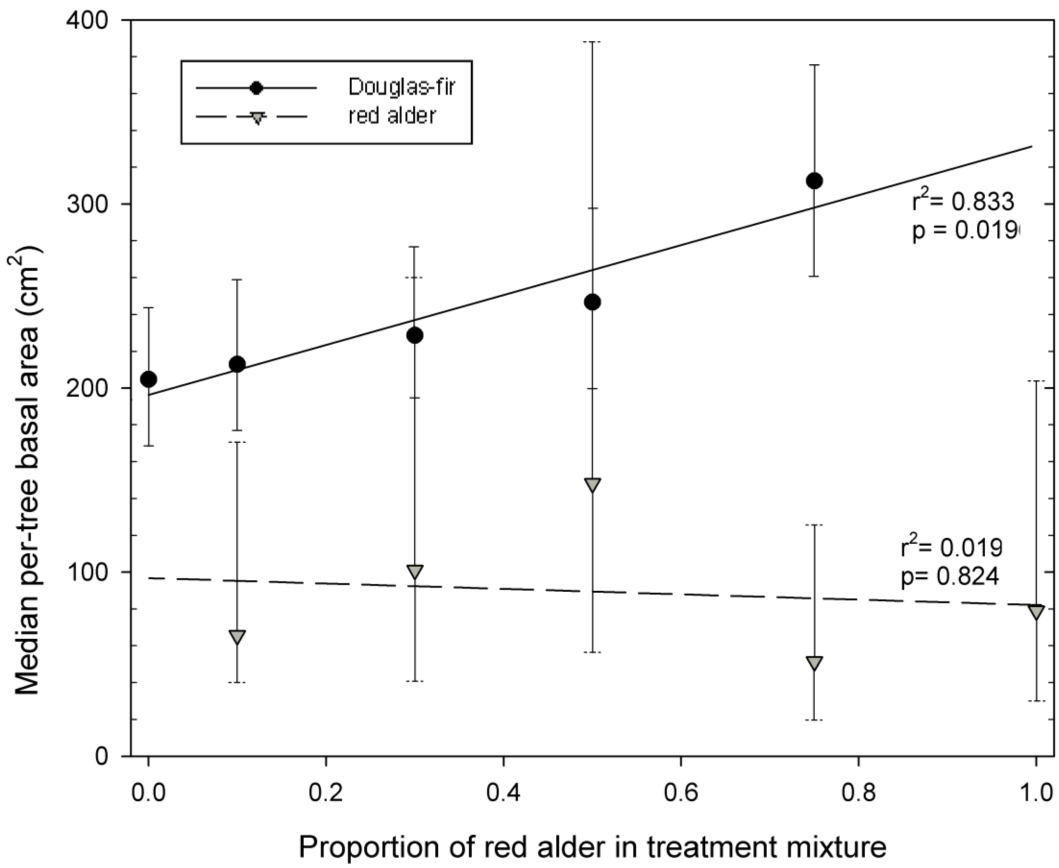


Figure 3.8: Mean height development at age 20 of Douglas-fir and 15 of red alder in delayed treatments across increasing densities of red alder (90% confidence intervals).

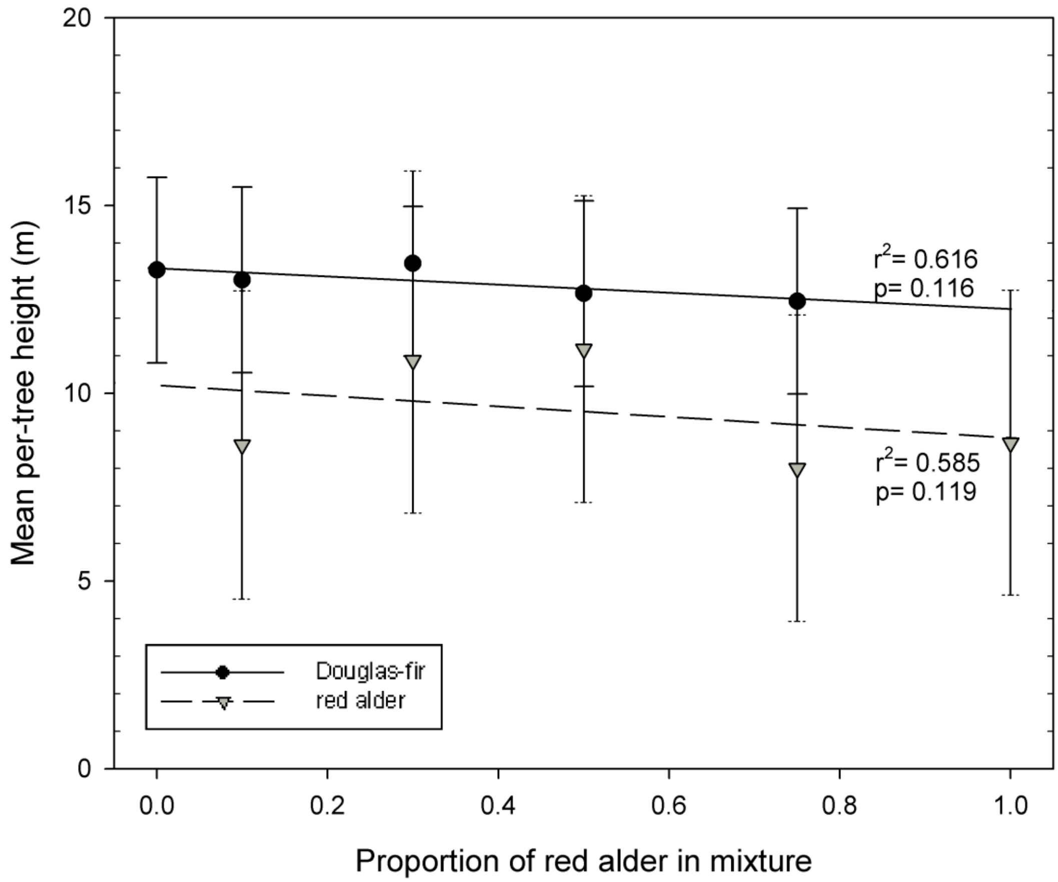
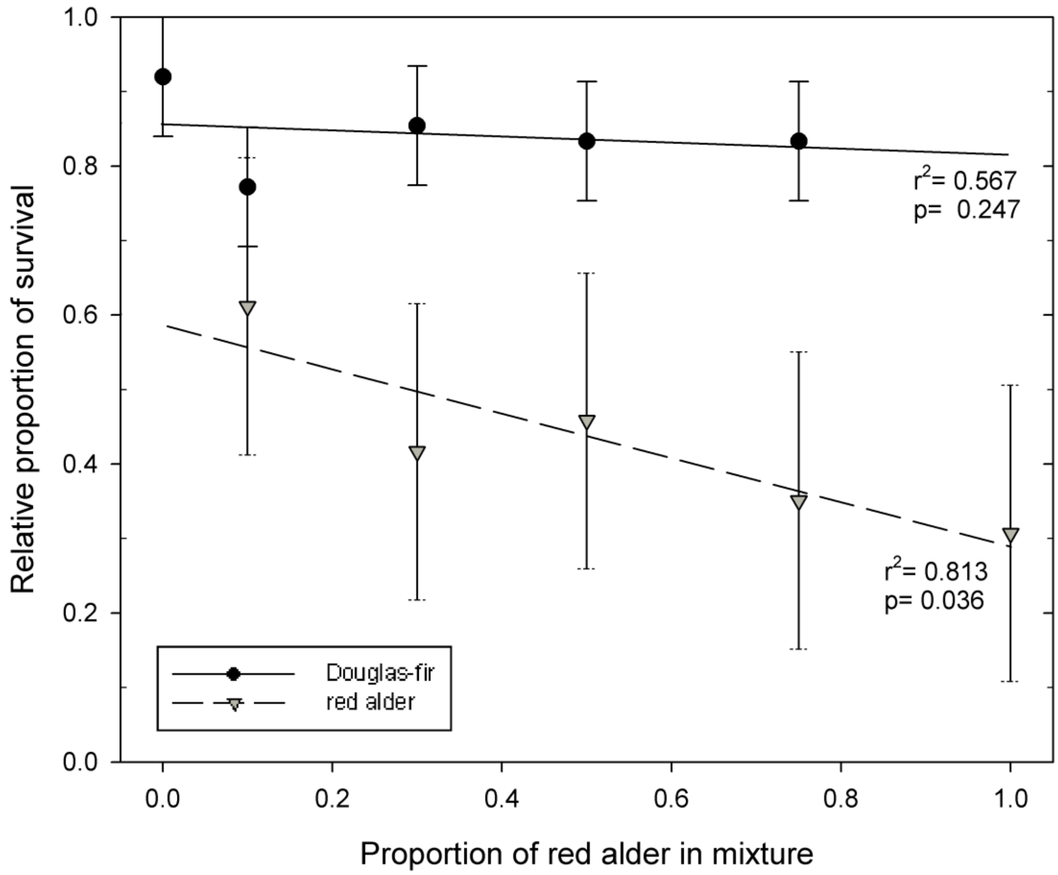


Figure 3.9: Proportion of surviving trees since planting at age 20 of Douglas-fir and 15 of red alder in delayed treatments across increasing densities of red alder (90% confidence intervals).



Mean per-tree basal area development over 20-years

Research Question 3: When does interference begin to affect individual tree growth over time in treatment mixtures?

The development of Douglas-fir and red alder was examined in two ways: (1) the median per-tree basal area development of each individual treatment by species and (2) each species within all treatments across all measurement years. Examining these results in this manner discerns and when interference began to influence the development of each treatment mixture.

Simultaneous treatments

The main effect of treatment and the treatment-year interaction analysis over the entire 20 years of growth were not significant for per-tree basal area of Douglas-fir in the simultaneous planted mixtures ($F_{4, 10}$=0.08, p=0.986 and $F_{28, 70}$=1.00 p=0.477, respectively). This indicates that there were no significant differences in tree basal area among treatments over all years and for each treatment in each measurement year since 1988.

The red alder experienced similar results. An overall treatment effect and treatment-year interaction effect were not significant ($F_{4, 10}$=1.09, p=0.413 and $F_{28, 70}$=1.09, p =0.376 respectively) for per-tree basal area of red alder in the simultaneous planted treatment mixtures.

Douglas-fir

There are two biologically noteworthy events taking place throughout the development of Douglas-fir in these treatment mixtures (Figure 3.10). First, all treatments developed similarly during their early years of establishment until age 9. At which point, mean per-tree basal area development of Douglas-fir begins to diverge indicating that different levels and/or types of interference begin to alter mixture development (Figure 3.10).

Red alder

The development of red alder has a wider distribution of variation than the Douglas-fir over time. From ages 1 to 6 all treatment mixtures developed on the same trajectory, with little variation between them. After 8 years of growth, the per-tree basal area begins to vary among treatment mixture. Between age 8 and 11, the variation becomes increasingly apparent, demonstrating the increases in interference (Figure 3.11).

Delayed treatments

The treatment main effect and the treatment-year interaction of median per-tree basal area of Douglas in the delayed were not significant ($F_{4,10}$=0.22, p=0.921 and $F_{28, 70}$=0.61, p=0.928 respectively).

Furthermore, the median per-tree basal area of red alder in the delayed planting treatments was also not significant among treatments alone ($F_{4,10}$=0.82, p=0.539) and treatment*years ($F_{8, 20}$=0.59, p=0.772).

Douglas-fir

The little variation in development of Douglas-fir in the first 9 years mirrors that of the simultaneous treatments. Variation in the delayed treatments does not take place until age 9, at which point the variation among treatment grows until final measurement at age 20. The presence of red alder, planted when the Douglas-fir was age 6, does not show up at that age. The variation among treatments remains relatively small until after age 12, indicating that interference was potentially small among treatments until after that age (Figure 3.12).

Red alder

Per-tree basal area development demonstrates a small increase between tree ages 3 and 6. From age 6 to age 15 there is a large amount of variation in basal area development among treatments, indicating that interference began to influence growth and structure among the treatments after age 6 (Figure 3.13).

Figure 3.10: Median per-tree basal area development of all simultaneous planted Douglas-fir treatments and monoculture control over 20 years. (DF=Douglas-fir, RA=red alder)

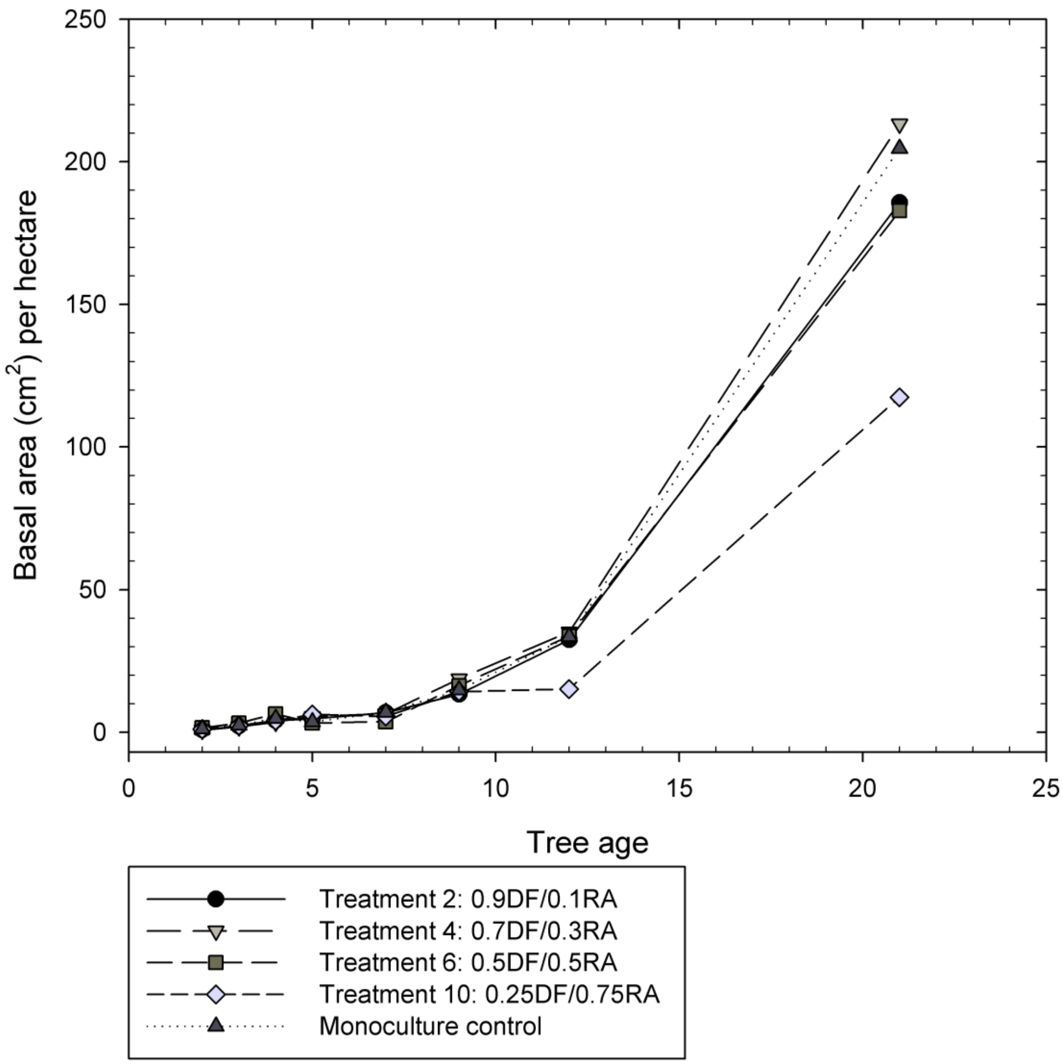


Figure 3.11. Median per-tree basal area development of all simultaneous planted red alder treatments and monoculture control over 20 years. (DF=Douglas-fir, RA=red alder)

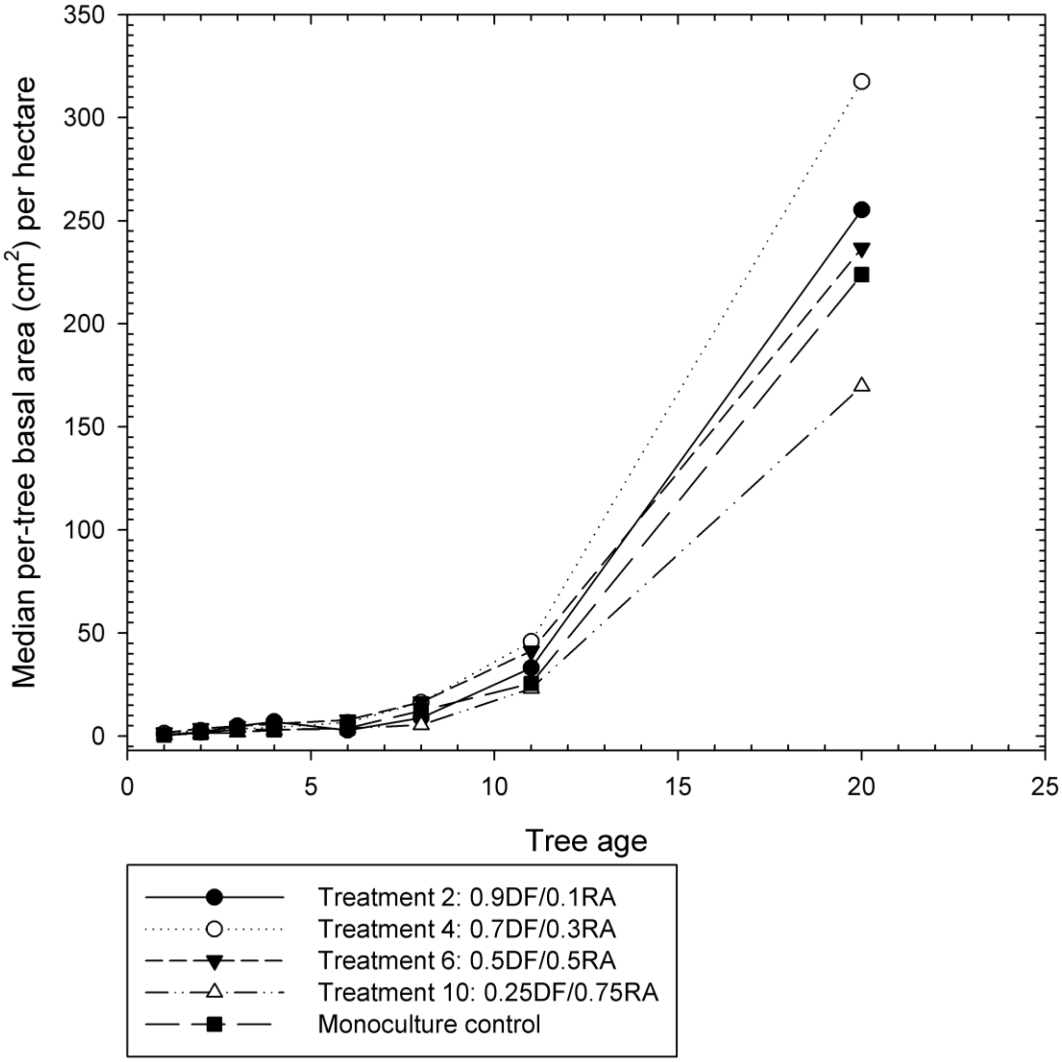


Figure 3.12: Median per-tree basal area development of all delayed planted Douglas-fir treatments and monoculture control over 20 years. (DF=Douglas-fir, RA=red alder)

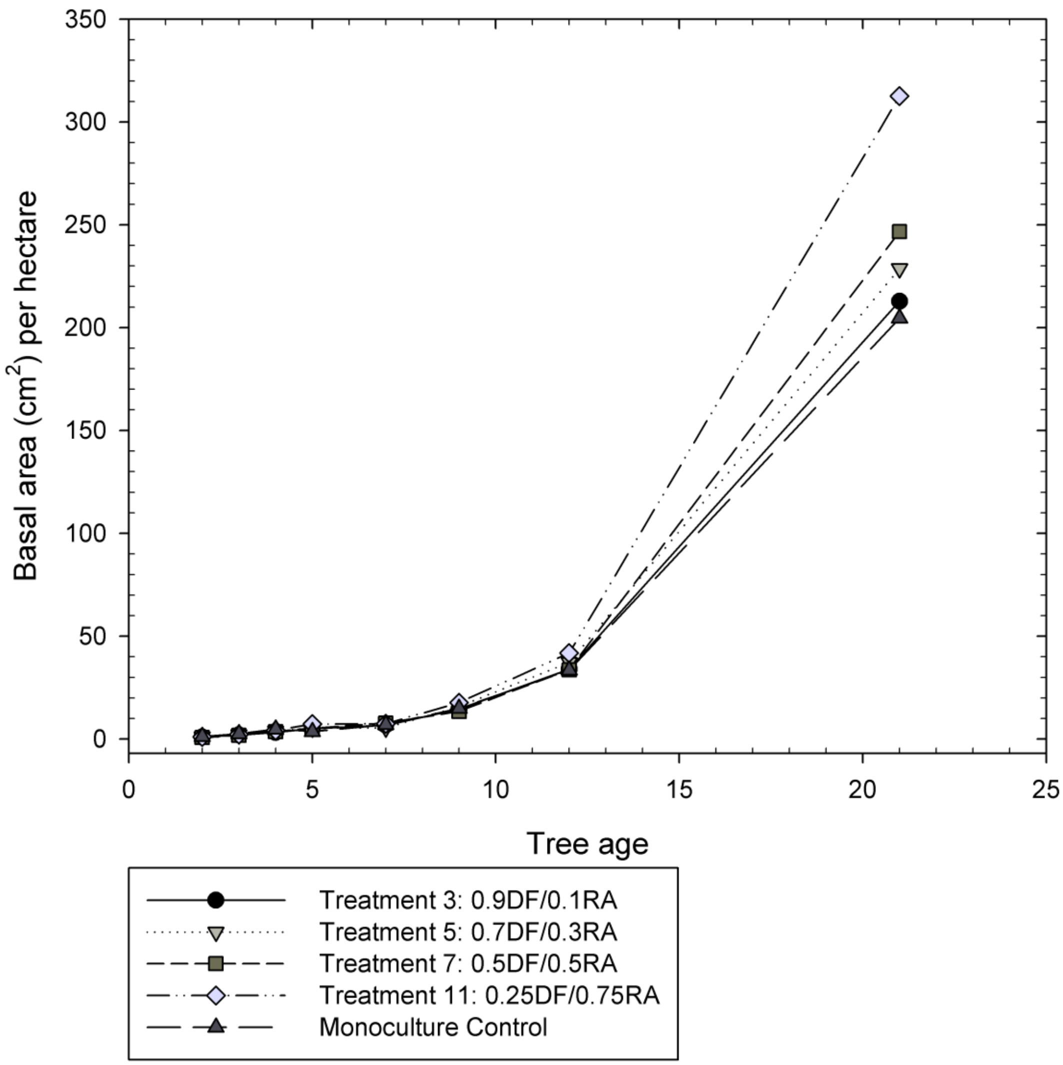
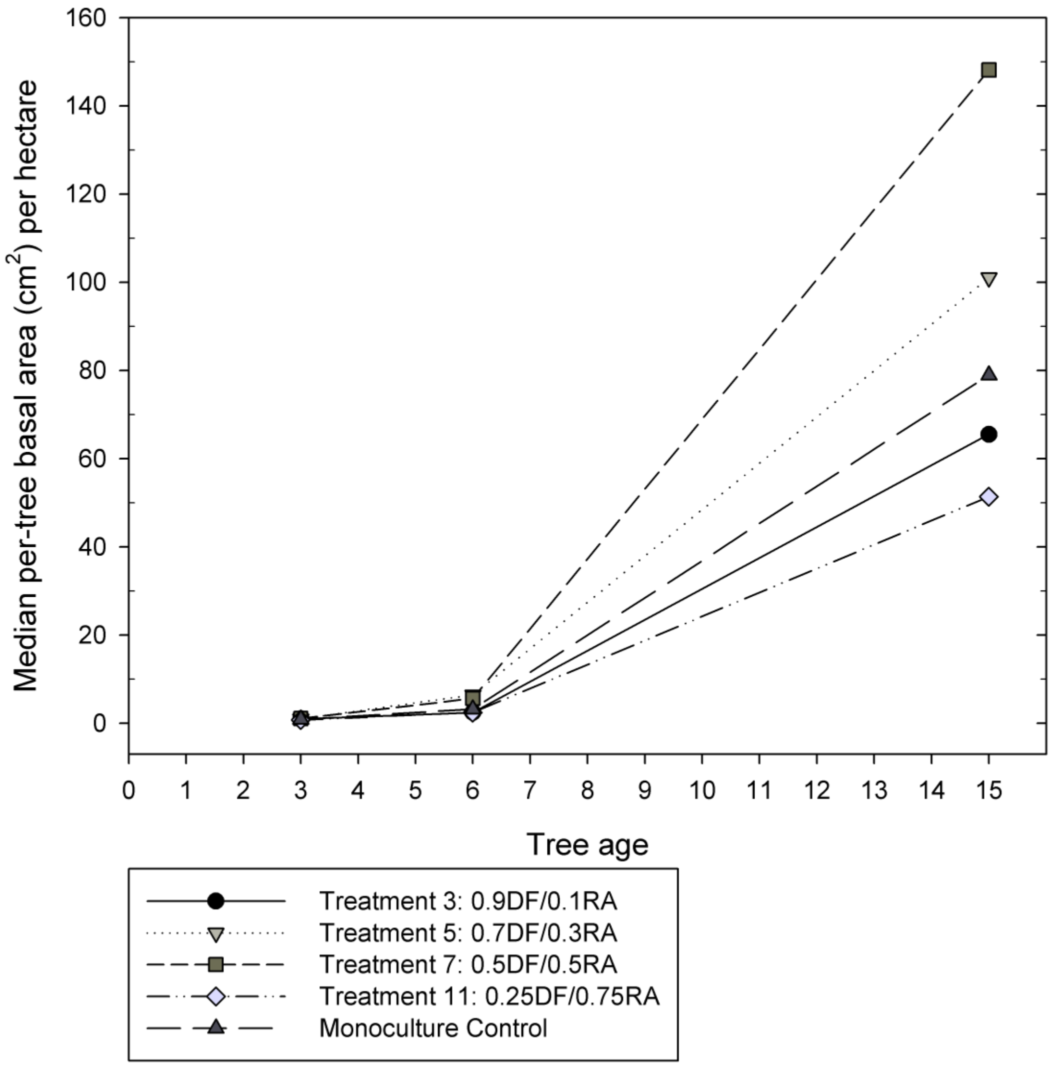


Figure 3.13: Median per-tree basal area development of all delayed planted red alder treatments and monoculture control over 15 years. (DF=Douglas-fir, RA=red alder)



CHAPTER THREE

DISCUSSION

The results of this experiment demonstrate the net effects of intra- and inter-specific competition, the influences of resource limitations, and the efficiency of resource capture/utilization. The important trends presented in the results fulfill the objective of this thesis *to determine how relative proportions of two tree species, one capable of facilitation and competition and another only competition, affect individual tree and stand development*. The ability of the different mixtures to capture and efficiently utilize resources results in interactions of inter- and intra-specific interference among treatments. The overall autoecological characteristics of the two species are consistent with the findings of other studies examining the mixed Douglas-fir/ red alder stands (Miller and Murray 1978; Cole and Newton 1986, 1987; Shainsky and Radosevich 1991, 1992, Radosevich et al. 2006). The measurements and analysis of this experiment describe the net effect of all the positive and negative interactions between Douglas-fir and red alder mixtures taking place over the past 20 years of development. In general, it is not possible to separate the effect of these positive or negative interactions. It is possible, however, to examine the net effect of interference and to discern what form of interference dominated development of two species in mixtures.

Interference

Interspecific competition

Interspecific competition is the prevailing form of interference for the Douglas-fir in the simultaneously planted treatments. Overall, the experiment demonstrates that after 20-years, Douglas-fir is negatively impacted by increasing the relative density of red alder in treatment mixtures. This is evident from the decrease in per-tree basal area, and significant decreases in mean height, and survival (Figures 3.4, 3.5, and 3.6). Similar relationships have been demonstrated in seedlings of the two species as well (Shainsky and Radosevich 1992). The negative curve demonstrates strong interspecific competition of red alder has Douglas-fir development in mixtures. Generally, Douglas-fir performance is affected by interspecific competition more than intraspecific competition as proportions and densities of Douglas-fir and red alder increase in mixtures (Shainsky and Radosevich 1992).

Examining the development during ages 1 through 8 of the simultaneously planted Douglas-fir (Figures 3.10) demonstrates little variation among treatment basal area, indicating that interspecific interference was either not present or did not influence development. Previous research demonstrates that individual tree size relative to the average of all trees within a treatment is the dominant force behind interference, indicating that smaller individuals provide less interference to their neighbors (Harper 1977; D'Amato 2002). In this experiment, after accounting for the wide spacing employed during planting (3m x 3m) and the small size of the trees during the first 6-8 years of development, it is expected that any interference would be minimal. At age 9, however, the development of the simultaneous treatments (Figures 3.10, 3.11) suggests that interspecific interference becomes a greater force. Per-tree basal area development of the two species diverges and red alder development exceeds that of Douglas-fir (Figures 3.10 and 3.11). Research conducted by Fuentes-Rodriguez (1993) demonstrated that the intensity of interspecific competition increased with stand age, which is suggested in this experiment as well. Trends in Fuentes-Rodriguez's results, indicating height development of Douglas-fir fell further behind that of red alder as stand ages increase, coincide with my results. The compounding interspecific competition suppressed the per-tree size and stand development of the Douglas-fir as both stand age increased and the relative density of red alder increased (Cole and Newton 1986, 1987).

Intraspecific competition

Intraspecific interference is the net driver for the development of the Douglas-fir in the delayed treatments. The significant increase in per-tree basal area (Figure 3.7) and lack of change in survival (Figure 3.9) for the Douglas-fir as its relative density decreased in mixtures is evidence for the net effect of decreasing intraspecific competition. An increase in basal area of Douglas-fir as its density decreases has also been demonstrated by Shainsky and Radosevich (1991), where decreases in intraspecific competition due to reduced density of Douglas-fir resulted in a greater stem volume index of Douglas-fir.

Red alder development in both the simultaneous and delayed planted treatments was unaltered by the changes in Douglas-fir density. Basal area development was not significantly related to increases in red alder relative densities (Figure 3.4 and 3.7). However, the significant decrease in survivorship as red alder density increases suggests that at some point intraspecific competition influenced the development of the treatment mixtures (Figure 3.6 and 3.9). Shainsky and Radosevich (1992) suggest that red alder seedling performance is most affected by intra- and not inter-specific competition. Newton and Cole (1994) also state that during early red alder development (5-15 years), individuals with lower competitive ability are highly subjected to mortality and suppressed growth.

I hypothesize that the insignificant decreases in red alder per-tree basal area in 2007 (Figures 3.4 and 3.7) are a consequence of the previous influence of intraspecific competition not captured in the 2007 data collection and analysis. This hypothesis is supported by the significant decreases in survival as relative density of red alder increases for both treatment types, which is a measure of all years since planting. The results from the development over time analysis indicate that red alder basal area variation among treatments began at an earlier age than Douglas-fir (Figures 3.10, 3.11, 3.12, and 3.13). The diverging slopes of per-tree basal area of red alder among treatments indicates when interference began influencing treatment development. Therefore, the net influence of past intraspecific competition of red alder, demonstrated by self-thinning mortality, has resulted in a more uniform per-tree basal area among treatments in 2007. This hypothesis is supported by previous research of Douglas-fir/red alder mixtures demonstrating that intraspecific competition causes mixtures to stabilize basal area among treatments as species the experience mortality from self-thinning (Puettmann et al. 1992).

Facilitation

Despite red alder's ability to fix nitrogen and enhance conifer growth (Tarrant 1961, Binkley 1983), the net effect of facilitation was not evident in this study. There are two reasons why net effects of facilitation may not be present. First, since facilitation is a highly energetic process (Tjepkema and Winship 1980), the increased competition for light due to the 5-year head start of Douglas-fir in the delayed planted treatments may have resulted in a reduction in the nitrogen fixing ability of the red alder. Second, the effect of facilitation from red alder in the simultaneously planted treatments may not be present because the influence of interspecific competition out-weights the affect of facilitation (Cole and Newton 1986, 1987). Previous research by D'Amato (2002) on tree to tree interaction of the same sample trees used in this experiment supports these conclusions. D'Amato observed that while facilitation between Douglas-fir and red alder may be occurring, competition is the dominant form of tree to tree interference. Without further soil and foliar analysis of the treatment mixtures, it is difficult to determine the degree of facilitation taking place among the treatment mixtures.

Resource limitation

The inter- and intra-specific interference occurring in this study does not influence per-tree development until an essential resource becomes limited. The success of a species when resources are limited depends on its ability to tolerate low levels of essential resources without perishing (Tillman 1988). The individuals in these treatment mixtures are in competition from their neighbors for light, water, and mineral nutrients; the limitations of these resources may vary throughout the day, season, or years. While this study documents the type of interference in mixtures, it is impossible to determine what resources are limited without further examination of the level of essential resources. However, previous research describes the potential mechanism for resource limitations of Douglas-fir/red alder mixture that may be applicable to this study.

Decreases in Douglas-fir development by interspecific competition in red alder mixtures is typically driven by light limitations (Chan 1990) and not water stress (Shainsky and Radosevich 1992). Light limitations are derived from red alder's superior ability to quickly grow taller than neighboring Douglas-fir and capture more space for light interception, i.e. red alder is capable of reaching half or more of its mature height by age 15 (Worthington et al. 1960; Newton et al. 1968) or 15m for red alder versus 4m for Douglas-fir (Deal, 2006). Previous research also demonstrates that imbalanced competition for light and other resources ensues when individuals are overtopped, thereby reducing their photosynthetic rate, above- and below-ground resource consumption and overall growth (Radosevich et al. 2007).

In this experiment it is presumed that once red alder reached dominant canopy position in the simultaneous mixtures, inter- and intra-specific competition increased, which was exhibited by the diverging developmental basal area slopes after stand age 9 (Figures 3.10, and 3.11). The Douglas-fir in the delayed treatments does not exhibit the same divergence of development until age 12 (Figure 3.12). Therefore, a reason for the increasing Douglas-fir basal area as red alder density increases in 2007 is because Douglas-fir growth was not influenced by red alder imposed light limitation since red alder was either absent (prior to planting) or smaller than the Douglas-fir.

Typically, red alder growth rates are more sensitive to soil moisture limitations, which significantly reduce its competitive ability relative to Douglas-fir (Shainsky 1988; Shainsky and Radosevich 1991, 1992; Giordano and Hibbs 1993; Fuchs and Livingston 1996). When moisture resources are limiting, red alder stomata close, limiting photosynthesis and growth (Hawkins and McDonald 1993). Conversely, Douglas-fir is capable of maintaining open stomatas in more limiting moisture conditions, thereby continuing photosynthesis after red alder photosynthesis has decreased (Shainsky and Radosevich 1992).

Numerous studies, (Newton et al. 1968; Miller and Murray 1978; Fuentes-Rodriguez 1993; Cole and Newton 1986, 1987; Shainsky and Radosevich 1991, 1992, Radosevich et al. 2006;) including this experiment, document that red alder is the superior competitor when grown in mixture with Douglas-fir. Its superior ability to capture and occupy growing space leads to increased inter- and intra-specific stress among neighbors. Eventually, the stress on individuals to capture resources essential for survival leads to increased mortality and decreased stand production. Puettmann et al. (1992b) found that over a 4- to 5-year period in a mixed stand, Douglas-fir had a 2% to 3% increase in average mortality than red alder due to competitive stress for resources. Previous research (Cole and Newton 1986) demonstrated that stress increases in stands as total tree density increases; this is well demonstrated in the current experiment by the decreasing basal area and survivorship of both species in the simultaneous and delayed treatments (Figure 3.4, 3.6, 3.7, and 3.9). In addition, Newton and Cole (1986) also demonstrated that in mixed stands stress increased with the presence of red alder, further supporting the findings in the simultaneous treatments where Douglas-fir basal area decreased as red alder density increased (Figure 3.4).

Resource efficiency

Given that both the simultaneously planted treatments and the delayed planted treatments demonstrate dominance by inter- and intra-specific competition, facilitation could not be a driver of overyielding of RLO in treatment mixtures. According to Jolliffe (personal communication 2008), the measure of relative land output is often uncorrelated with productivity, i.e. basal area growth, and does not demonstrate the most productive mixture, but rather the most efficient. Given this and significant reduction of basal area development of Douglas-fir in the simultaneous treatments as well as the increase in intraspecific competition for red alder in both treatment types (simultaneous and delayed), it is possible that treatments with the greatest RLO values are most efficient in resource use (Jolliffe, 1997). RLO also suggests that resource efficiency of the mixtures increases in both treatment types as the density of red alder increases from 0.1 to 0.5 and decreases once the density reaches 0.75 (Figure 3.1, 3.2, and 3.3). Further replication of these treatments would more clearly define these results.

It is plausible that the cause of enhanced resource capture/utilization efficiency of the treatments is because the species respond to enhanced microsite conditions for tree growth (Knowe et al. 1992). Or, that species mixtures are also capable of sustaining productivity and performance when environmental conditions destabilize (McNaughton 1993) because they qualitatively and quantitatively utilize resources differently than monocultures. More likely however, the species in certain treatments partake in resource partitioning (Vandermeer 1989), leading to increased efficiency. For example, mixed species systems are often capable of intercepting light qualitatively and quantitatively differently than monocultures (Vandermeer 1989), due to differences in autoecological characteristics and resource requirements. Thus, it is reasonable that different proportions of species mixtures would have unique rates of efficiency to capture and utilize light. The same idea is also possible for other essential resources. Therefore, it appears that the 0.5/0.5 mixtures of Douglas-fir and red alder of both the simultaneously and delayed plantings are the most efficient systems of their respective treatment definition. The delayed 0.5DF/0.5RA mixture is the most efficient of all treatment proportions and planting times examined.

In conclusion, this experiment demonstrates the important role that interference, resource limitation, and resource utilization have on individual and species development. The results of this experiment further support the general claim that among mixtures of planted species, the net effect of intraspecific competition is greater than interspecific competition (Radosevich et al. 2007). These results exhibit clear trends and relationships which define the type of effect that inter- and intra-specific competition and how resource limitation and efficiency in mixed stand influences development. It is also clear that interference is dynamic and changes with relative density of species in forest communities and that competition is an important determinant of structural development over time. Additionally, these results coincide with previous research that explore the positive and negative affects that autoecological development and interference have on one another. Therefore, the results reported in this research may improve the understanding of the interference process on the long-term development of Douglas-fir and red alder mixtures.

Study limitations

The lack of strong statistical significance of many of the results does not diminish the biological significance of the results; suggesting that increasing the density of either red alder or Douglas-fir in treatment mixtures impacts the relative land output of treatment mixtures, the per-tree basal area development, height growth, or survival of either species, and development over 20 years. Given the high degree of variability in forest research as well as the small number of repetitions of this experiment, it comes as little surprise that the statistical analysis of these data does not display highly significant statistical results that coincide with the observed trends (Johnson 1999). The natural variability of forest ecosystems, influence that microsite variation, limited repetitions, and 20 years of growth increased the variability of this experiment and diluted the statistical significance of the biologically important trends present.

References

Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Canadian Journal of Forest Research 33, 2274-2279.

Chan, S.S., 1990. Effects of light and soil moisture availability on Douglas-fir and red alder sapling development, carbon allocation, and physiology. In, College of Forestry. Oregon State University, Corvallis.

Cole, E.C., Newton, M., 1986. Fifth year responses of Douglas-fir to crowding and non-coniferous competition. Canadian Journal of Forest Research 16, 727-737.

Cole, E.C., Newton, M., 1987. Nutrient moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. Canadian Journal of Forest Research 17, 181-186.

Deal, R.L. 2006. Red Alder Stand Development and Dynamics. In: R.L. Deal, C.A. Harrington (Eds.), Red alder: a state of knowledge. USDA Forest Service: General Technical Report PNW-GTR-669. Pp. 150.

D'Amato, A.W., 2002. Interference dynamics in mixed red alder/Douglas-fir forests. Master of Science Thesis. In, College of Forestry. Oregon State University, Corvallis.

Fuchs, E.E., Livingston, N.J., 1993. Hydraulic control of stomatal conductance in Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] and alder [Alnus rubra (Bong)] seedlings. Plant, Cell and Environment 19, 1091-1098.

Fuentes-Rodriguez, L.A. 1993. Factors influencing growth of young Douglas-fir and red alder in the Oregon coast range: interference, nitrogen availability, and animal damage. Master of Science Thesis. College of Forestry. Oregon State University, Corvallis.

Hawkins, B.J., McDonald, S. 1993. The influences of temperature and soil water on growth, photosynthesis, and nitrogen fixation of red alder (*Alnus rubra*) seedlings. Canadian Journal of Forest Research. 24, 1029-1032.

Johnson, J.H., 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63(3), 763-770.

Jolliffe, P.A., 1997. Are mixed populations of plant species more productive than pure stands? Oikos 80, 595-601.

Jolliffe, P.A., 2008. Personal communication.

Knowe, S.A., 1991. Simultaneous prediction of the development of loblolly pine and woody competitors in young plantations. New Forestry 5, 26-33.

McNaughton, S.J., 1993. Biodiversity and function of grazing ecosystems. Oikos 80, 595-601. In: Jolliffe, P.A. 1997. Are mixed populations of plant species more productive than pure stands? Oikos 80(3): 595-601.

Miller, R.E., Murray, M.D., 1978. The effects of red alder on the growth of Douglas-fir. In: Briggs, D.G., DeBell, D.S., Atkinson, W.A. (Eds.), Utilization and Management of Alder. USDA Forest Service: General Technical Report PNW-70.

Newton, M., Cole, E.C., 1994. Stand development and successional implication: Pure and Mixed Stands. In: Hibbs, D.E., DeBell, D.S., Tarrant, R.F. (Eds.), The Biology and Management of Red Alder. Oregon State University Press, Corvallis.

Newton, M., El Hassan, B.A., Zavitkovski, J., 1968. Role of red alder in western Oregon forest succession. In: Trappe, J.M. (Ed.), Biology of alder. USDA Forest Service: General Technical Report PNW-70, Portland, Oregon.

Puettmann, K.J., Hibbs, D.E., Hann, D.W., 1992b. The dynamics of mixed stands of Alnus rubra and Pseudotsuga menziesii: extension of size-density analysis to species mixtures. Journal of Ecology 36, 769-782.

Radosevich, S.R., Hibbs, D.E., Ghersa, C.M., 2006. Effects of species mixtures on growth and stand development of Douglas-fir and Red Alder. Canadian Journal of Forest Research 36, 769-782.

Radosevich, S.R., Holt, J.S., Ghersa, C.M., 2007. Ecology of Weeds and Invasive Plants. Wiley-Interscience Publication. John Wiley & Sons, Hoboken, New York.

Shainsky, L.J., 1988. Competitive interactions between Douglas-fir and red alder: growth analysis, resource use and physiology. In, College of Forestry. Oregon State University, Corvallis.

Shainsky, L.J., Radosevich, S.R., 1991. Analysis of yield-density relationships in experimental stands of Douglas-fir and red alder seedlings. Forest Science 37, 574-592.

Shainsky, L.J., Radosevich, S.R., 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology 73 30-45.

Tarrant, R.F., 1961. Stand development and soil fertility in a Douglas-fir/red alder plantation. Forest Science 7, 238-246.

Tillman, G. D., 1988. Plant strategies and the dynamics and structure o plant communities. Princeton Monographs, Princeton, New Jersey

Tjepkema, J.D., Winship, L.J., 1980. Energy requirement for nitrogen fixation in actinorhizal and legume root nodules. Science 209, 279-281.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge university press. Cambridge, New York.

Wagner, R.G., Radosevich, S.R., 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecological Applications 8, 779-794.

Worthington, N.P., Johnson, F.A., Staebler, G.R., Lloyd, W.J., 1960. Normal yield tables for red alder. USDA Forest Service: Research Paper PNW-36.

CHAPTER FIVE

CONCLUSIONS

The results of this study demonstrate the important impact that interference has on the development of forest ecosystems. This study and other studies of interference also demonstrate the strong competitive influence that red alder has among other species and itself. Its dominant height growth at age 20 clearly influenced the development of Douglas-fir and other red alder individuals in the mixtures. Similar results also have observed which indicates the importance of individual size relative to the population in determining growth and development of an individual within a mixture (D’Amato 2002; Radosevich et al 2007).

This study also demonstrates the difficulty of studying intercropping. The results indicate that per-tree productivity decreased as inter- and intra-specific competition increased, but efficiency at the stand level increased and peaked once the mixtures reached 0.5/0.5 proportions. This observation is indicative of the difficulty in drawing conclusions between productively at the tree level and efficiency at the stand level. Relative land output is a resourceful tool for examining which species mixtures are most efficient at interspecific resource use, but less powerful in examining the species-to-species interactions. While, examining interference at the per-tree scale demonstrates the interference among neighbors, it displays little information about their efficiency.

Facilitation did not appear to be a net interference effect in this study. However, that does not imply that facilitation by red alder is not occurring to some degree within these mixtures. Further analysis of foliar and soil nitrogen would potentially be beneficial in discovering if facilitation is apart of the gross interference effect occurring within these stands. Examining if or to what degree facilitation is taking place may better explain the increased efficiency of the 0.5/0.5 species mixtures indicated in the RLO analysis.

Silviculture implications

It is clear from this study that understanding the autoecological characteristics of tree species and the interference among the species is necessary. This observation has several implications for mixed species silviculture and the goals of sustainable forestry.

Red alder is clearly the superior early competitor and its ability to suppress conifer growth must be recognized. If conifer productivity is the primary landowner goal, but overstory diversity is also important then delaying red alder planting may be an appropriate option. This will provide increased horizontal and vertical structural diversity as well as increased species diversity for wildlife. Overall, interspecific competition by the Douglas-fir will be limited.

If the goal is total species diversity are the driver in management decisions, the 0.5/0.5 species mixture may be a management option. However, the results of this experiment may not necessarily coincide with what could result in a different geographic location. A replication of this study at Cascade Head, on the Oregon Coast developed dramatically different results (Radosevich et al. 2006). Given the results of this experiment, however, a 0.5/0.5 species mixture may produce a highly efficient system with enhanced structural and species heterogeneity in the central Cascade Range.

Finally, if commercial Douglas-fir and red alder are the desired objective planting alternating rows of Douglas-fir and red alder may be a viable option, as suggested by Hibbs and DeBell (1994). This option reduces the interference effects of red alder on Douglas-fir within the mixture and leaves potential for facilitation by red alder. In addition to the Hibbs and DeBell suggestion, delaying the planting of red alder until conifer establishment is sufficient will further reduce the interference effect of red alder on Douglas-fir. Given red alder's superior height growth under good growing conditions little red alder development may potentially be lost overall. This option also increases the ease of harvesting of one species while minimizing the damage to another during thinning.

Regardless of the silviculture planting prescription chosen, planting mixtures of Douglas-fir and red alder increase the ecological complexity of the forest community as well as the economic options for the land owner. The results of this study demonstrate that interference can influence the yield and efficiency of planted systems. Mixed species systems generally improve the biodiversity of those systems as well (Liebman and Staver 2001; Radosevich et al. 2006). In addition, with the current capricious log market, having a species mixture of two valuable species increases the options for the land manager to select the more valuable species for harvest. In the Pacific Northwest red alder log prices have increased steadily since the early 1980's, while the softwood prices for Douglas-fir have experienced great volatility. Moreover, red alder reaches senescent age before Douglas-fir and typically is harvested age by 30 years, while Douglas-fir rotations are upward from 50 to 300 years. Harvesting mixed stands of red alder on a shorter rotation than Douglas-fir increases profitability, while concurrently opening more growing space for the remaining Douglas-fir cohort, which further supports ecological health by not completely denudating the forest canopy between harvests.

References

D'Amato, A.W., 2002. Interference dynamics in mixed red alder/Douglas-fir forests. Master of Science Thesis. In, College of Forestry. Oregon State University, Corvallis.

Liebman, M., Staver, C.P., 2001. Crop diversification for weed management. In: Liebman, M., Mohler, C.M., Staver, C.P. (Eds.), Ecological Management of Agricultural Weeds. Cambridge University Press, New York.

Radosevich, S.R., Hibbs, D.E., Ghersa, C.M., 2006. Effects of species mixtures on growth and stand development of Douglas-fir and Red Alder. Canadian Journal of Forest Research 36, 769-782.

Radosevich, S.R., Holt, J.S., Ghersa, C.M., 2007. Ecology of Weeds and Invasive Plants. Wiley-Interscience Publication. John Wiley & Sons, Hoboken, New York.

BIBLIOGRAPHY

Binkley, D., 1982. Nitrogen fixation and net primary production in a young Sitka alder stand. Canadian Journal of Botany 60, 281-284.

Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Canadian Journal of Forest Research 33, 2274-2279.

Bormann, B.T., DeBell, D.S., 1981. Nitrogen content and other soil properties related to age or red alder stands. Soil Science Society of America Journal 45(2), 428-432.

Burkholder, P.R., 1952. Cooperation and conflict among primitive organisms. American Scientist 40, 601-631.

Chan, S.S., 1990. Effects of light and soil moisture availability on Douglas-fir and red alder sapling development, carbon allocation, and physiology. In, College of Forestry. Oregon State University, Corvallis.

Clements, F.E., Weaver, J.E., Hanson, H.C., 1929. Plant competition. Carnegie institute of Washington, Washington, D.C. *In.* Jolliffe, P.A., Nimjas, A.N., and Reuneckles, V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology. 21: 227-243.

Cole, D.W., Gessel, S.P. and Turner, J. 1978. Utilization and management of alder: comparative mineral cycling in red alder and Douglas-fir. USDA Forest Service General Technical Report PNW-70.

Cole, E.C., Newton, M., 1986. Fifth year responses of Douglas-fir to crowding and non-coniferous competition. Canadian Journal of Forest Research 16, 727-737.

Cole, E.C., Newton, M., 1987. Nutrient moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. Canadian Journal of Forest Research 17, 181-186.

Deal, R.L. 2006. Red Alder Stand Development and Dynamics. In: R.L. Deal, C.A. Harrington (Eds.), Red alder: a state of knowledge. USDA Forest Service: General Technical Report PNW-GTR-669. Pp. 150.

D'Amato, A.W., 2002. Interference dynamics in mixed red alder/Douglas-fir forests. Master of Science Thesis. In, College of Forestry. Oregon State University, Corvallis.

Franklin, J.F., Dryness, C.T., 1971. A checklist of vascular plants on the H.J. Andrews experimental forest. USDA Forest Service PNW-RN-138.

Fuchs, E.E., Livingston, N.J., 1993. Hydraulic control of stomatal conductance in Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] and alder [Alnus rubra (Bong)] seedlings. Plant, Cell and Environment 19, 1091-1098.

Fuentes-Rodriguez, L.A. 1993. Factors influencing growth of young Douglas-fir and red alder in the Oregon coast range: interference, nitrogen availability, and animal damage. Master of Science Thesis. College of Forestry. Oregon State University, Corvallis.

Giordano, P.A., Hibbs, D.E., 1993. Morphological response to competition in red alder: the role of water. Functional Ecology 7, 462-467.

Goldberg, D.E., 1990. Components of resource competition in plant communities. In: J.B.Grace, Tillman, D. (Eds.), Prospectives in plant competition Academic Press, New York, pp. 27-40.

Gordon, J.C., Wheeler, C.T., 1983. Biological nitrogen fixation in forest ecosystems: foundations and applications. Dr. W. Junk Publishers, Boston.

Grotta, A.T., Gartner, B.L., Radosevich, S.R., 2004. Influence of species proportion and timing of establishment on stem quality in mixed red alder- Douglas-fir plantations. Canadian Journal of Forest Research 34, 863-870.

Harper, J.L., 1961. Approaches to the study of plant competition. In, Symposia of the Society for Experimental Biology, pp. 1-39. *In* Jolliffe, P.A., Nimjas, A.N., and Reuneckles, V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology. 21: 227-243.

Harrington, C.A., 1990. Alnus rubra Bong.: red alder. Silvics of North America 2, 116-123.

Hawkins, B.J., McDonald, S. 1993. The influences of temperature and soil water on growth, photosynthesis, and nitrogen fixation of red alder (*Alnus rubra*) seedlings. Canadian Journal of Forest Research. 24: 1029-1032.

Herman, R.K., Lavender, D.P., 1990. Pseudotsuga menziesii [Mirb.] Ranco: Douglas-fir. Silvics of North America 1, 527-540.

Hibbs, D.E., DeBell, D.S., 1994. Management of young red alder. The Biology and Management of Red Alder. In: Hibbs, D.E., DeBell, D.S., Tarrant, R.F. (Eds.), The Biology and Management of Red Alder. Oregon State University Press, Corvallis, pp. 202-214.

Hibbs, D.E., Emmingham, W.H., Bondi, M.C., 1989. Thinning red alder: effects of method and spacing. Forest Science 35, 16-29.

Johnson, J.H., 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63, 763-770.

Jolliffe, P.A., 1997. Are mixed populations of plant species more productive than pure stands? Oikos 80, 595-601.

Jolliffe, P.A., 2008. Personal communication.

Jolliffe, P.A., Nimjas, A.N., Reuneckles, V.C., 1984. A reinterpretation of yield relationships in replacement series experiments. Journal of Applied Ecology 21, 227-243.

Knowe, S.A., 1991. Simultaneous prediction of the development of loblolly pine and woody competitors in young plantations. New Forestry 5, 26-33.

Knowe, S.A., Hibbs, D.E., 1996. Stand structure and dynamics of young red alder as affected by plant density. Forest Ecology and Management 82, 69-85. *In* Knowe, S.A., Harrington, T.B., and Shula, R.G. 1992. Incorporating the effects of interspecific competition and vegetation management treatments in distribution models for Douglas-fir saplings. Canadian Journal of Forest Research. 22: 1255-1257.

Liebman, M., Staver, C.P., 2001. Crop diversification for weed management. In: Liebman, M., Mohler, C.M., Staver, C.P. (Eds.), Ecological Management of Agricultural Weeds. Cambridge University Press, New York.

McNaughton, S.J., 1993. Biodiversity and function of grazing ecosystems. Oikos 80, 595-601. In: Jolliffe, P.A. 1997. Are mixed populations of plant species more productive than pure stands? Oikos 80(3): 595-601.

Miller, R.E., Murray, M.D., 1978. The effects of red alder on the growth of Douglas-fir. In: Briggs, D.G., DeBell, D.S., Atkinson, W.A. (Eds.), Utilization and Management of Alder. USDA Forest Service: General Technical Report PNW-70.

Miller, R.E., Reukema, D.L., Max, T.A., 1993. Size of Douglas-fir trees in relation to distance from a mixed alder-Douglas-fir stand. Canadian Journal of Forest Research 23, 2413-2418.

Newton, M., Cole, E.C., 1994. Stand development and successional implication: Pure and Mixed Stands. In: Hibbs, D.E., DeBell, D.S., Tarrant, R.F. (Eds.), The Biology and Management of Red Alder. Oregon State University Press, Corvallis.

Newton, M., El Hassan, B.A., Zavitkovski, J., 1968. Role of red alder in western Oregon forest succession. In: Trappe, J.M. (Ed.), Biology of alder. USDA Forest Service: General Technical Report PNW-70, Portland, Oregon.

Puettmann, K.J., Hibbs, D.E., Hann, D.W., 1992b. The dynamics of mixed stands of Alnus rubra and Pseudotsuga menziesii: extension of size-density analysis to species mixtures. Journal of Ecology 36, 769-782.

Puettmann, K.J., Hibbs, D.E., Hann, D.W., 1992a. Extending the size-density analysis to mixed species populations and investigation of underlying dynamics using red alder and Douglas-fir stands. Journal of Ecology 80, 448-459.

Radosevich, S.R., Hibbs, D.E., Ghersa, C.M., 2006. Effects of species mixtures on growth and stand development of Douglas-fir and Red Alder. Canadian Journal of Forest Research 36, 769-782.

Radosevich, S.R., Holt, J.S., Ghersa, C.M., 2007. Ecology of Weeds and Invasive Plants. Wiley-Interscience Publication. John Wiley & Sons, Hoboken, New York.

Roth, A., Cormack, K.J., Sigrid, S.C., Makineci, E., Son, Y., 2002. Soil carbon and nitrogen changes under Douglas-fir with and without red alder. Soil Science Society of America Journal 66, 1955-1988.

Roth, A., Jörg, E., Hibbs, D.E., 2003. Do admixed broadleaves improve foliar nutrient status of conifer tree crops. Forest Ecology and Management 172, 328-329.

Shainsky, L.J., 1988. Competitive interactions between Douglas-fir and red alder: growth analysis, resource use and physiology. In, College of Forestry. Oregon State University, Corvallis.

Shainsky, L.J., Radosevich, S.R., 1991. Analysis of yield-density relationships in experimental stands of Douglas-fir and red alder seedlings. Forest Science 37, 574-592.

Shainsky, L.J., Radosevich, S.R., 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology 73 30-45.

Shainsky, L.J., Rose, C.L., 1995. Effects of competition on the foliar chemistry of young Douglas-fir in monoculture and mixed stands with young red alder. Canadian Journal of Forest Research 25, 1969-1973.

Stubblefield, G., Oliver, C.D., 1978. Silvicultural implications of the reconstruction of mixed alder/conifer stands. In: Briggs, D.G., DeBell, D.S., Atkinson, W.A. (Eds.), Utilization and Management of alder. USDA Forest Service, pp. 307-320.

Tappeiner, J.C., Maguire, D.A., Harrington, T.B., 2007. Silviculture and ecology of western U.S. Forests. Oregon State University Press, Corvallis, Oregon.

Tarrant, R.F., 1961. Stand development and soil fertility in a Douglas-fir/red alder plantation. Forest Science 7, 238-246.

Tillman, G. D., 1988. Plant strategies and the dynamics and structure o plant communities. Princeton Monographs, Princeton, New Jersey

Tjepkema, J.D., Winship, L.J., 1980. Energy requirement for nitrogen fixation in actinorhizal and legume root nodules. Science 209, 279-281.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge university press. Cambridge, New York.

Wagner, R.G., Radosevich, S.R., 1991. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. Canadian Journal of Forest Research 21, 821-828.

Wagner, R.G., Radosevich, S.R., 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecological Applications 8, 779-794.

Weiner, J., Thomas, S.C., 1986. Size variability and competition in plant monocultures. Oikos 47, 211-222.

Weldon, C.W., Slauson, W.L., 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61, 23-44.

Worthington, N.P., Johnson, F.A., Staebler, G.R., Lloyd, W.J., 1960. Normal yield tables for red alder. USDA Forest Service: Research Paper PNW-36.