Nutrient and Establishment Density Effects on Structural Development and Growth Processes in Juvenile Western Redcedar and Western Hemlock Stands on Northern Vancouver Island

By

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Abstract

Conifer plantations established on sites formerly occupied by old-growth cedar-hemlock (CH) forests have exhibited poor growth compared to plantations established on sites previously occupied by early-seral hemlock amabilis fir (HA) stand on northern Vancouver Island. Poor growth on CH sites has been associated with low nutrient supply capacity, compared to HA sites, and competition from the ericaceous shrub salal. Fertilization with N and P has been shown to improve conifer growth and increasing plantation establishment density has been suggested as a method to competitively exclude salal from CH sites. A trial was established in 1988 to examine the effects of fertilization and establishment density on the growth of western redcedar and western hemlock plantations established on CH and HA sites. In this thesis, I examine the effects of these silvicultural treatments on the growth and structure of juvenile conifer stands 14 years after establishment and attempt to determine structural and functional mechanisms by which these treatments have affected community growth and site productivity. I also used the trial to examine current theories regarding the influence of soil resource availability on competition processes.

Fertilization improved the height and basal area growth of both species on both sites 10 years after its application. Fertilization increased total stand mass and the masses of wood, foliage, bark and branches. Hemlock responded more strongly to fertilization than cedar. Elevated foliar concentrations of P were associated with fertilization treatments on both CH and HA sites but N concentrations were only elevated on HA sites. Other nutrients, not applied in fertilizer, also had elevated foliar concentrations associated with fertilization. Increasing establishment density was associated with greater stand basal area

and mass. However, individual component masses of wood, foliage, bark and branches different in their response to increasing establishment density on each site. The magnitude of all mass components increased with establishment density on HA sites. On CH sites, wood and foliage mass declined with increasing establishment density while stand masses of bark and branches tended to increase.

Fertilization increased stand mass proportion in wood and decreased mass proportion in foliage. Increasing establishment density increased stand mass proportion in foliage and decreased mass proportion in wood. Hemlock tended to have greater mass proportion in wood while cedar tended to have greater mass proportions in bark and branches and, on HA sites, in foliage.

The presence and influence of competition on mass structure of stands was greatest on the least productive areas associated with CH sites and unfertilized treatments and increased with site productivity.

Fertilization decreased or did not influence foliar efficiency. Increasing establishment density decreased foliar efficiency. Hemlock generally had greater foliar efficiency than cedar. Foliar efficiency varied with tree size and was positively correlated with tree size in cedar but negatively correlated with size in hemlock.

Light interception was increased by fertilization and increasing establishment density. Light use efficiency was not influenced by fertilization and declined with increasing establishment density. Light use efficiency increased exponentially with stand light interception for growth of foliage, wood and total dry mass.

Nutrient use efficiencies of N, P, K, S, Ca, Mg, Zn and B were increased by fertilization. Nutrient use efficiencies tended to be greatest in cedar on CH sites and greater

in hemlock on HA sites. Establishment density generally did not influence nutrient use efficiencies.

Growth of cedar and hemlock stands on both sites showed a consistent positive linear relationship with stand foliage mass.

Size hierarchies were reduced by fertilization and were not influenced by establishment density or absolute biological density. Cedar had greater structural inequality on HA sites and structural inequality of hemlock was greater on CH sites. Degree of structural inequality tended to be negatively associated with growth response to treatments and site: stands with greater growth had lower structural inequality. Development of structural inequality over the experimental period varied with site and species. Reduction in structural inequality was associated with increased relative growth rates of smaller versus larger individuals in stands. Stands developed positive skewness that was reduced by fertilization.

It was concluded that fertilization continued to increase stand growth 10 years after treatment. In structural or functional terms, the only growth mechanism positively influenced by fertilization was increased nutrient use efficiency. Symmetric competition was likely the dominant mode on these sites and increasing site productivity and fertilization decreased its presence and influence. No evidence for increased asymmetric competition development associated with increased site productivity and fertilization was found.

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Chapter 1

General Introduction and Background

1.1 Introduction

Extensive areas of coastal British Columbia are occupied by forest stands dominated either by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes), known as Hemlock-Amabilis Fir or HA sites, or by western redcedar (*Thuja plicata* Donn) with a minor hemlock component, known as Redcedar-Hemlock or CH sites. Geographic areas with significant occupancy by HA and CH stands include regions of strong oceanic influence on the central and north coasts. These areas are classified as maritime or hypermaritime subzones of the Coastal Western Hemlock (CWH) zone under the Biogeoclimatic Ecosystem Classification (BEC) system (Banner *et al.* 1993, Green and Klinka 1994). HA stands span all seral stages and occur with a range of structures, although mid-seral with an even-aged structure predominate on northern Vancouver Island (Prescott *et al.* 1996). CH stands on northern Vancouver Island are typically late seral with an uneven-aged structure and irregular canopy (Prescott *et al.*1996). There has been significant scientific and managerial interest in the ecology of CH and HA sites due to their widely divergent patterns of plantation development in response to clear-cut logging and to slash-burning.

Following logging, the ericaceous shrub salal, (*Gaultheria shallon* Pursh.), invades plantations established on CH sites and rapidly establishes a high cover (Prescott *et al.* 1996). Approximately 5 to 8 years following establishment, plantations of hemlock, amabilis fir and Sitka spruce (*Picea sitchensis* (Bong.) Carriere), and to a lesser extent redcedar, experience severe growth check associated with N and P deficiency (Weetman *et al.* 1989, Weetman *et al.* 1990). The growth of all three of these species is related to soil nutrient availability on a range of sites across an edatopic gradient on the British Columbia coast (Kranabetter *et al.* 2002). Salal competes with planted conifers for soil nutrients (Messier 1993, Chang and Preston 2000) and reduces conifer growth (Messier 1993, Fraser *et al.* 1995). However, salal invasion merely exacerbates a low nutrient supply situation on CH sites that results from a complex set of conditions (Prescott *et al.* 1996). Redcedar growth on CH sites is greater than that of hemlock (Weetman *et al.* 1989), possibly because redcedar fine roots tend to be evenly distributed through the soil profile or concentrated in the top 10 cm of the mineral horizons, while hemlock and salal fine roots are concentrated in the upper forest floor (Bennett *et al.* 2002, Wang *et al.* 2002). Hemlock and salal may therefore compete more strongly with each other for soil resources and have less access to nutrient pools deeper in the soil than redcedar (Bennett *et al.* 2002). In contrast to CH sites, HA sites have greater nutrient supply and lower salal abundance. Consequently growth check of juvenile plantations does not occur on HA sites (Prescott *et al.* 1996). Hemlock growth exceeds that of redcedar on HA sites.

Poor conifer plantation performance associated with ericaceous species has been noted in other cool-temperate regions with maritime climates, e.g. Heather Check Syndrome occurs on afforestation sites that were previously dominated by heather (*Calluna vulgaris* (L.) Hull) in Britain (de Montigny and Weetman 1990). Despite extensive investigation to date, the question of divergent juvenile stand growth on CH and HA sites remains a challenge.

1.2 Differences in Plantation Growth on CH vs. HA Sites

Early seral HA stands on northern Vancouver Island typically have a dense, even-aged structure with uniformly closed crowns and very little understory (Lewis 1982). These stands are generally regarded as having arisen as the result of an extra-tropical cyclone in 1906, which caused extensive windthrow and widespread initiation of HA stands on the landscape (Lewis 1982). In contrast, CH stands have an uneven-aged structure with irregular canopies that contain many openings. The well-developed understory on CH sites is strongly dominated by salal. Forest floors tend to be deep on CH sites and relatively shallow on HA sites. Lewis (1982) regards both CH and HA stands as being different phases that occur on circum-mesic sites that have otherwise similar topographic and edatopic characteristics. CH stands may thus be a late-seral stage in stand development on zonal sites, while HA stands may be early to mid-seral stages on the same sites. While acknowledging that redcedar-salal complexes can arise on sites that can also promote the growth of HA stands, Green and Klinka (1994) note that redcedar-salal complexes also occupy wetter sites in lower topographic positions.

The primary reason for poor plantation growth performance on CH sites is the low nutrient supply capability of the forest floor, relative to HA sites, especially for N and P (Prescott and Weetman 1994). Slower organic matter decomposition on CH sites, and under redcedar stands in general (Prescott *et al.*2000) may be the result of the chemical composition of redcedar litter, which resists decomposition and has lower mineralization rates than the litter of other conifers (Prescott *et al.* 1995, Prescott *et al.* 2000). Slower organic matter decomposition may also be the result of CH forest floors that are saturated for a greater portion of the year (Prescott and Weetman 1994). The resulting poor aeration may contribute to slower decomposition and mineralization of N and P (Prescott *et al.* 1996). Litter chemistry parameters and litter decomposition rates have been shown to correlate poorly with N mineralization rates and site factors, except for salal abundance in the understory, which is closely related to N mineralization rates (Prescott *et al.* 2000).

Fertilization with supplemental N and P eliminated growth check in conifer plantations on CH sites and increased foliar nutrient content (Weetman *et al.* 1989). Post-establishment fertilization of existing plantations with N and P increased growth of dominant trees, elevated forest floor N and P content, increased the tree growth potential of the forest floor in bioassays, and increased foliar P concentration of hemlock up to 10 – 13 years after a single fertilizer application compared to unfertilized plantations (Bradley *et al.* 2000, Bennett *et al.* 2003). Where fertilization does promote growth and enhance foliar nutrient content, hemlock tends to respond more strongly than redcedar (Bennett *et al.* 2003). The growth and presence of salal in stands decreased with increasing canopy closure and with reduction in light reaching the forest floor (Vales 1986, Messier *et al.* 1989, Messier 1992). In response to accumulating evidence showing the importance of fertilization and the role of salal in growth check on CH sites, a trial was established in 1988 to examine the effects of stand establishment density, fertilization at planting and five years later, and mechanical site preparation, on tree and stand growth on CH and HA sites. This trial was established through the Salal Redcedar Hemlock Integrated Research Program (SCHIRP) and is referred to as the SCHIRP Installation. The single and combined effects of fertilization, density and hoe-raking on tree and stand growth were to be examined. It was reasoned that denser conifer plantings would promote more rapid canopy closure and light attenuation with consequent reduction in salal presence. This effect would be amplified by fertilization, which would increase tree growth rates and further hasten canopy closure. Hoe-raking would remove salal from stands at establishment and promote stand growth and salal exclusion, particularly in conjunction with fertilization.

Early observations from this trial indicated that fertilization did increase tree growth and site occupancy by stands up to 10 years after stand establishment, five years after the last fertilization. Results from a nearby trial indicated that fertilization and salal removal both increased tree growth on CH sites 10 – 13 years after last fertilization (Bennett *et al.*2003); however, only fertilization increased N and P content in the forest floor and nutrient supply capacity (Bennett *et al.* 2003).

1.3 Fertilizer and Density Effects on Stand Structure, Function and Size Hierarchies

Fertilization increases growth of trees and stands by increasing nutrient availability (Weetman *et al.* 1989, Bennett *et al.* 2003), and this effect can last up to 30 years after a single fertilizer application, although most of the additional growth occurs within 10 years of treatment (Nohrstedt 2001, Jandl *et al.* 2002). However, fertilization may also influence tree structure and function to promote growth. Fertilization significantly increased total tree size and aboveground stem, branch and foliage biomass components in loblolly pine (*Pinus taeda* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), red pine (*Pinus resinosa* Ait.), and Scots pine (*Pinus sylvestris* L.; Brix 1981, Gower *et al.* 1993, Valinger 1993, Gillespie *et al.* 1994, Albaugh *et al.* 1998, Retzlaff *et al.* 2001) or stand leaf area in Douglas-fir and loblolly pine (Vose 1988, Vose and Allen 1988, Albaugh *et al.* 1998, Balster and Marshall 2000). Fertilization increased production of both fine (Braekke 1995, Retzlaff *et* *al.* 2001) and coarse roots (Braekke 1995, Albaugh *et al.* 1998, Retzlaff *et al.* 2001) in loblolly and Scots pines, although fine root production decreased in loblolly pine (Albaugh *et al.* 1998). Increased foliage biomass or leaf area resulting from fertilization has been associated with increased tree and stand growth of Douglas-fir, loblolly pine and Scots pine (Brix 1983, Vose and Allen 1988, Valinger 1993, Albaugh *et al.* 1998, Balster and Marshall 2000), however, increased proportional allocation to foliage biomass is less well documented and more complex. Proportional increases in biomass allocation to foliage may or may not result from fertilization and tend to be detectable for less than seven years after treatment (Brix 1983, Barclay *et al.* 1986, Gower *et al.* 1993, Valinger 1993, Albaugh *et al.* 1998, Yang 1998, King *et al.* 1999, Retzalff *et al.* 2001). Age-related declines in stand growth were associated with changes in stand structure, including a reduction in stand leaf area (Smith and Long 2001). Declining nutrient supply is associated with consequent reductions in stand leaf area and growth as lodgepole pine stands age (Binkley *et al.* 1995). Loblolly pine stand leaf area and foliar nutrient concentration increased following fertilization (Vose and Allen 1988). Fertilization alone did not increase foliar nutrient contents of N, K and Mg due to dilution of these nutrients in the expanded leaf area in Douglas-fir: reduction of initial stand foliage density through pruning was necessary to increase foliar nutrient concentrations (Velazquez-Martinez *et al.* 1992). The influence of fertilization on biomass allocation and the relation of foliar nutrient concentrations to foliage development are not well documented for western hemlock and western red redcedar.

Fertilization increased foliar efficiency (biomass growth increment per unit of foliage biomass or leaf area) in loblolly pine, Scots pine and Douglas-fir (Brix 1982, Vallinger 1993, Albaugh *et al.* 1998), although efficiency per unit of leaf area declined asymptotically with increasing stand leaf area in Douglas-fir and loblolly pine stands (Vose and Allen 1988, Velazquez-Martinez 1992). However, increases in foliar efficiency due to fertilization tend to be short-lived and decline to equal or below those of unfertilized controls 7 to 9 years after treatment (Brix 1982, Barclay *et al.* 1986, Valinger 1993, Mitchell *et al.* 1996). The effect of fertilization on foliar efficiency of western hemlock and western red redcedar is not well documented.

Competition is a significant factor influencing the structure and function of ecosystems, including plant communities (Keddy 1989, Goldberg and Barton 1992, Gurevitch *et al.* 2000) and competition theory continues to evolve. Many definitions of competition exist; however, in the studies described in this thesis the definition given by Keddy (1989) will be used where competition is defined as: "The negative effects which one organism has upon another by consuming, or controlling access to a resource that is limited in availability." When the aggregate resource demand of an individual organism and its neighbours exceeds resource supply, the negative influence of resource limitation experienced by the individual results from density (Newton and Jolliffe 1993). Competition is thus a measurable effect that results from density. When dealing with plants this effect may consist of reduced growth, increased mortality, changes in plant form and altered reproductive output (Harper 1977, Keddy 1989, Weiner *et al.* 1990). The degree to which competition is present, can be detected, and influences plant community growth and structure is closely connected to the degree of concurrent herbivory (Gurevitch *et al.* 2000). In this thesis, reduced growth associated with increasing establishment density will be used to determine the presence and degree of competition.

Competition has been shown to reduce tree size and growth and alter biomass allocation patterns, however, these effects vary with species, conditions and are not consistent. Increasing establishment density reduced both average height and diameter growth, especially on sites with lower growth potential (e.g. Nilsson 1994). Density limits individual tree growth in close-canopied stands and thinning, especially when combined with fertilization, produced greater average tree growth in Scots pine (*Pinus sylvestris* L.) western red redcedar, and Douglas-fir stands (Barclay and Brix 1985, Harrington and Wierman 1990, Valinger 1993). Competition influences biomass allocation patterns at both tree and stand levels, however, the exact effect of the effect varies with species and situation. For example, density may increase biomass allocation to foliage and decrease allocation to stems and branches (Newton and Jolliffe 1993), but it may also decrease allocation to foliage and increase allocation to stems and roots, especially when individuals are reduced to a subordinate crown position (Barclay *et al.* 1986, Nilsson and Albrektson 1993, Naidu *et al.* 1998, Vanninen and Makela 2000). In contrast to intraspecific competition, interspecific competition from salal did not alter allocation to shoot versus root components in hemlock, red redcedar or Sitka spruce (*Picea sitchensis* (Bong.) Carr.; Chang *et al.* 1996). The effect of competition on biomass allocation in juvenile hemlock and western red redcedar stands is not well documented.

Increasing stand density in closed-canopied stands results in a trade-off between increasing stand growth due to more foliage, and a reduction in growth per unit of foliage. Stratification in growing space use efficiency between larger and smaller trees may also occur. Total stand biomass production increases with stand density and increasing amounts of foliage (Ford 1982, Espinosa Bancalari and Perry 1987, Vose and Allen 1988, Velazquez-

Martinez *et al.* 1992). However, foliar efficiency tends to decline with increasing stand leaf area or foliage biomass, and greater foliage biomass in a stand tends to be offset by reduced foliar efficiency (Waring *et al.* 1981, Ford 1982, Velzquez-Martinez *et al.* 1992). In some cases, however, increasing stand density may increase foliar efficiency where light levels are not significantly reduced (Nilsson and Albrektson 1993). Reduction of stand density through thinning has been shown to increase foliar efficiency of Douglas-fir stands for longer periods than stand fertilization, although the effect is slower to develop (Brix 1983, Mitchell *et al.* 1996). As trees increase in size, an increase in resource availability, especially light, is likely necessary to prevent reduction in foliar efficiency (Maguire *et al.* 1998). Stand development with age, and consequent increases in stand density due to increased site occupancy, has been shown to result in increased growing space use efficiency by smaller compared to larger trees, based on sapwood basal area, crown projection and foliar biomass, although stand structure will influence which tree size is most efficient (O'Hara 1988, Larocque and Marshall 1994, Sterba and Amateis 1998, Vanninen and Makela 2000). The effect of density on foliar efficiency in western hemlock and western red redcedar are not well documented.

Nutrient use efficiency (biomass growth increment per unit nutrient content or concentration) tends to be strongly influenced by species but can be influenced by fertilization and density. Nutrient use efficiency varies with species and reflects different physiological investment strategies and response to external conditions (Prescott *et al.* 1989, Gower *et al.* 1993, Bothwell *et al.*2001, Dicus and Dean 2001, Ripullone *et al.* 2003). For example, the superior growth of lodgepole pine compared to Sitka spruce (*Picea sitchensis* (Bong.) Carr.) under conditions of low nutrient availability on CH sites was attributed to greater nutrient use efficiency of pine (Bothwell *et al.* 2001). Nutrient use efficiency tends to decline with increasing soil availability of nutrients following fertilizer application (Barclay and Brix 1985, Elliott and White 1993, Elliott and White 1994, Mitchell *et al.*1996), possibly because photosynthetic rates tend to initially increase as foliar nutrient concentration rises, but then plateau at higher concentrations (Reich and Schoettle 1988, Brown *et al.* 1996a, 1996b). Foliar N use efficiency declined with increasing N concentrations in both hemlock and western red redcedar, but tended to be higher for hemlock than for redcedar at lower N concentrations (Brown *et al.* 1996a, 1996b). Competition had mixed effects on nutrient use efficiency. Increasing planting density, and associated increases in intraspecific competition, resulted in lower N and P use efficiency in stands of loblolly and slash pine (*Pinus elliottii* Englem.) (Dicus and Dean 2001). However, increasing interspecific competitive stress, associated with increasing cover of non-timber species, has been shown to increase N use efficiency in red pine (*Pinus resinosa* Ait.) (Elliott and White 1993). The net effect of both interspecific competition, from salal, and intraspecific competition, as stand establishment density increases, on nutrient use efficiency is thus likely to be complex and vary as conditions influence the relative competitive ability of both tree species and salal (Keddy 1989, Goldberg *et al.* 1992, Grime 2001). The effect of fertilization and density on nutrient use efficiencies of western hemlock and western red redcedar in the field are not well documented.

Fertilization may increase stand growth by influencing light use efficiency (growth per unit of absorbed photosynthetically active radiation). Fertilization resulted in increased absorbed-light use efficiency in Douglas-fir stands eight years after treatment (Balster and Marshall 2000).

Size hierarchies describe concentration of biomass within populations (Weiner and Solbrig 1984, Weiner and Thomas 1986) and can offer insight into mode of competition and factors influencing stand development (Newton 1990, Sarkkola *et al.* 2003). The influence of density and environmental factors on the development of competition and size hierarchies in trees is unclear. Competition may increase with soil resource supply in natural communities (Goldberg and Barton 1992, Grime 2001), however, the addition of fertilizer to artificially enhance soil nutrient supply has tended not to increase the magnitude of competition (Goldberg and Barton 1992). Alternatively, soil resource supply may not affect the magnitude of competition (Tilman 1988, Wilson and Tilman 1993). Herbivory that occurs in conjunction with resource supply may also significantly influence the degree of competition detected and its influence on community structure (Gurevitch *et al.* 2000). One-sided, or asymmetric, competition occurs when larger plants obtain size-disproportionably more resources compared to smaller plants, while two-sided, or symmetric, competition occurs when resource uptake occurs independently of the relative size of competitors (Schwinning and Weiner 1998). Factors that increase asymmetric competition are typically associated with pre-emption of light and are hypothesized to increase differences in size between individuals and lead to more strongly developed size hierarchies, with a greater proportion of biomass concentrated in fewer individuals (Weiner and Solbrig 1984, Weiner 1990). Conversely, symmetric, or two-sided, competition, which is typical for soil resources (Nambiar and Sands 1993), is thought to produce more weakly developed hierarchies with more uniformly sized individuals composing the population (Schwinning and Weiner 1998). In a forestry context, asymmetric competition results in the expression of dominance by large individuals and stand differentiation, while symmetric competition results in stagnation of stand development (Oliver and Larson 1996).

The influence of density and environmental factors on the development of size hierarchies in trees is unclear. Competition has been shown to increase size inequity within populations of trees (Knox *et al.* 1989, Newton 1990, Laroque and Marshall 1993) and non-woody species (Weiner 1985, Schmitt *et al.* 1986, Weiner 1986), although the response may vary with species (Lieffers and Titus 1989). However, the role of site factors, such as soil moisture and nutrient supply are not as clear. Increased availability of soil moisture has been shown to increase growth rates and competition, and enhance the development of size inequality within tree stands and populations of non-tree plants through increased competitive pressure (Weiner 1985, Briones *et al.* 1998, Wichmann 2001). However, the influence of soil nutrient availability on size hierarchies is complex. Peat land drainage of boreal sites, which presumably enhances nutrient supply in the root zone through increased mineralization rates, reduced size inequity within stands, by increasing the growth rate of smaller trees relative to that of larger trees (MacDonald and Yin 1999). Drainage caused an initial increase then decrease of size inequality within stands across southern Finland, which was presumed to have resulted from an increase in relative importance of symmetric competition (Sarkkola *et al.* 2003). In this latter case, though, size distribution pattern rather than size inequity (a measure of differences in sizes within the population), *per se*, was examined (Sarkkola *et al.* 2003). Irrigation and fertilization, both separately and in combination, did not influence within-stand size hierarchy development stands, relative to non-treated controls, although the growth rate of small trees was increased by combined fertilization and irrigation relative to that of larger trees (Nilsson *et al.* 2002). The lack of influence of resource supply on competition and size hierarchy development could have resulted from an increase in site carrying capacity or 'stockability' in this experiment (DeBell *et al.* 1989, Nilsson *et al.*2002). Size hierarchies decline with stand age in regenerating stands on poor sites, consistent with an increase in significance of symmetric competition (Newton 1990). The role of site and species differences in size hierarchy development is not well documented, particularly under field conditions.

1.4 A Conceptual Framework of Fertilization and Density Effects on Stand Growth and Structure

The influence of fertilization and establishment density on the growth of western redcedar and western hemlock stands up to 14 years after establishment and 10 years after the last fertilization are unknown. Increased nutrient supply, associated with fertilization, may continue to increase stand growth. However, possible structural and functional effects of the treatments may be affecting stand growth as well, as outlined above. The preceding information may be summarized into a conceptual framework describing the possible effects of fertilization and establishment density on growth, stand structure and functional mechanisms at the SCHIRP Installation and used to generate the following testable hypotheses:

1. Fertilization of forest stands increases both tree size and site occupancy by the stand. Given the time since fertilizer was last applied, growth increment may or may not still be affected by the fertilizer application. Hemlock responds more strongly to fertilization than redcedar on northern Vancouver Island.

   <u>Hypotheses:</u>

   a) Fertilization results in larger individual trees, in terms of basal area and height.
   b) Fertilization results in greater basal area per ha.
   c) Fertilization does not result in greater growth increment, in terms of annual increment of tree basal area, height and basal area/ha, in the most recent measurement period.
   d) Hemlock responds more strongly (fertilization x species interaction presence) than redcedar to fertilization.

2. Fertilization may change biomass allocation; specifically increased proportion of the foliage component and decreased allocation to wood, but this effect tends to diminish with time. Density affects biomass allocation patterns but effects differ among species.

   <u>Hypotheses:</u>

   a) Fertilization increases total tree biomass and component biomasses per ha.
   b) Fertilization does not change stand-level biomass proportions.

c) Increasing establishment density affects proportional allocation to biomass components.

3. Fertilization may increase foliar efficiency but this increase dissipates with time. Density reduces foliar efficiency.

<u>Hypotheses:</u>

a) Fertilization did not increase foliar efficiency

b) Increasing establishment density reduces foliar efficiency.

4. Fertilization can increase foliar nutrient concentration of P in hemlock up to 13 years after treatment.

<u>Hypothesis:</u>

Fertilization increases foliar nutrient concentrations of N,P, K, S, Ca, Mg, SO_4-S, Fe, Mn, Cu, Al and B ten years after treatment in both redcedar and hemlock.

5. Nutrient use efficiency is strongly species dependent; is greater for hemlock than for redcedar; and tends to decline with increasing foliar nutrient concentration for these species.

<u>Hypotheses:</u>

a) Stand level nutrient use efficiency is reduced by fertilization.

b) Stand level nutrient use efficiency is greater for hemlock than for redcedar.

6. Fertilization may increase absorbed light use efficiency.

   Hypothesis:

   Fertilization increases growth efficiency per unit of absorbed light.

7. Increasing stand density reduces tree sizes and growth rates but increases stand-level growth.

   Hypotheses:

   a) Increasing establishment density reduces tree size, in terms of height and diameter.

   b) Increasing establishment density reduces growth increment, in terms of annual increment of tree basal area, height and basal area/ha, in the most recent measurement period.

   c) Increasing establishment density increases stand-level growth, in terms of basal area and biomass accumulation

8. Size hierarchy development may be reduced by increasing soil resource availability and may be unaffected by density in juvenile conifer stands. It is not known how or if size hierarchy development varies with species.

   Hypotheses:

   a) Increasing establishment density does not affect size hierarchy development.

   b) Fertilization does not affect size hierarchy development.

   c) Size hierarchy development is not influenced by species.

This thesis will examine the effect of establishment density and fertilization, singly and in combination, on the growth response of redcedar and hemlock on CH and HA sites 14 years after establishment, 10 years after last fertilizer application at the SCHIRP Installation. Objectives of this thesis will be to test the above hypotheses to determine the effect of:

1. Size development, growth of trees and site occupancy continue to be elevated by fertilization.
2. Establishment density has influenced tree size and growth.
3. Overstory density and fertilization on salal occupancy of CH sites.
4. Fertilization on stand-level changes in foliage biomass proportion.
5. Fertilization on foliar or resource-use efficiency.
6. Establishment density on biomass allocation to foliage, foliar and resource-use efficiency.
7. Site, species, fertilization and establishment density on size hierarchy development and competition process.

Hypotheses regarding the effects of establishment density and fertilization on tree and stand growth are examined in Chapter 2. Treatment effects and the influence of species are determined through the examination of tree size variables (average basal area at breast height; leading height; average height), stand variables (stand basal area; mortality) and growth between the two most recent measurement years in the experimental period. Chapter 2 also examines hypotheses regarding the influence of treatment and species on foliar nutrient concentrations. Chapter 2 is intended to provide context for further hypothesis investigation by providing a summary of stand growth, both over the entire experimental period and in the most recent growth interval, and by summarizing the effect of treatment on nutritional status by species.

Hypotheses regarding the influence of site productivity and fertilization on the development of competition and the influence of competition on stand biomass structure are examined in Chapter 3. Chapter 3 expands on Chapter 2 by examining treatment effects on total biomass accumulation; total accumulation of biomass in various components and; proportional biomass accumulation in different components. In Chapter 3, competition is specifically examined though the examination of total size (biomass) rather than through indirect measures of size (height, basal area). The presence and influence of competition on stand biomass structure is examined across a gradient of nutrient supply/site productivity for each species in this chapter.

Chapter 4 explores growth processes by testing hypotheses regarding treatments on foliar and resource use efficiencies for each species. Treatment effects on foliar efficiency are further examined by including an effect for tree size in the analysis. In addition to foliar efficiency, foliar capacity of stands is examined by relating total stand growth to foliage mass in Chapter 4. Treatment effects on total light absorption by stands and growth of different biomass components with increasing light absorption are examined for redcedar stands on CH sites in Chapter 4.

Chapter 5 explores current theories about the influence of site productivity on competition development by examining size hierarchy development. Hypotheses regarding the effect of establishment density and fertilization are tested to determine whether size hierarchy development is decreased by fertilization and uninfluenced by density and whether these effects vary with species.

Chapter 6 summarizes conclusions described in previous chapters and provides suggestions for future research.

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Chapter 2

Growth and Foliar Nutrient Response to Fertilization and Establishment Density in Juvenile Western Redcedar and Western Hemlock Stands on Northern Vancouver Island

2.1 Introduction

Measures to protect non-timber values and competition from other land-uses have reduced the operating land base for commercial timber production in coastal British Columbia. Wood production on the remaining operable land base must therefore increase in order to avoid or limit reductions in annual allowable cut. Historically, timber was predominantly harvested in old-growth forests but, as these forests are logged or protected, forest stands of plantation origin will become the dominant source of wood supply in coastal British Columbia.

Conifer plantations on sites formerly occupied by old-growth western redredcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands (CH sites) develop differently than plantations established on sites formerly occupied by mid-seral stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes (HA sites). Plantations located on CH sites typically experience nutrition related growth check 5 to 8 years after establishment, while plantations located on HA sites typically do not experience growth check and develop unimpeded (Weetman *et al.* 1990). Poor growth on CH sites resulted from low availability of soil N and P (Weetman *et al.* 1989, Prescott *et al.* 1996) exacerbated by competition with salal for available soil nutrients, including fertilizer-applied nutrients (Chang and Preston 2000). Reduction of early plantation growth on CH sites was strongly and positively associated with salal presence (Messier 1993, Fraser *et al.* 1995).

Silvicultural solutions have been found to increase plantation growth on CH sites. Fertilization with N and P relieved growth check on CH sites (Weetman *et al.* 1989). Fertilization with N and P increased conifer-available nutrient supply, as well as growth and foliar P concentration of dominant hemlock trees in dense stands (> 3000 stems per ha) on CH sites 10 to 13 years after a single application (Bradley *et al.* 2000, Bennett *et al.* 2003). Tree-layer canopy cover was increased by a combination of fertilization and salal removal (Bennett *et al.* 2003). Salal cover was negatively correlated with increasing canopy cover across a range of treatments, including an untreated control, fertilization treatment and combined fertilization and salal removal treatments (Bennett *et al.* 2003). Salal growth and cover declined with increasing tree cover and light attenuation (Messier *et al.* 1989), although the interaction of declining light levels and soil nutrient availability on salal growth was unclear (Messier 1992). Generally, increased stocking and fertilization are the only silvicultural cultural activities that can increase wood production from a stand within a given period of time. The combined effect of early fertilization with establishment density has not been documented in redcedar and hemlock stands in coastal British Columbia and is generally poorly documented for species in other locations.

A factorial trial was established in 1988 (the SCHIRP Installation) to examine the separate and combined effects of stand establishment density and fertilization on the growth of redcedar and hemlock on both CH and HA sites. Earlier observations from this trial indicated that fertilization increased growth of both redcedar and hemlock on CH and HA sites, however, density effects were not examined. Single fertilizer applications have been shown to increase stand volumes and foliar nutrient concentrations up to 30 years after treatment (Jandl *et al.* 2002), although most of the volume gain was accrued within the first 10 years of treatment (Nohrstedt 2001). In this chapter, tree size and site occupancy by the stand (basal area/ha) were examined at the SCHIRP Installation to detect cumulative treatment effects on growth. It was anticipated that fertilizer effects on growth may have dissipated in the interval between the 1997 and 2002 measurements and that competition effects on growth may have developed only later in stand development. Therefore, tree and stand basal area growth rate between 1997 and 2002 were examined to better determine whether fertilization increased growth 5 – 10 years after application and whether intra-specific competition had developed at this time. Specific objectives of this study were to re-examine the trial 14 years after establishment and 10 growing seasons since the last fertilizer application, in order to address the following questions:

1) Have fertilization and establishment density affected tree size, site occupancy by the stand, cumulative mortality and do effects vary with species?
2) Have fertilization and establishment density affected recent tree and stand growth rates (1997 – 2002) and do effects vary with species?
3) Have fertilization and establishment density affected foliar nutrient concentrations and do effects vary with species?
4) Does a significant relationship exist between tree growth and foliar nutrient concentration?

5) Have fertilization and establishment density affected salal biomass development on CH sites?

Based on results from previous studies, it was hypothesized that fertilization would increase tree size, stand basal area and growth rates in the 1997 – 2002 period; increasing establishment density would decrease average tree basal area and basal area growth rate but increase stand-level basal area and growth rate; redcedar growth would be greater on CH sites while hemlock growth would be greater on HA sites; foliar P would be increased by fertilization; and growth of both species would be closely correlated with foliar N and P concentrations.

2.2 Materials and Methods

2.2.1 Study Sites

The study was located on northern Vancouver Island, British Columbia, Canada, between Port Hardy and Port McNeill (50° 60'N, 127° 35' W) in the Submontane Very Wet Maritime variant of the Coastal Western Hemlock Biogeoclimatic, or CWHvm1, zone (Green and Klinka 1994). The study site was approximately 50m ASL in undulating terrain with frequent rocky knolls and wetlands located in depressions. Surface materials consist of unconsolidated glacial moraine and fluvial outwash deposits that range from blankets over 1m in depth to shallow veneers with exposed bedrock. Mineral soils ranged from silty clay loams to fine sand with high coarse fragment content. Organic soils of wetland or upland origin are also common within the study site.

The area receives approximately 1900 mm of precipitation annually, most of which falls as rain. Growing season soil moisture deficits typically do not occur (Lewis 1982).

Average daily mean temperature ranges from 3.3° C in January to 14.1° C in August. A relatively high percentage of the annual solar radiation is received as diffuse radiation (McKay and Morris 1985), reflecting overcast conditions throughout the year and frequent summer fog. Direct sunlight exposure ranges from 1.5 h/day in December to 6.4 h/day in July. Global solar radiation incident of a horizontal surface averages 10.212 MJ/m^2 per day and ranges from a low of 2.043 MJ/m^2 per day in December to 18.935 MJ/m^2 per day in July (McKay and Morris 1985).

Two common CWHvm1 forest types were examined at the study site. Hemlock Amabilis Fir (HA) types are occupied by stands composed of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) while Redcedar Hemlock (CH) types are occupied by stand composed of western red redcedar (*Thuja plicata* Donn) and western hemlock. Both forest types are typically found on well to imperfectly drained Duric Humo-Ferric Podzols and are considered zonal sites (Lewis 1982, Green and Klinka 1994). HA sites typically occur on areas that have historically been subject to stand-replacing wind throw events (Lewis 1982). HA stands are mid-seral and have a dense, even-aged structure with uniform canopies. Due to the dense canopy cover, HA stands have poorly developed understory vegetation layers. Surface organic layers in HA stands are comparatively thin (5 – 10 cm) and friable. CH stands likely represent a climatic climax state, with an uneven-aged structure and open, irregular canopies. CH stands typically have well developed understory plant communities dominated by dense salal (*Gaultheria shallon* Pursh) growth. Surface organic layers in CH stands are thicker (10 – 45 cm) and more compact than on HA sites. Soil nutrient availability is lower on CH sites than on HA sites (Prescott *et al* 1996).

The study site was clear-cut logged in 1986, broadcast burned and planted with western hemlock and western red redcedar in 1987.

2.2.2 *Treatments*

Ninety-six treatment plots, each containing 64 sample trees were established in 1987. Plot size and tree spacing varied with density. Treatments consisted of a fully crossed factorial combination with two levels of fertility (fertilized and unfertilized) and three levels of density (500, 1500 and 2500 stems per ha). Trees in the 500 sph plots were planted 4.5 m apart, resulting in a central (core) measurement area of 36 x 36 m and a total plot size of 54 x 54 m, including a buffer zone. Buffer zones were planted at the same spacing as the core areas they surrounded. The 1500 sph treatment had a tree spacing of 2.6 m, a core measurement area of 21 x 21 m and a total area plot size of 32 x 32 m. Between tree spacing was 2 m in the 2500-sph treatment, with a 16 x 16m core measurement area and total plot size of 36 x 36 m.

Fertilized plots received a 60 g dressing of Nutricoat™ controlled release fertilizer at time of planting. The fertilizer was raked into 15-cm radius areas around each seedling and provided 10 g of N, 2.5 g of P and 5 g of K to each seedling. Total application rated per ha varied with density. All fertilized plots were refertilized before the beginning of the growing season in 1993 with a broadcast application of 225 kg of N and 100 kg of P per ha.

The 2 x 3 combination of fertilizer/no-fertilizer by densities was duplicated for each of redcedar and hemlock on both CH and HA sites. Each fertilization-density-species combination was randomly assigned within four blocks on each site, with a single treatment level replicate per block. Thus, a total of 48 plots examined 12 treatments with 4 replications per treatment level.

Height and diameter of each living sample tree within core measurement areas were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997 and 2002. Height was recorded to the nearest cm. Diameter was measured in mm at the root collar for the years 1988 – 1997. Diameter was measured at 1.3 m above the root collar (breast height) in 1997 and 2002.

Leading-height was determined from heights of the ten largest diameter trees in each plot.

2.2.3 Salal Biomass Sampling

Clip plots were established in the late summer and early fall of 2002 to sample the salal-dominated shrub layer. Only CH sites planted to redcedar were sampled, as initial site inspections indicated that the young redcedar stands were growing more vigorously than hemlock and had the greater likelihood of closing and competitively excluding salal through light attenuation. Six clip plots were randomly located in each experimental unit planted to redcedar on CH sites, avoiding very wet areas dominated by skunk cabbage (*Lysichitum americanum* Hultén & St. John) or sedges. A total of 144 plots were clipped and analyzed (24 for each density x fertility combination). Clip plots were 0.75 x 0.75 m square and were delineated using a frame made of polyvinyl chloride tubing. All vegetation rooted within the frame was clipped, although only salal data are reported here.

All salal stems from a clip plot were combined and the biomass determined to the nearest 50 g in the field. Ten stems were then randomly subsampled and removed to a lab facility in Port McNeill where their combined fresh biomass was determined to the nearest

0.01 g within four hours of clipping. Plot sub samples were then dried in a drying oven at 70 °C for at least 72 hours or until they ceased to lose biomass. Dry biomass of subsamples was determined to the nearest 0.01g and dry biomass conversion factors were determined for each clip plot as follows:

$$\textit{proportional plot dry biomass} = \frac{\textit{sub-sample dry biomass}}{\textit{sub-sample fresh biomass}}$$

Total clip-plot dry biomass was determined by multiplying fresh biomass by proportional plot dry biomass. Clip-plot dry biomass estimates were averaged to yield an estimate for standing salal biomass in each experimental unit sampled.

2.2.4 Foliar Nutrient Concentration Determination

Samples of current-year foliage were collected from the upper crowns of trees within each plot. Approximately 500g of fresh foliage was collected from about 60 trees in each plot and combined into one composite sample per plot. Composite samples were dried to constant weight at 70 °C and ground. Nutrient concentration was determined following sulphuric-acid hydrogen-peroxide digestion (Parkinson and Allen 1975). Nitrogen and P concentrations were determined colorimetrically on a Technicon auto-analyzer. K, Ca, Mg, Mn and Al concentrations were determined by atomic absorption specrography. Cu, Zn, and Fe concentrations were determined through dry-ashing and subsequent analysis with atomic absorption spectography. Boron concentration was determined colorimetrically with the azomithine-H method. Total S concentration was determined using a LECO Sulfur Analyzer. Available sulphate-sulphur concentration was determined using 0.01 N HCl extractions and determined colorimetrically in a HI-Bismuth reducible distillate. All analyses were conducted at Pacific Soils Analysis Incorporated of Richmond, British Columbia.

2.2.5 Statistical Analysis

A general linear model approach (PROC Mixed in SAS) was used to examine the cumulative effect of treatments on stand and tree growth after 14 years of stand development on each site and on current foliar nutrient concentrations. A mixed-effects model was used for each site type with species, fertilization and density tested as fixed effects and block included as a random effect:

$$y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + (abc)_{ijk} + \varepsilon_{ijkl}$$

Where: y_{ijk} = Response of the *i*th species at the *j*th fertility level at the *k*th density level
μ = General Mean
a_i = Species Effect
b_j = Fertility Effect
c_k = Density Effect
ε_{ijkl} = Residual Error

A randomized complete block design with a 2 x 3 factorial combination of treatment levels was used. Where interaction terms were significant, given significance of at least one constituent fixed effect, simple effects were compared by adjusting least-square means for Tukey's Honestly Significant Difference test. Where interactions were significant, density, fertilizer and species effects were examined together. Where interaction terms were not significant, simple effects were compared using Tukey's HSD test. The following variables were analyzed in this fashion: average tree height, leading-height, average tree basal area, average annual height and average basal area growth rates for 1997 – 2002; stand basal area and average stand basal area growth rate for 1997 – 2002; salal biomass and foliar nutrient concentration (N, P, K, S, Ca, Mg, Mn, Cu, Al, Fe, B and available sulphate-sulphur). To homogenize variances, analysis was conducted on $\log_e$- transformed tree and stand growth variables. The correlation between foliar nutrient concentration and recent tree growth, using average annual height increment for the 1997 – 2002 period, was determined using Pearson Correlation Analysis. All statistical analyses were conducted using SAS Version 8.2 with a significance level of $p < 0.05$ used for hypothesis testing.

2.3 Results

Average tree height, leading-height, basal area (tree), stand basal area (BA) per ha and percent mortality are presented in Table 2.1. Average annual tree height, leading-height and BA growth rate for the 1997 – 2002 period are presented in Table 2.2, with average annual stand BA growth rate. Foliar nutrient concentrations are presented in Table 2.3. Statistical tests are summarized in Appendix 1.

Stand development, described using mean treatment leading-height, over the experimental period, is presented in Figures 2.1 to 2.4.

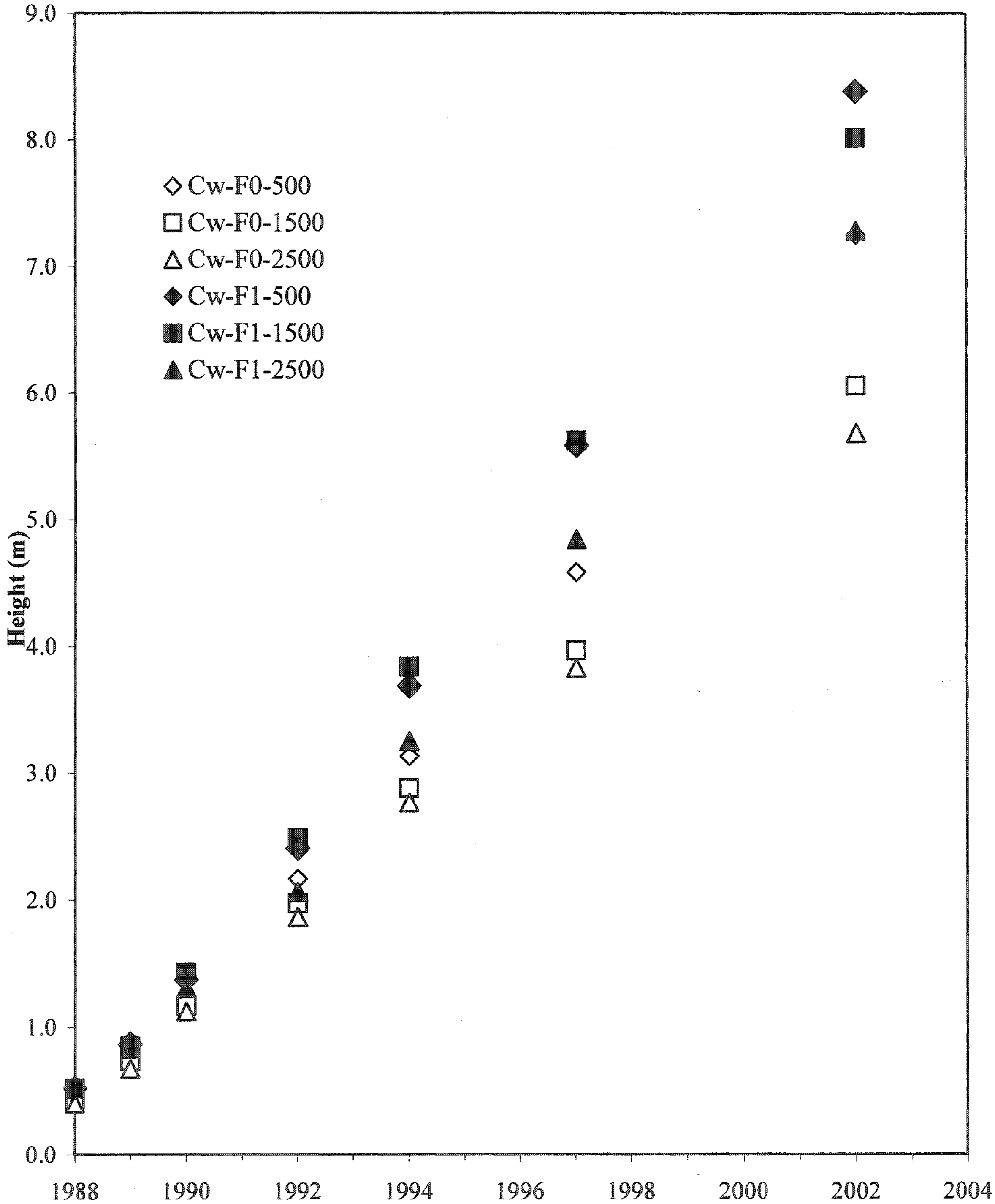

Figure 2.1. Leading-height development of Cw on CH sites, 1988 – 2002.

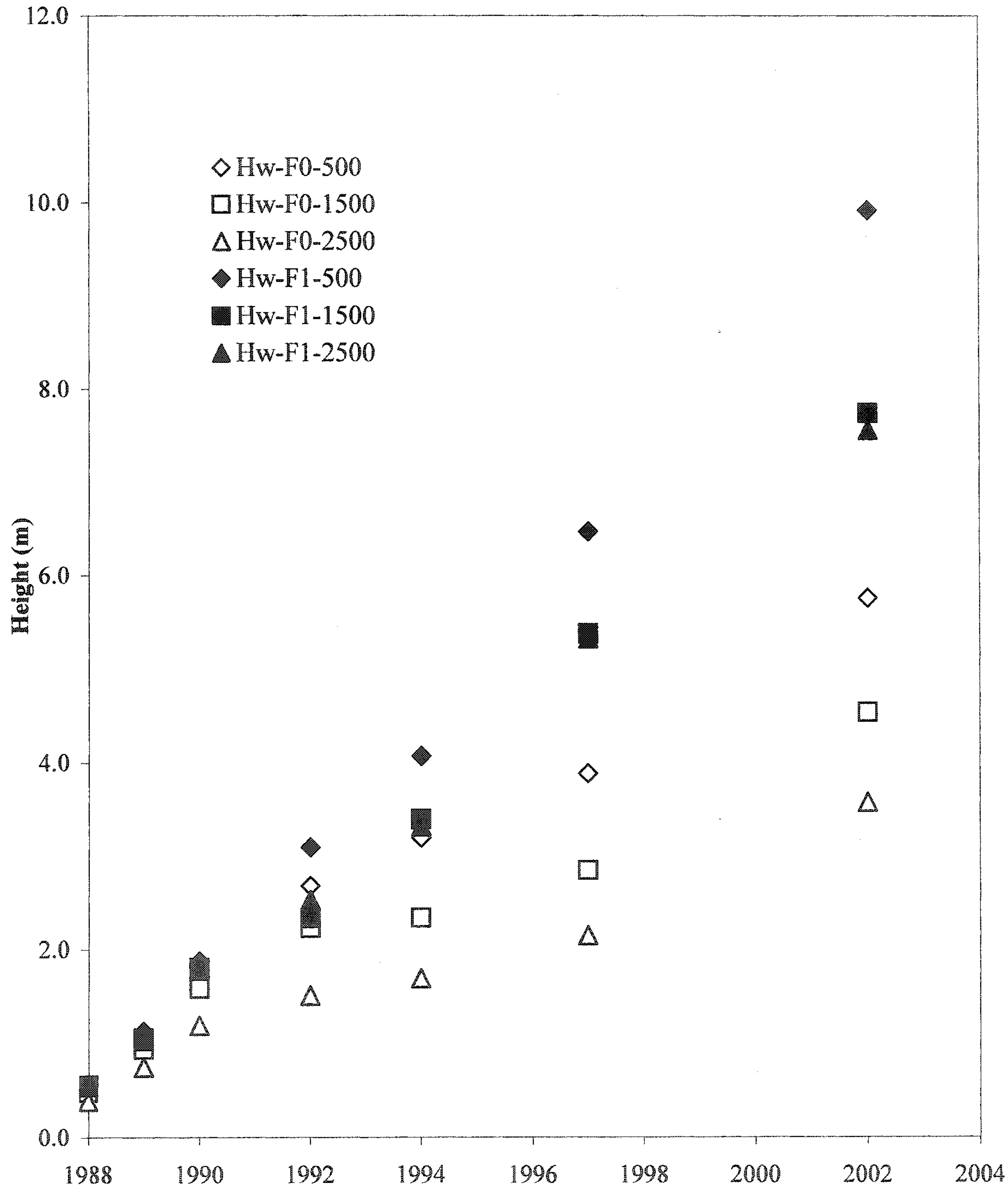

Figure 2.2. Leading-height development of Hw on CH sites, 1988 – 2002.

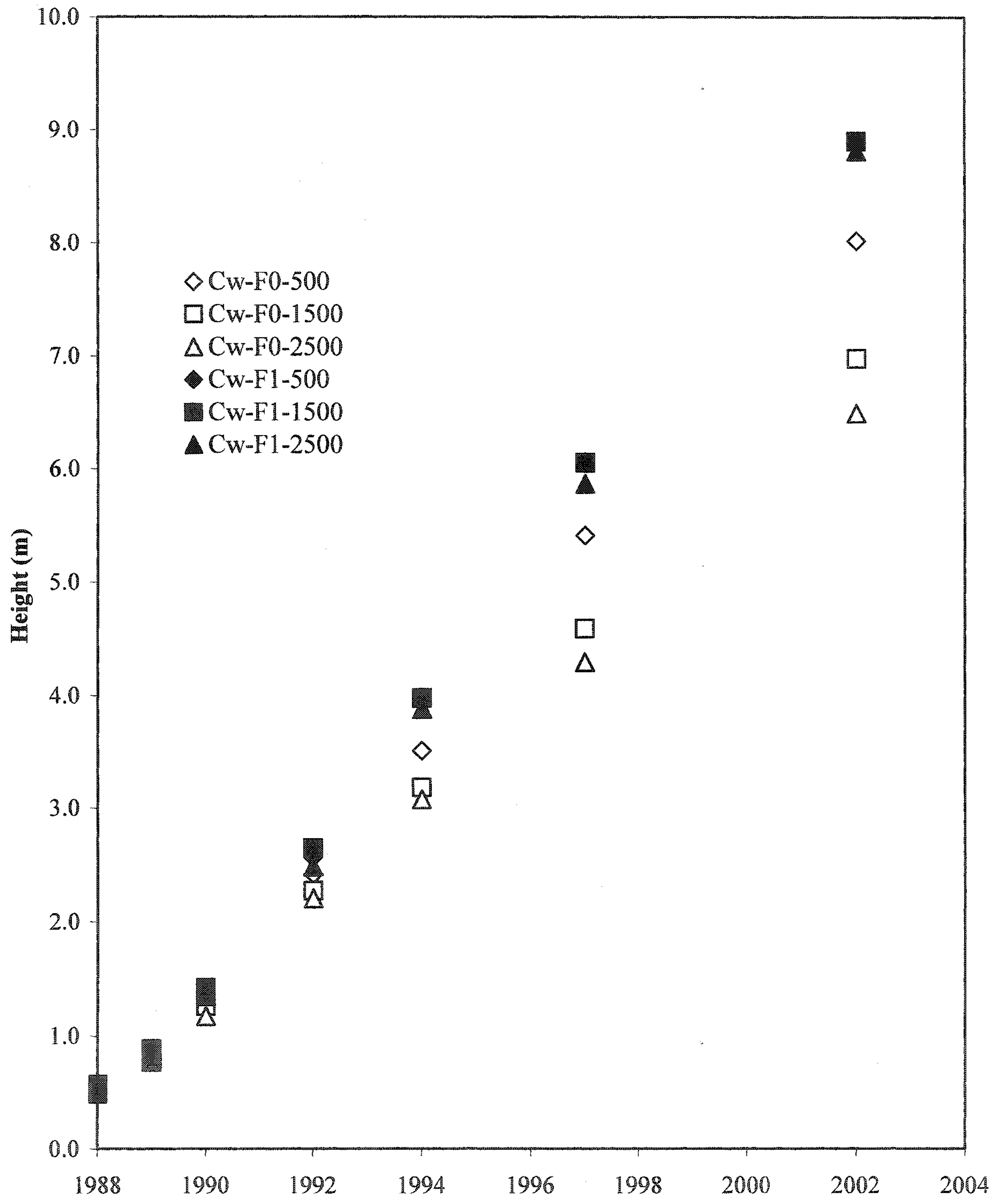

Figure 2.3. Leading-height development of Cw on HA sites, 1988 – 2002.

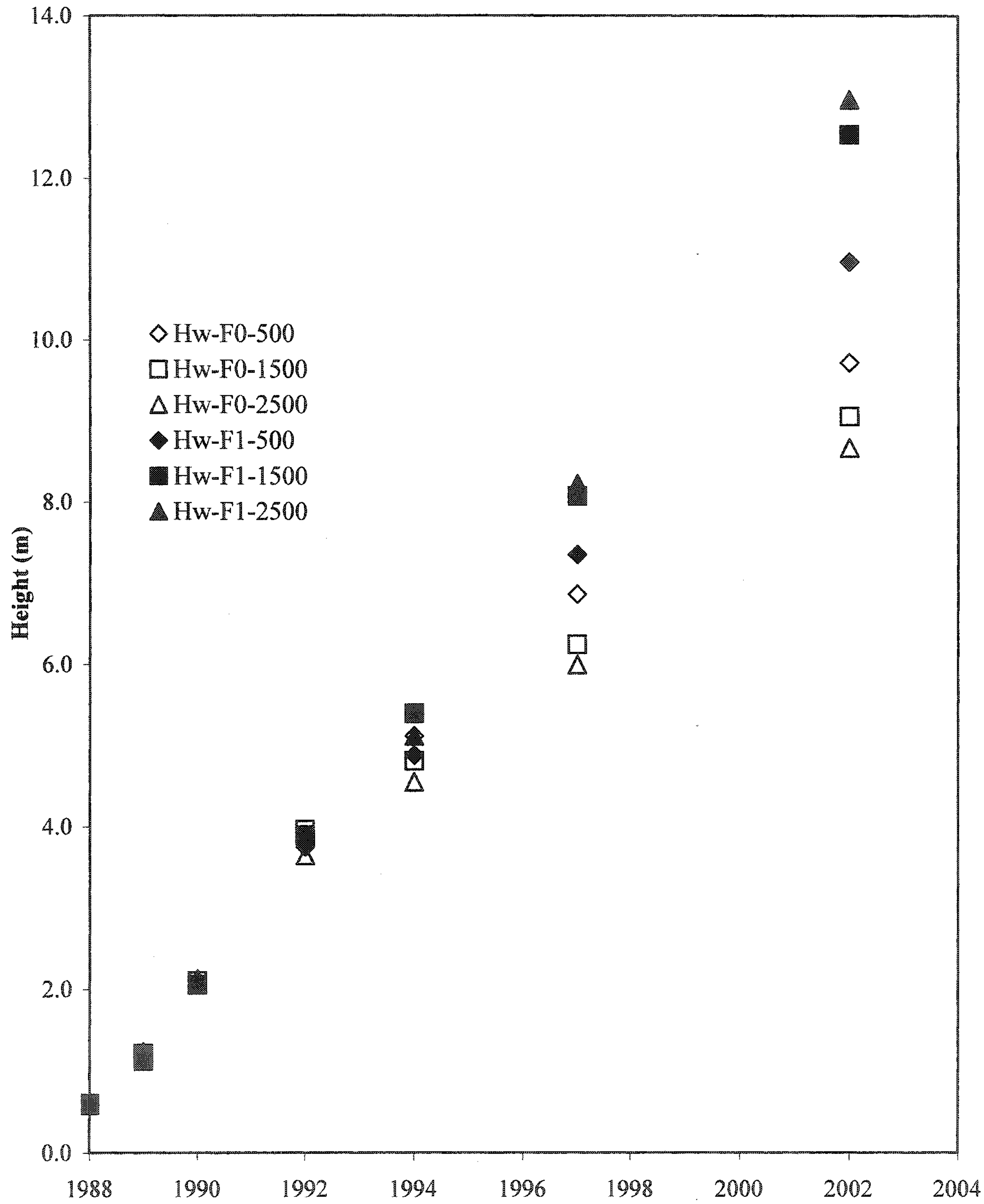

Figure 2.4. Leading-height development of Hw on HA sites, 1988 – 2002

2.3.1 Height and Basal Area

Fertilization increased height development of stands (Figures 2.1 to 2.4). This increase in height growth has generally not lessened with time since fertilizer application. The exception to this is fertilized hemlock on CH sites planted at 1500 and 2500 sph, which show a reduction in growth between 1997 and 2002, compared to the fertilized 500 sph treatment. Leading-heights declined with increasing establishment density for redcedar and hemlock, on both fertilized and unfertilized CH sites, and for redcedar and hemlock on unfertilized HA sites. Fertilized hemlock on HA sites show a pattern opposite to this: leading-heights increased with decreasing establishment density. Fertilized redcedar leading-height was unaffected by density.

Fertilization increased average and leading-heights for both species on HA sites (Table 2.1, A1.1 and A1.3). Hemlock stands had greater average and leading heights than redcedar stands on HA sites.

Treatment and species effects on height growth were more complex on CH than on HA sites (Tables 2.1, A1.1 and A1.3). Significant species x fertilization interactions were present for average and leading heights on CH sites. These interactions indicated that average height and leading height of redcedar is greater than that of hemlock on unfertilized. Fertilization increased height growth more in hemlock than in redcedar and eliminated species differences so that average and leading heights of the two species did not differ on fertilized CH sites. A significant species x establishment density interaction was present for leading height on CH sites. This interaction indicated that hemlock leading-height was reduced more by increasing establishment density than was leading-

Table 2.1. Average tree height, leading-height and basal area; stand basal area (BA) and mortality (standard errors in brackets).

Species	Fert.	Planting Density (Stems/ha)	Height (m)	Leading-Height (m)	Tree Basal Area (cm^2)	Stand Basal Area (m^2/ha)	Mortality (%)
CH Sites:							
Cw	F0	500	5.36(0.59)	7.26(0.76)	53.29(16.19)	2.60(0.77)	0.8(1.6)
Cw	F0	1500	4.53(0.55)	6.07(0.69)	27.43(11.16)	4.35(1.74)	0.4(0.8)
Cw	F0	2500	4.08(0.33)	5.69(0.23)	19.46(3.52)	4.79(0.90)	0.4(0.8)
Cw	F1	500	7.15(0.49)	8.39(0.40)	126.31(24.61)	5.95(1.15)	4.3(3.5)
Cw	F1	1500	6.73(0.61)	8.02(0.52)	86.59(25.29)	13.77(4.12)	0.8(0.9)
Cw	F1	2500	5.72(1.05)	7.29(0.75)	50.54(21.26)	12.40(1.53)	2.3(2.7)
Hw	F0	500	3.65(0.26)	5.76(0.43)	16.10(4.45)	0.73(0.22)	6.3(4.4)
Hw	F0	1500	3.17(0.29)	4.54(0.48)	9.34(2.92)	1.35(0.21)	5.9(3.9)
Hw	F0	2500	2.27(0.19)	3.58(0.25)	3.36(0.57)	0.72(0.12)	3.1(2.2)
Hw	F1	500	8.06(1.21)	9.92(1.15)	122.99(36.89)	5.58(0.70)	8.2(3.7)
Hw	F1	1500	5.92(1.01)	7.75(1.02)	53.62(17.17)	8.10(1.02)	6.3(6.1)
Hw	F1	2500	5.95(1.35)	7.57(1.60)	49.39(21.08)	12.07(1.39)	2.3(2.7)
HA Sites:							
Cw	F0	500	5.85(1.24)	8.03(1.14)	70.32(32.12)	3.25(0.41)	5.5(4.7)
Cw	F0	1500	5.08(0.84)	6.98(0.73)	37.46(12.73)	5.85(0.76)	1.6(1.3)
Cw	F0	2500	4.23(1.75)	6.50(1.59)	31.12(25.88)	7.29(0.92)	1.6(1.3)
Cw	F1	500	7.29(0.99)	8.89(0.71)	135.68(53.60)	6.11(0.76)	7.4(8.1)
Cw	F1	1500	7.66(1.17)	8.91(1.17)	133.03(49.16)	20.29(2.40)	3.5(4.5)
Cw	F1	2500	7.27(0.78)	8.82(0.75)	105.47(30.75)	25.42(3.01)	3.1(2.9)
Hw	F0	500	7.65(1.99)	9.73(1.82)	103.56(57.20)	4.87(0.58)	5.5(2.7)
Hw	F0	1500	7.12(2.67)	9.07(2.54)	79.23(54.00)	11.40(1.26)	7.0(6.6
Hw	F0	2500	7.04(3.45)	8.68(3.06)	65.73(53.25)	14.89(1.68)	7.42(5.6)
Hw	F1	500	9.65(0.63)	10.97(0.54)	236.56(42.21)	9.60(1.05)	16.4(13.6)
Hw	F1	1500	11.68(0.73)	12.54(0.42)	227.31(31.84)	31.51(3.33)	12.9(9.0)
Hw	F1	2500	11.61(1.16)	12.98(1.50)	159.06(36.11)	36.39(3.65)	8.6(0.9)

Fert.=Fertilization, Cw = Western Redredcedar, Hw = Western Hemlock; F0 = Unfertilized, F1 = Fertilized

Table 2.2. Average annual tree height, leading-height and BA growth rates for the 1997 – 2002 period; average annual stand BA growth rate (standard errors in brackets).

Species	Fertilization	Planting Density (Stems/ha)	Average Height Growth (m/yr)	Leading Height Growth (m/yr)	Tree Basal Area Growth (cm^2/year)	Stand Basal Area Growth (m^2/year)
CH Sites:						
Cw	F0	500	0.39(0.05)	0.53(0.06)	7.96(2.59)	0.39(0.12)
Cw	F0	1500	0.31(0.04)	0.42(0.04)	3.85(1.48)	0.61(0.23)
Cw	F0	2500	0.24(0.04)	0.37(0.05)	2.58(0.59)	0.65(0.15)
Cw	F1	500	0.48(0.04)	0.56(0.03)	16.91(3.00)	0.79(0.14)
Cw	F1	1500	0.39(0.05)	0.48(0.07)	9.99(2.81)	1.59(0.46)
Cw	F1	2500	0.37(0.07)	0.49(0.05)	6.23(2.55)	1.53(0.63)
Hw	F0	500	0.20(0.05)	0.37(0.10)	2.24(0.48)	0.10(0.02)
Hw	F0	1500	0.20(0.03)	0.34(0.10)	1.41(0.36)	0.21(0.06)
Hw	F0	2500	0.10(0.03)	0.29(0.04)	0.55(0.10)	0.12(0.04)
Hw	F1	500	0.53(0.12)	0.69(0.13)	15.62(4.42)	0.70(0.20)
Hw	F1	1500	0.33(.11)	0.47(0.13)	6.84(2.34)	1.02(0.38)
Hw	F1	2500	0.32(0.14)	0.45(0.17)	5.70(2.25)	1.39(0.56)
HA Sites:						
Cw	F0	500	0.35(0.06)	0.52(0.05)	8.86(3.53)	0.41(0.16)
Cw	F0	1500	0.32(0.07)	0.48(0.08)	4.76(1.44)	0.76(0.23)
Cw	F0	2500	0.21(0.15)	0.44(0.13)	3.77(2.98)	0.92(0.73)
Cw	F1	500	0.47(0.07)	0.57(0.07)	17.00(6.42)	0.76(0.26)
Cw	F1	1500	0.49(0.10)	0.57(0.10)	15.96(6.12)	2.40(0.88)
Cw	F1	2500	0.46(0.03)	0.59(0.03)	12.64(3.60)	3.01(0.81)
Hw	F0	500	0.46(0.12)	0.57(0.17)	12.44(6.44)	0.58(0.30)
Hw	F0	1500	0.43(0.23)	0.56(0.25)	8.88(5.99)	1.26(0.78)
Hw	F0	2500	0.44(0.27)	0.53(0.21)	7.53(5.72)	1.68(1.25)
Hw	F1	500	0.61(0.05)	0.72(0.09)	26.93(4.65)	1.05(0.12)
Hw	F1	1500	0.81(0.09)	0.89(0.10)	24.15(3.18)	3.33(0.61)
Hw	F1	2500	0.83(0.09)	0.95(0.11)	16.25(2.60)	3.65(0.60)

Cw = Western Redredcedar, Hw = Western Hemlock; F0 = Unfertilized, F1 = Fertilized

Table 2.3. Average foliar nutrient concentration of N, P, K, S and SO_4-S (standard errors in brackets).

Species	Fert.	Planting Density (Stems/ha)	N (%)	P (%)	K (%)	S (%)	SO_4-S (ppm)
CH Sites:							
Cw	F0	500	1.09(0.06)	0.15(0.01)	0.59(0.06)	0.10(0.01)	131.03(17.20)
Cw	F0	1500	0.97(0.04)	0.16(0.02)	0.53(0.04)	0.09(0.01)	117.05(27.03)
Cw	F0	2500	1.06(0.13)	0.15(0.02)	0.48(0.02)	0.09(0.00)	109.65(19.97)
Cw	F1	500	1.06(0.08)	0.17(0.01)	0.53(0.04)	0.10(0.00)	149.35(25.35)
Cw	F1	1500	0.97(0.11)	0.16(0.01)	0.46(0.06)	0.09(0.01)	133.44(23.01)
Cw	F1	2500	0.98(0.03)	0.16(0.01)	0.46(0.10)	0.09(0.01)	145.50(29.25)
Hw	F0	500	0.79(0.07)	0.09(0.02)	0.62(0.10)	0.08(0.01)	240.00(56.27)
Hw	F0	1500	0.76(0.02)	0.11(0.03)	0.68(0.08)	0.08(0.01)	265.86(66.76)
Hw	F0	2500	0.78(0.05)	0.10(0.01)	0.66(0.04)	0.09(0.01)	309.94(44.16)
Hw	F1	500	0.78(0.02)	0.19(0.02)	0.63(0.11)	0.08(0.00)	243.85(39.41)
Hw	F1	1500	0.71(0.05)	0.18(0.03)	0.61(0.04)	0.08(0.00)	273.01(56.28)
Hw	F1	2500	0.74(0.09)	0.20(0.04)	0.58(0.04)	0.08(0.00)	255.20(40.05)
HA Sites:							
Cw	F0	500	1.02(0.06)	0.16(0.03)	0.47(0.08)	0.09(0.00)	145.95(21.95)
Cw	F0	1500	1.02(0.02)	0.16(0.01)	0.50(0.04)	0.09(0.01)	129.68(22.40)
Cw	F0	2500	0.99(0.06)	0.17(0.01)	0.55(0.07)	0.09(0.01)	148.11(25.75)
Cw	F1	500	1.11(0.12)	0.18(0.02)	0.41(0.08)	0.09(0.01)	125.67(49.44)
Cw	F1	1500	1.18(0.15)	0.18(0.01)	0.51(0.03)	0.09(0.01)	109.92(47.99)
Cw	F1	2500	1.12(0.05)	0.19(0.02)	0.50(0.06)	0.09(0.01)	100.59(27.69)
Hw	F0	500	0.92(0.11)	0.11(0.01)	0.65(0.10)	0.10(0.02)	261.76(73.01)
Hw	F0	1500	0.86(0.15)	0.09(0.01)	0.56(0.04)	0.10(0.01)	290.36(32.10)
Hw	F0	2500	0.92(0.19)	0.10(0.02)	0.54(0.09)	0.10(0.02)	257.87(65.28)
Hw	F1	500	0.79(0.04)	0.19(0.04)	0.55(0.04)	0.08(0.00)	171.11(52.90)
Hw	F1	1500	1.01(0.04)	0.18(0.02)	0.47(0.03)	0.10(0.01)	196.41(38.99)
Hw	F1	2500	1.06(0.09)	0.18(0.05)	0.49(0.14)	0.11(0.01)	276.79(47.92)

Fert.=Fertilization, Cw = Western Redredcedar, Hw = Western Hemlock; F0 = Unfertilized, F1 = Fertilized

Table 2.3 (cont.). Average foliar nutrient concentration of Ca, Mg, Fe, Cu and Zn.

Species	Fert.	Planting Density (Stems/ha)	Ca (%)	Mg (%)	Fe (ppm)	Cu (ppm)	Zn (ppm)
CH Sites:							
Cw	F0	500	0.73(0.10)	0.13(0.01)	40.51(12.77)	3.38(0.27)	12.29(0.66)
Cw	F0	1500	0.69(0.05)	0.13(0.01)	37.82(4.47)	3.37(0.65)	12.69(1.04)
Cw	F0	2500	0.71(0.07)	0.13(0.01)	33.77(2.77)	3.24(0.77)	10.81(1.59)
Cw	F1	500	0.79(0.08)	0.13(0.01)	45.99(10.10)	3.39(0.30)	13.26(1.36)
Cw	F1	1500	0.85(0.09)	0.11(0.01)	33.54(2.64)	3.62(0.81)	12.21(1.80)
Cw	F1	2500	0.86(0.09)	0.12(0.02)	29.34(5.32)	3.47(0.31)	12.80(1.13)
Hw	F0	500	0.24(0.02)	0.09(0.01)	45.37(13.75)	12.98(10.76)	9.08(3.10)
Hw	F0	1500	0.22(0.02)	0.08(0.01)	38.84(6.91)	5.16(2.79)	6.85(0.85)
Hw	F0	2500	0.23(0.03)	0.08(0.01)	40.22(7.48)	3.51(0.52)	6.36(0.88)
Hw	F1	500	0.25(0.04)	0.09(0.00)	49.33(14.99)	25.72(40.39)	11.82(10.50)
Hw	F1	1500	0.24(0.05)	0.11(0.02)	37.63(10.06)	3.89(1.23)	6.35(1.54)
Hw	F1	2500	0.27(0.06)	0.11(0.02)	37.68(6.42)	3.64(0.40)	6.76(0.72)
HA Sites:							
Cw	F0	500	0.83(0.05)	0.11(0.02)	37.68(6.22)	4.04(0.93)	12.12(2.12)
Cw	F0	1500	0.83(0.13)	0.13(0.01)	44.40(9.24)	3.36(0.26)	12.64(0.68)
Cw	F0	2500	0.86(0.10)	0.12(0.00)	41.66(13.51)	3.36(0.27)	12.76(0.45)
Cw	F1	500	1.05(0.07)	0.11(0.02)	36.34(8.01)	3.64(0.28)	12.92(0.36)
Cw	F1	1500	0.98(0.09)	0.11(0.01)	43.32(9.70)	4.61(0.71)	15.05(2.87)
Cw	F1	2500	0.99(0.05)	0.12(0.01)	37.84(11.72)	4.59(0.73)	14.32(2.17)
Hw	F0	500	0.22(0.03)	0.09(0.01)	46.85(9.30)	4.69(2.04)	6.64(1.04)
Hw	F0	1500	0.22(0.04)	0.09(0.02)	40.28(8.45)	4.93(2.89)	7.28(1.70)
Hw	F0	2500	0.29(0.11)	0.09(0.03)	42.84(9.83)	4.80(2.40)	7.79(2.35)
Hw	F1	500	0.23(0.05)	0.12(0.01)	42.72(8.53)	3.50(0.90)	5.82(1.38)
Hw	F1	1500	0.42(0.11)	0.12(0.04)	40.21(5.00)	5.97(2.90)	9.20(1.02)
Hw	F1	2500	0.44(0.12)	0.11(0.01)	41.78(14.75)	4.18(0.73)	9.13(2.68)

Fert.=Fertilization, Cw = Western Redredcedar, Hw = Western Hemlock; F0 = Unfertilized, F1 = Fertilized

Table 2.3 (cont.). Average foliar nutrient concentration of Mn, Al and B.

Species	Fertilization	Planting Density (Stems/ha)	Mn (ppm)	Al (ppm)	B (ppm)
CH Sites:					
Cw	F0	500	337.37(115.41)	38.49(3.90)	9.72(0.55)
Cw	F0	1500	254.24(62.81)	40.50(6.41)	9.98(1.13)
Cw	F0	2500	494.42(109.46)	40.51(6.53)	9.27(0.46)
Cw	F1	500	318.45(114.12)	38.57(13.74)	10.21(0.94)
Cw	F1	1500	385.52(270.53)	48.26(6.23)	10.18(0.21)
Cw	F1	2500	270.99(46.05)	30.00(3.96)	9.97(1.04)
Hw	F0	500	2375.31(391.13)	281.75(99.05)	25.07(2.78)
Hw	F0	1500	2143.26(599.01)	260.06(78.87)	24.58(3.56)
Hw	F0	2500	2408.74(290.92)	194.79(21.82)	24.34(0.92)
Hw	F1	500	2049.31(315.28)	360.07(99.75)	22.78(1.56)
Hw	F1	1500	1718.70(584.23)	260.84(55.53)	23.65(3.27)
Hw	F1	2500	1768.04(666.87)	290.73(59.14)	22.78(2.18)
HA Sites:					
Cw	F0	500	324.85(112.56)	36.33(10.48)	10.95(1.43)
Cw	F0	1500	405.32(131.26)	38.35(7.82)	10.22(0.96)
Cw	F0	2500	264.84(73.84)	32.24(0.23)	9.55(0.97)
Cw	F1	500	439.86(127.05)	36.36(8.13)	11.87(1.40)
Cw	F1	1500	319.87(84.92)	40.63(6.51)	12.53(2.71)
Cw	F1	2500	343.00(84.91)	34.47(8.00)	12.98(3.45)
Hw	F0	500	1854.21(738.32)	370.83(54.04)	20.96(3.03)
Hw	F0	1500	1763.33(523.27)	281.00(61.17)	21.88(3.46)
Hw	F0	2500	2229.50(254.59)	284.02(85.41)	19.71(5.21)
Hw	F1	500	1354.56(323.68)	396.98(84.47)	19.94(3.63)
Hw	F1	1500	2067.60(454.04)	456.91(115.09)	17.99(3.18)
Hw	F1	2500	1660.90(440.12)	391.98(75.63)	15.16(1.15)

Cw = Western Redredcedar, Hw = Western Hemlock; F0 = Unfertilized, F1 = Fertilized height of redcedar. Increasing establishment density reduced average height on CH sites, with significant differences existing between each establishment density (Table A1.1

Fertilization increased average tree basal area on HA sites (Tables 2.1 and A1.6). Increasing establishment density significantly reduced basal area of trees on HA sites, with trees established at 2500 sph significantly smaller than those established at 1500 and 500 sph (Table A1.6). No difference in basal area existed between 1500 and 500-sph treatments on HA sites (Table A1.6).

Significant species x establishment density x fertilization and species x fertilization interactions for average tree basal area on CH sites indicated that hemlock basal area tended to be most reduced by increasing density and that it responded more strongly to fertilization, compared to redcedar (Table A1.5). No differences in average basal area of trees existed between redcedar and hemlock at the three establishment density levels on fertilized CH sites (Table A1.5).

2.3.2 Stand Basal Area and Mortality

Fertilization increased stand basal area on HA sites (Tables 2.1, A1.8). Stand basal area tended to be increased by establishment density on HA sites. Stands established at 500 sph had significantly less basal area than those planted at either 1500 or 2500 sph. However, no significant differences in stand basal area existed between 1500 and 250-sph treatments. Hemlock stands had significantly greater basal area than redcedar stands on HA sites.

Treatment and species effects on stand basal area were more complex on CH sites (Table 2.1, A1.8). Species x fertilization and species x establishment density x fertilization interactions were both significant on CH sites. These interactions indicated that unfertilized redcedar had significantly greater stand basal area than unfertilized hemlock but fertilization increased growth of hemlock more than growth of redcedar and eliminated species differences in stand basal area. Further, while increased establishment density tended not to result in significantly different stand basal area in unfertilized hemlock stands, increasing establishment density did increase stand basal area of redcedar in unfertilized areas. Fertilization combined with increased density resulted in increased site occupancy for both species but this increase was greater for hemlock than for redcedar.

Cumulative morality differed by species on CH sites with hemlock experiencing significantly greater mortality than redcedar (Tables 2.1, A1.10). A similar pattern, with hemlock having greater mortality than redcedar, was evident on HA sites. Mortality was increased by fertilization on HA sites but was not significantly influenced by increasing establishment density. Mortality was therefore not related to establishment density. Clustered mortality also suggested that root pathogens may be a factor, especially on HA sites. Armillaria root rot was positively identified in the local area where the study site was located (personal communication, D. Mogensen, North Island Area Forester, Western Forest Products Inc.).

2.3.3 Recent (1997 – 2002) Growth Rates

Average annual height growth rate of stands on HA sites was significantly increased by fertilization (Tables 2.2 and A1.2). Average annual height growth rate of hemlock was significantly greater than that of redcedar on HA sites (Tables 2.2 and A1.2).

Significant species x fertilization interactions existed for average annual height growth rate on CH sites and average leading height growth rates on both CH and HA sites (Tables A1.2 and A1.4). In the case of average annual height growth rate on CH sites, redcedar grew at a greater rate than hemlock on unfertilized sites but hemlock responded more strongly to fertilization and no differences existed between the species for annual height growth rate on fertilized sites (Table A1.2). In the case of annual leading height growth rate on CH sites, no differences existed between growth rates in unfertilized stands but hemlock responded to fertilization and redcedar did not. The result was that no differences existed between unfertilized redcedar and fertilized stand of both species in terms of leading height growth rate (Table A1.4). In the case of leading height growth rate on HA sites, only hemlock responded to fertilization. The result was that no differences existed between unfertilized stands and fertilized redcedar, while fertilized hemlock had significantly greater annual leading height growth rate on HA sites (Table A1.4).

Significant establishment density effects were present for average height and leading height growth rates on CH sites (Tables A1.2 and A1.4). In both cases, establishment density reduced growth rates with stands established at the 500-sph treatment having greater growth rates than the 1500 and 2500-sph treatments, between which no differences existed (Tables A1.2 and A1.4).

On HA sites, tree and stand basal area growth rates were increased by fertilization compared to unfertilized stands (Tables A1.7 and A1.9). Average annual tree and stand basal area growth rates of hemlock were significantly greater than those of redcedar on HA sites (Tables A1.7 and A1.9).

Establishment density decreased basal area growth rates of trees on HA sites, the 500-sph treatment having significantly greater growth rate than the 2500-sph treatment. No differences existing between the 1500-sph treatment and either other establishment density levels (Table A1.7). Establishment density also reduced basal area growth rates of trees on CH sites with significant differences existing between all three establishment density levels (Table A1.7). Establishment density increased stand basal area growth rates on both CH and HA sites with growth rates in the 2500 and 1500-sph treatments significantly exceeding those in the 500-sph treatments. No differences existed between the 2500 and 1500-sph treatments for stand basal area growth rate (Table A1.9).

Significant species x fertilization interactions existed for both tree and stand basal area growth rates on CH sites (Tables A1.7 and A1.9). In both cases, growth rates of redcedar were greater than hemlock on unfertilized sites but fertilization increased growth rates of hemlock more than those of redcedar with the result that no species differences existed for tree and stand basal area growth rates on fertilized CH sites.

2.3.4 Foliar Nutrient Concentrations Ten Years After Fertilization

Fertilization increased foliar concentration of N and Zn on HA sites but did not influence foliar concentrations of these nutrients on CH sites (Tables 2.3, A1.11 and A1.20). Fertilization increased the foliar concentrations of P on CH sites (Tables 2.3 and A1.12). Foliar concentration of K decreased after fertilization on both sites. Fertilization did not influence foliar nutrient concentrations of S or Fe on either site or on concentration of B on HA sites (Tables 2.3, A1.14, A1.18 and A1.23).

Foliar nutrient concentrations varied with establishment density in the case of N and Fe on CH sites and Zn on HA sites. Foliar concentration of N was least in the 1500-sph treatment on CH sites and did not differ between the 500- and 2500-sph establishment densities. Concentration of Fe was significantly greatest in the 500-sph treatment and did not differ between the 1500- and 2500-sph treatments on CH sites. Concentration of Zn was significantly least in the 500-sph treatment and did not differ between the 1500- and 2500-sph treatments on HA sites.

Foliar concentrations of N were greater in redcedar than in hemlock on both sites (Tables 2.3 and A1.11). Foliar concentrations of K, SO_4-S and Al were significantly greater in hemlock than in redcedar on CH sites (Tables 2.3, A1.13, A1.15 and A1.22). Concentrations of Fe, Mn and B were greater in hemlock than in redcedar on HA sites (Tables 2.3, A1.18, A1.21 and A1.23).

Significant species x fertilization interactions were present on both sites. On CH sites, foliar concentrations of Mn and B in were lower in fertilized compared to unfertilized hemlock, while foliar concentrations of these nutrients were not influenced by fertilization in redcedar stands and were lower than concentrations in hemlock (Tables 2.3, A1.21 and A1.23). Ca concentration was greater in redcedar than in hemlock on CH site and fertilization increased Ca concentration in redcedar on CH sites but did not influence concentration in hemlock (Tables 2.3 and A1.16). Fertilization increased foliar Mg concentration in hemlock on both CH and HA sites but did not influence concentration in redcedar. Mg concentration was greater in redcedar than in hemlock on CH sites (Tables 2.3 and A1.17). On HA sites, unfertilized redcedar had greater foliar concentration of P but fertilization increased P concentration more in hemlock than in redcedar and eliminated species differences (Tables 2.3 and A1.12). Fertilization increased foliar concentration of Al on HA sites but did not affect concentration in redcedar. Al concentration was lower in redcedar than in hemlock on HA sites (Tables 2.3 and A1.22).

Significant species x establishment density interactions existed on both sites. On HA sites, redcedar established at 500 sph had significantly the lowest K concentration and differed significantly from hemlock at 500 sph, which had the highest foliar K concentration (Tables 2.3 and A1.13). Foliar Ca concentration in redcedar did not vary with establishment density on HA sites but Ca concentration increased with density in hemlock stands (Tables 2.3 and A1.16). On CH sites, redcedar established at 500 sph had significantly greater foliar S concentration than hemlock at all densities (Tables 2.3 and A1.14).

A significant species x establishment density x fertilization interaction was present on HA sites for foliar SO_4-S concentration. Fertilization did not increase foliar SO_4-S concentration in redcedar and decreased concentration in hemlock. However, foliar SO_4-S concentrations in hemlock stands tended to increase with establishment density when stands were fertilized (Tables 2.3 and A1.15).

2.3.5 Growth – Foliar Nutrient Concentration Relationships

Average annual height growth rate in redcedar for the 1997 – 2002 period on both CH and HA sites combined was significantly correlated with foliar nutrient concentrations of N, P, S, Ca, Zn, Cu and B (Table A1.24). Average annual height growth rate in hemlock was significantly and positively correlated with foliar concentrations of N, P, S, Ca, Mg and Zn for CH and HA sites combined and significantly negatively correlated with concentrations of K, Mn and B. On CH sites only, redcedar height growth was significantly correlated with concentrations of N, P, S, Zn, B and SO_4-S. Hemlock growth was correlated with concentrations of P and Al and negatively correlated with B concentration on CH sites. On HA sites, redcedar height growth was correlated with concentrations of N, S, Ca, Mg, Zn, Al and B. Hw growth on HA sites was correlated with concentrations of N, P, S, Ca, Mg, Zn and Al and negatively correlated with K and B concentrations.

2.3.6 Salal Biomass

Average biomass of salal is summarized in Table 2.4. Salal biomass was significantly increased (Table A1.25) by fertilization but was not significantly influenced by establishment density of the overstory. Although average salal biomass tended to be greater at lower establishment densities, high variability prevented significant test results for establishment densities.

Table 2.4. Salal Biomass and Standard Error.

Fertilization	Establishment Density (stems/ha)	Salal Biomass (g/plot)	Standard Error
F0	500	402.7	218.44
F0	1500	318.3	47.4
F0	2500	300.3	99.2
F1	500	899.3	376.5
F1	1500	791.9	80.1
F1	2500	820.0	220.5

2.4 Discussion

Results of this study confirm earlier observations from this trial regarding the positive influence of fertilization on tree and stand growth. They also document fertilizer-enhanced growth of redcedar and hemlock on CH and HA sites up to 10 years after treatment. Growth of dominant trees (leading-height individuals) documented in this study support the results of Bennett *et al.* (2003) who earlier found increased growth of hemlock arising from fertilizer application on CH sites. These results expand on those of Bennett *et al.* (2003) by showing that redcedar and hemlock growth was increased by fertilization on both CH and HA sites 10 years after treatment. Hemlock mortality was significantly greater than that of redcedar on both sites. Fertilization increased mortality in other studies (e.g. Yang 1998) and significantly increase mortality on hemlock stands on HA sites in this study but not on CH sites. Increased mortality associated with fertilization may have resulted from interactions with suspected root pathogens on HA sites, although this is speculative.

That tree and stand growth continued to be promoted by fertilization 10 years after treatment is suggested by net significant increases in 1997 – 2002 periodic growth rates in fertilized stands; the significant correlations between foliar P and 1997 – 2002 periodic growth on both sites and between foliar N and periodic growth on HA sites; greater foliar P concentration in fertilized stands on both sites and greater foliar N concentration on HA sites. However, it is possible that growth may have ceased to be greater in fertilized compared to non-fertilized stands towards the end of the 1997 – 2002 period. Continued increased growth of fertilized stands is consistent with results showing elevated growth rates from a single application for up to 30 years (Nohrstedt 2001, Jandl *et al.* 2002). A mechanism for continued growth following fertilization on CH sites is likely elevated nutrient supply rate. A single application of fertilizer containing N and P elevated soil supply of available N and P on CH sites 10 - 13 years after treatment (Bradley *et al.*2000, Bennett *et al.* 2003). Fertilization also resulted in significantly increased growth and foliar P concentration of dominant hemlock compared to unfertilized stands (Bennett *et al.* 2003). The lack of fertilization effect on foliar N concentration and continued elevation of foliar P in this study suggests that N availability is no longer elevated on fertilized CH sites but higher P availability persists. However, the generally greater correlation between foliar P concentration and growth than between foliar N and growth suggests that P may be the more limiting resource on CH sites. In contrast, the closer correlation between foliar N concentration and growth rate suggests that N may be the more limiting nutrient on HA sites. Foliar concentration of fertilizer-applied ^{15}N did not exceed that of unfertilized foliage 6 years after fertilization of CH sites (Chang and Preston 2000). Increased foliar N and P concentrations on fertilized HA sites and significant correlations between N and P foliar concentrations and tree growth suggests that availability of N and P may also be elevated by fertilization on HA sites. Increased foliar concentrations of SO_4-S, Ca, Mg, Zn, Al and B on fertilized CH or HA sites suggest an indirect fertilizer effect on the cycling or availability of these nutrients. Otchere-Boateng and Ballard (1981) found that urea fertilizer increased leaching of Cu, Zn, Fe, Mn and Al in forest soils and thus increased their availability for plant uptake. Kranabetter *et al.* (2003) noted that foliar nutrient concentrations increased proportionally with the availability of N. Foliar nutrient concentration of N, P, K, S, Ca, Mg, Zn, Cu, Fe and B all fell within the range of those reported for redcedar and hemlock on similar sites (Weetman *et al.* 1989, Kranabetter *et al.* 2003). Foliar concentrations of N and P indicated: moderate to severe deficiencies for both redcedar and hemlock on both CH and HA sites; adequate P nutrition for redcedar growth on both fertilized and unfertilized treatments on both sites and; moderate P deficiencies in unfertilized hemlock stands on both sites with adequate to slightly deficient levels in fertilized hemlock treatments (Carter 1992). Foliar concentrations of K, Ca and Mg were considered adequate for growth of redcedar and hemlock in fertilized and unfertilized treatments on both CH and HA sites (Carter 1992).

Density effects on foliar nutrient concentrations may reflect varying overstory influence on the understory plant community, through increased shading. Salal competition reduced N and P supply available for tree growth (Weetman *et al.* 1989, Chang and Preston 2000); however, its influence on the availability of other nutrients is undocumented. Understory vegetation has been demonstrated to significantly facilitate and influence the biogeochemical cycling of nutrients elsewhere in conifer-dominated ecosystems of British Columbia with a high ericaceous plant component in the understory (Yarie 1980).

Increased growth in fertilized stands may also be the result of a change in stand structure or function that results in greater photosynthetic capacity. This change in structure or function may be achieved through increased proportional growth of foliage, higher foliage growth efficiency or greater efficiency per unit of resource acquired. Fertilization may increase stand growth by increasing: biomass allocation to foliage; total foliage biomass or leaf area; increasing foliar efficiency and; light interception and use efficiency (Brix 1981, Brix 1983, Barclay *et al.* 1986, Vose and Allen 1988, Gower *et al.* 1993, Valinger 1993, Albaugh *et al.* 1998, Balster and Marshall 2000). Any tendency for fertilization to increase biomass allocation to foliage may be negated by environmental conditions, such as low or excess soil moisture, which affect the ability of individual trees to support proportionally more foliage and increased growth associated with fertilization does not necessarily result from increased biomass allocation to foliage (Gower *et al.* 1993, King *et al.* 1999, Retzlaff *et al.* 2001). On CH sites, superior growth of lodgepole pine compared to Sitka spruce (*Picea sitchensis* (Bong.) Carr.) has been attributed to greater nutrient use efficiency by the pine (Bothwell *et al* 2001) and a similar difference in nutrient use efficiency may explain growth differences between redcedar an hemlock on CH and HA sites. The effects of nutritional status, fertilization and density on biomass allocation and resource use efficiency in redcedar and hemlock have not previously been documented but will be explored in subsequent chapters of this thesis.

The generally stronger growth response of hemlock than redcedar to fertilizer application may be explained by species rooting characteristics. Redcedar tends to root more deeply within the soil profile than hemlock (Bennett *et al.* 2002, Wang *et al.* 2002). This may give hemlock an initial advantage in acquiring surface-applied fertilizer nutrients. It may also explain the declining growth of the denser plantings of hemlock on CH sites with time as nutrients of fertilizer origin are incorporated into biomass of trees, understory vegetation and leaked to soil pools, thus becoming more limiting. Growth begins to slow because the hemlock cannot access nutrients located deeper in the soil profile, whereas redcedar, with its ability to root and access nutrient pools deeper in the soil, does not experience such an apparent decline in growth. The greater flood tolerance of redcedar (Krajina *et al.* 1982) may also partly explain its generally greater growth on CH sites, which experience fluctuating water tables. The ability to tolerate saturated soils may allow redcedar to access nutrients deeper in saturated soils than can hemlock.

Establishment density affected growth on CH sites but the effect has generally been weakly expressed on HA sites. Total tree size and growth increments show consistent declines with increasing density on CH sites. On HA sites, only average tree basal area was influenced by increasing establishment density. These observations are likely explained by the inherently lower soil nutrient supply capacity of CH sites versus HA sites (Weetman *et al.* 1990, Prescott *et al.* 1996). On CH sites, higher planting densities would reduce the smaller pool of available soil nutrients sooner than lower densities. Greater nutrient availability on HA sites has minimized density stress and allowed competition to only weakly develop. The similarity of density effect on height and top-height increment on CH sites suggests that stands there are not differentiating as a result of density and competition is therefore symmetric (Weiner 1985, 1986, Lieffers and Titus 1989). Symmetric competition develops in response to limitations in soil resources (Weiner 1985, 1986, Lieffers and Titus 1989, Nambiar and Sands 1993) and is likely to occur sooner in denser plantings because the aggregate nutrient demand of the stand is greater than in less dense stands. Establishment density reduced tree size development and resulted in symmetric competition in other studies (e.g. Nilsson 1994).

Salal growth was increased by fertilization but was not influenced by stand density. Lack of overstory density influence on salal growth may have resulted because overstory crowns may not have closed to the same degree as those reported by Bennett *et al.* (2003), where stem densities were greater (> 3000 sph).

2.5 Conclusion

Fertilizer applied 10 years previously increased stand and tree growth and likely continued to positively influence growth of redcedar and hemlock on both CH and HA sites to the end of the experimental period.

Competition resulting from density stress developed on the relatively nutrient-poor CH sites but was less pronounced on the relatively more nutrient-medium HA sites. Mortality was greater for hemlock than for redcedar was not influenced by establishment density. The similarity of leading-height and average- height growth trajectories suggests that fertilization did not promote asymmetric competition on these sites.

On CH sites, unfertilized redcedar had greater growth than unfertilized hemlock. Fertilization resulted in greater growth response in hemlock and eliminated species differences in tree size, incremental growth and site occupancy on CH sites. Hemlock had greater growth than redcedar under both unfertilized and fertilized conditions on HA sites.

Fertilization increased foliar nutrient concentrations of P on both CH and HA sites and of N on HA sites. Foliar concentrations of nutrients not applied in the fertilizer were also affected by fertilization. Generally, redcedar had greater foliar concentrations of macronutrients, Ca and Mg, except for K, which was greater in hemlock. Growth was positively correlated with foliar concentrations of both N and P. However, growth tended to be more closely correlated with P concentration on CH sites and more closely correlated with N concentration on HA sites.

Fertilization increased salal growth comparable to increases in tree growth. Increasing stand establishment density did not affect salal biomass development on CH sites.

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Chapter 3

Aboveground Biomass Growth and Partitioning in Juvenile Western Redcedar and Western Hemlock Plantations

3.1 Introduction

A better understanding of the factors that control forest productivity, and how these factors may be influenced by silvicultural practices, is necessary to enable managers to balance wood production with environmental concerns in forest management (Velazquez-Martinez *et al.* 1992, Albaugh *et al.* 1998). Recent desire to conserve non-timber forest values has resulted in a reduction in size of the land base available for commercial forestry in coastal British Columbia. Therefore, wood production on the remaining operable land base must increase, in order to maintain current levels of annual allowable cut. Fertilization and establishment density both have the potential to increase stand and site productivity. Greater understanding of the mechanisms by which these silvicultural practices influence stand growth will allow them to be more effectively employed in forest management. Increased understanding of stand growth processes will also enhance our knowledge of other ecological processes.

The concept that site productivity or quality is a fixed quantity (Miller 1981) has given way to an understanding that site quality is a function of resource availability and that site nutrients and their supply rates can be manipulated (Albaugh *et al.* 1998, Bennett *et al.* 2003). Fertilization increases growth of trees and stands by increasing nutrient availability (Weetman *et al.* 1989, Bennett *et al.* 2003); although this effect can last up to 30 years, most of the additional growth occurs within 10 years of treatment (Binkley and Reid 1984, Nohrstedt 2001, Jandl *et al.* 2002). Fertilization influences stand structure; increasing total biomass, biomass components and biomass allocation patterns i.e. the proportional amount of biomass in stems, branches and foliage. Fertilization has been noted to significantly increase total tree size and aboveground stem, branch and foliage biomass components in loblolly pine (*Pinus taeda* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), red pine (*Pinus resinosa* Ait.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Scots pine (*Pinus sylvestris* L.) (Gower *et al.* 1993, Valinger 1993, Gillespie *et al.* 1994, McWilliams and Therien 1996, Albaugh *et al.* 1998, Retzlaff *et al.* 2001) and stand leaf area in Douglas-fir and loblolly pine (Vose 1988, Vose and Allen 1988, Velazquez-Martinez *et al.* 1992, Albaugh *et al.* 1998, Balster and Marshall 2000). Increased foliage biomass or leaf area resulting from fertilization was associated with increased tree and stand growth of Douglas-fir, loblolly pine and Scots pine (Brix 1983, Vose and Allen 1988, Valinger 1993, 2000 Albaugh *et al.* 1998, Balster and Marshall 2000).

As trees increase in size the proportional amount of perennating structures, such as stems, large woody roots and branches, have been shown to increase and the amount of more ephemeral tissue, such as fine roots and foliage, to decrease (Brix 1983, Barclay *et al.* 1986, Gower *et al.* 1993, King *et al.* 1999, Retzlaff *et al.* 2001). The proportional size relationship, or allometry, between different biomass components is influenced by site conditions, including soil resource availability, and may be altered by fertilization (Gower *et al.* 1993, King *et al.* 1999). Increased proportional allocation to foliage biomass occurred in ponderosa and red pine after two years of fertilization and after four years of fertilization and irrigation in loblolly pine (Gower *et al.* 1993). In another study, however, fertilization did not increase proportional allocation to foliage biomass in loblolly pine following either four years of annual fertilization and irrigation or five years of annual fertilization (King *et al.* 1999, Retzlaff *et al.* 2001). Foliage growth rates increased for four years after a single fertilizer application in Douglas-fir but declined to unfertilized control levels after seven years (Brix 1983). Changes to allometry resulted in increased allocation to branch biomass but did not alter allocation to stem components or foliage in Douglas-fir nine years after fertilization (Barclay *et al.* 1986). Total stand foliage biomass was not increased by fertilization nine years post-treatment (Mitchell *et al.* 1996). Environmental factors that reduce needle longevity or the site's ability to support foliage, such as water availability, may also affect the size and duration of changes in biomass allocation patterns in response to fertilization and their duration (Gower *et al.* 1993). In summary, fertilization can increase tree size and stand growth in the long term by increasing the amount of foliage in stands but studies show that proportional allocation to foliage has not been increased longer than four years post-treatment.

Competition has been shown to alter biomass allocation at the stand level due to reductions in tree size and changes in proportional allocation associated with size. Competitive status and extreme stocking densities may also alter allometry patterns to favour stem biomass and height. Average height and diameter growth of Norway spruce (*Picea abies* (L.) Karst.) decreased with increasing establishment density but height and diameter allocation patterns were unaffected (Nilsson 1994). Naturally regenerated stands of black spruce (*Picea mariana* (Mill.) B.S. P.) increased stand-level allocation to foliage and decreased stem and branch biomass proportions with increasing density stress and commensurately decreasing tree size (Newton and Jolliffe 1993). Loblolly pine (*Pinus taeda* L.) in lower or suppressed canopy positions allocated proportionally more biomass to its stems and less to foliage, possibly in an effort to gain height and increased access to light, compared to dominant trees in upper canopy positions (Naidu *et al.* 1998). Scots pine in a subordinate lower crown position had a higher priority of allocation to stems than to foliage, compared to trees in upper crown positions (Nilsson and Albrektson 1993, Vanninnen and Makela 2000). Scots pine in very dense stands (more than18 000 stems per ha) allocated proportionally more biomass to stem wood and less to foliage than did trees in sparse stands.

Competition influences the structure of plant populations but interactions between site resource availability and competition in forest stands are not well understood. Symmetric or two-sided competition for soil resources is thought to limit growth of individuals in proportion to their size and reduce differentiation within stands (Newton 1990, Nambiar and Sands 1993, Schwinning and Weiner 1998). Asymmetric or one-sided competition for light is thought to limit the growth of smaller individuals more than that of larger individuals and increase differentiation within stands (Weiner 1990, Newton and Jolliffe 1998, Schwinning and Weiner 1998). However, competition among neighbours exists on a continuum between one- and two-sided modes, and the dominant mode is determined by site conditions (Weiner 1990, Schwinning and Weiner 1998). Asymmetric competition may also be two-sided with differentiation accompanied by a general reduction in tree size (Brand and Magnussen 1988). The dominant mode of competition may vary with stage of stand development (Larocque and Marshall 1993). Sites with greater nutrient availability and growth potential may allow asymmetric competition to develop sooner and more severely than sites with lower growth potential (Goldberg and Barton 1992, Grime 2001). Conversely, site growth potential may not affect competition (Tilman 1988), possibly because decreased competition for soil resources on more productive sites is offset by increased competition for light

(Wilson and Tilman 1993) or because levels of herbivory may change with site growth potential, effectively altering competitive relations (Gurevitch *et al.* 2000). Increased site 'stockability' or resource supply in the Hawaiian Islands delayed the onset of competition in loblolly pine stands of similar stocking compared to sites of lower resource availability in the south-eastern United States (DeBell *et al* 1989). Increased site resource supply prevented or reduced both symmetric and asymmetric competition and consequent differentiation of Scots pine, loblolly pine and tamarack (*Larix laricina* (Du Roi) K. Koch) stands by increasing the growth rate of subordinate size classes more than that of larger size classes (MacDonald and Yin 1999, Nilsson *et al.* 2002, Sarkkola *et al.* 2003). Competition affects tree and stand biomass allocation patterns, but effects differ depending on species and mode of competition (Newton and Jolliffe 1993, Naidu *et al.* 1998). Identification of symmetric competition in commercial stands may be used as a prescriptive tool indicating the need for fertilization to maintain growth and encourage stand differentiation.

Application of N and P fertilizer has been shown to improve stem growth of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red redcedar *(Thuja plicata* Donn*)* on CH and HA sites (Weetman *et al.* 1989, Bennett *et al.* 2003, Chapter 2), however, the influence of fertilization and establishment density on stand-level biomass allocation patterns for hemlock and redcedar on CH and HA sites are undocumented. Examination of the influence of fertilization and establishment density on biomass allocation and competition in redcedar and hemlock stands is poorly documented.

A study was initiated in a 14-year-old silvicultural trial to examine the influence of fertilization and establishment density on biomass structure and competition development in juvenile western red redcedar and western hemlock stands on CH and HA sites. Foliage and stem wood biomass components are of particular interest because foliage abundance is closely associated with stand growth and wood is the intended commercial product of these stands. The objectives of this study were to determine how fertilization and establishment density, singly and in combination, influenced total and component biomass development in stands, whether competition had developed in these stands, and how competition was related to site productivity. Based on previous studies it was hypothesized that: 1) tree-level biomass allocation pattern will not be influenced by either fertilization or density; 2) stand, component and tree biomasses will be increased by fertilization; 3) increasing establishment density will increase stand and component biomasses but decrease individual tree biomass; 4) fertilization will shift stand-level biomass allocation to wood, while increasing establishment density will shift stand-level allocation to foliage biomass; 5) fertilization will promote biomass development, shift stand-level allocation to stem wood and decrease competition; 6) competition will develop more strongly on less productive CH sites and have more influence on stand structure; 7) no species differences will exist between redcedar and hemlock in terms of fertilization and establishment density effects on biomass development, proportional biomass allocation and competition.

3.2 Materials and Methods

3.2.1 Study Sites

The study site was located on northern Vancouver Island, British Columbia, Canada, between Port Hardy and Port McNeill (50° 60'N, 127° 35' W) in the Submontane Very Wet Maritime variant of the Coastal Western Hemlock Biogeoclimatic, or CWHvm1, zone (Green and Klinka 1994). The site was approximately 50m ASL in undulating terrain with frequent rocky knolls and wetlands located in depressions. Surface materials consist of unconsolidated glacial moraine and fluvial outwash deposits that range from over 1m in depth to shallow with exposed bedrock. Mineral soils ranged from silty clay loams to fine sand with high coarse fragment content. Organic soils of wetland or upland origin are also common within the study site.

The area receives approximately 1900 mm of precipitation annually, most of which falls as rain. Growing season soil moisture deficits typically do not occur (Lewis 1982). Average daily mean temperature ranges from 3.3° C in January to 14.1° C in August. A relatively high percentage of the annual solar radiation is received as diffuse radiation (McKay and Morris 1985), reflecting overcast conditions throughout the year and frequent summer fog. Direct sunlight exposure ranges from 1.5 h/day in December to 6.4 h/day in July. Global solar radiation incident of a horizontal surface averages 10.212 MJ/m^2 per day and ranges from a low of 2.043 MJ/m^2 per day in December to 18.935 MJ/m^2 per day in July (McKay and Morris 1985).

Two common CWHvm1 forest types were examined at the study site. Hemlock Amabilis Fir (HA) types are occupied by stands composed of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) while Redcedar Hemlock (CH) types are occupied by stand composed of western red redcedar (*Thuja plicata* Donn) and western hemlock. Both forest types are typically found on well to imperfectly drained Duric Humo-Ferric Podzols and are considered zonal sites (Lewis 1982, Green and Klinka 1994). HA sites typically occur on areas that have historically been subject to stand-replacing wind throw events (Lewis 1982). HA stands are mid-seral and have a dense, even-aged structure with uniform canopies. Due to the dense canopy cover, HA stands have poorly developed understory vegetation layers. Surface organic layers in HA stands are comparatively thin (5 – 10 cm) and friable. CH stands likely represent a climatic climax state, with an uneven-aged structure and open, irregular canopies. CH stands typically have well developed understory plant communities dominated by dense salal (*Gaultheria shallon* Pursh) growth. Surface organic layers in CH stands are thicker (10 – 45 cm) and more compact than on HA sites. Soil nutrient availability is lower on CH sites than on HA sites (Prescott *et al* 1996).

The study site was clear-cut logged in 1986, broadcast burned and planted with western hemlock and western red redcedar in 1987.

3.2.2 Treatments

Ninety-six treatment plots, each containing 64 sample trees were established in 1987. Plot size and tree spacing varied with density. Treatments consisted of a fully crossed factorial combination with two levels of fertility (fertilized and unfertilized) and three levels of density (500, 1500 and 2500 stems per ha). Trees in the 500 sph plots were planted 4.5 m apart, resulting in a central (core) measurement area of 36 x 36 m and a total plot size of 54 x 54 m, including a buffer zone. The 1500-sph treatments had a tree spacing of 2.6 m, a core measurement area of 21 x 21 m and a total area plot size of 32 x 32 m. Between tree spacing was 2 m in the 2500-sph treatments, with a 16 x 16 m core measurement area and total plot size of 36 x 36 m.

Fertilized plots were received a 60 g dressing of Nutricoat™ controlled-release fertilizer at time of planting. The fertilizer was raked into a 15 cm radius areas around each seedling, provided 10 g of N, 2.5 g of P and 5 g of K to each seedling. Total application rated per ha varied with density. All fertilized plots were refertilized before the beginning of the growing season in 1993 with a broadcast application of 225 kg of N and 100 kg of P per ha.

The 2 x 3 combination of fertilizer/no-fertilizer by densities was duplicated for each of redcedar and hemlock on both CH and HA sites. Each fertilization-density-species combination was randomly assigned within four blocks on each site, with a single treatment level replicate per block. Thus, a total of 48 plots examined 12 treatments with 4 replications per treatment level.

Height and diameter of each sample tree within core measurement areas were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997 and 2002. Height was recorded to the nearest cm. Diameter was measured in mm at the root collar for the years 1988 – 1997. Diameter was measured at 1.3 m above the root collar (breast height) in 1997 and 2002.

3.2.3 Biomass Determination

Regression equations were developed to predict individual tree total biomass and biomass of foliage, branch, bark and wood components. Saplings were destructively sampled after growth had ceased in the fall of 2001 and 2002. Saplings were selected from buffer areas to represent the existing size range within treatment levels based on measurements at breast height. Both redcedar and hemlock were sampled from across the range of treatment levels on both sites. Sample trees were selected using a two-stage process. In the first stage, several sample trees were initially selected using a random procedure within each treatment level. Diameter at breast height was measured for all neighbouring trees within a 4.3 m radius of randomly selected trees to establish a size range for the treatment level. In the second stage, sample trees were selected to span the size range determined in the first stage. Sample trees were selected to be free of significant stem and crown damage. Sample trees were felled and their height and diameter at breast height were measured. Stems were then cut into 1 m segments and branches removed by severing at the point of branch contact with the stem section. Total fresh biomass of the stem section and the branches was then determined to the nearest 50 g. A 3-cm-wide disk was subsampled from each stem section. These subsamples were removed approximately 30 cm from the bottom of each stem section such that they were located within the tree beginning at 30 cm from the root collar and thence at 100 cm intervals up the stem, with an additional section extracted where the stem narrowed to a diameter of 1 cm. The portion of the stem above this point was designated the terminal and analyzed separately as a branch. Two or three undamaged branches were randomly sub sampled from each section. In some cases, no branches could be sampled from the bottom stem section, as no living branches were present. Dead branches were discarded and not included in calculations. Stem disks and branch sub samples were removed to a lab facility in Port McNeill for further analysis.

Dry biomass conversion factors were determined for stem wood, stem bark, branch foliage and woody branch components (twig) for each section of each sample tree. In the lab, bark was manually stripped from each stem section and branches were dissected into manageable-sized segments. Fresh biomass of each of the components was determined to the nearest 0.01 g. Bark, stem wood components and dissected branches were dried at 70^0C for 72 hours, or until they ceased to lose biomass. Foliage components were separated from woody branch components by shaking and stripping. Dry biomass of bark, wood, foliage and twig components was measured to the nearest 0.01g. Dry biomass conversion factors for each section were determined as:

$$\textit{proportional dry biomass (foliage or twig)} = \frac{\textit{dry biomass of foliage or twig}}{\textit{fresh biomass of branch}}$$

$$\textit{proportional dry biomass (wood or bark)} = \frac{\textit{dry biomass of wood or bark}}{\textit{fresh biomass of stem section}}$$

Foliage and twig conversion factors were averaged for each section. Total component dry biomass was determined for each section by multiplying fresh biomass of the stem and branches by respective conversion factors. Total section dry biomass was determined by summing all components. Total and component dry biomasses for each sample tree were determined by summing section-level values.

Initial analysis of sample tree data in 2001 indicated greater variability between component biomasses in redcedar compared to hemlock. Consequently, a total of 84 redcedar saplings were destructively sampled compared to 41 for hemlock. Due to the greater variability among biomass components of redcedar, it was assumed that if biomass allocation patterns were influenced at the tree level, this was more likely to be observed in redcedar. In order to examine assumptions regarding the influence of density and fertility level on biomass allocation, the 2002 redcedar sampling was balanced across nine fertility-density combinations. Fertility level included unfertilized CH, fertilized CH and fertilized HA. It was reasoned that sampling from these three levels would include the full range of nutrient availability regimes available at the installation. Each of the three tree establishment density levels was sampled from each fertility level. Eight redcedar saplings were sampled from each fertility-density combination.

Covariate analysis, described more fully below, indicated that neither fertility level nor establishment density significantly affected within-tree biomass allocation patterns in redcedar. Consequently, all sample trees were combined to produce a single set of prediction equations for each species, rather than a separate set of equations for each fertility-density combination.

3.2.4 Biomass Prediction Equations

Predictive equations from total and component biomass were developed based on tree diameter and height as predictive variables. Both diameter at breast height squared (d^2) and height multiplied by d^2 (d^2h) were investigated as predictor variables. Two regression models commonly used for biomass estimation were examined: a second degree polynomial model using weighted least squares regression (1) and an allometric model using ordinary least squared regression on logarithmically transformed data (2):

$$Y_{ij} = \beta_{0i} + \beta_{1i}X_{1j} + \beta_{2i}X_{2j} + \varepsilon_{ij} \qquad [1]$$

Where Y_{ij} is the oven dry biomass (g) of the ith component (i is bark, stem wood, twig or foliage biomass) of the jth sample tree (j ranging from 1 to 84 for redcedar and 1 to 41 for hemlock); X_{1j} and X_{2j} are d^2 and $(d^2)^2$ or d2h and $(d^2h)^2$, respectively for the jth sample tree and β_{0i}, β_{1i}, and β_{2i} are parameters estimated by weighted least squares. Two weights were attempted: the inverse of the predictor variable ($1/d^2$ and $1/d^2h$) and the inverse of the predictor variable squared ($1/d^4$ and $1/d^2h)^2$). These weights were selected based on the pattern of variability in the predictor variables (variances proportional to the weight used).

The allometric model tested was:

$$\log_e Y_{ij} = \log_e \beta_{0i} + \log_e \beta_{1i}X_j + \log_e \varepsilon_{ij} \qquad [2]$$

where $\log_e \beta_{0i}$ and loge β_{1i} are parameters estimated by ordinary least squares regression on $\log_e$-transformed data for the ith component and $\log_e \varepsilon_{ij}$ is the residual term for the ith component.

Predictive models were assessed based on the proportion of biomass variation explained (r^2), the standard error of estimate for the regression (SE), residual plots, and a positive test for normality using the Shapiro-Wilks test. Model-fitting was conducted using the Statistical Analysis System (SAS), Version 8.2.

Results indicated that the allometric model [2] using d^2h as the predictor variable explained the greatest biomass variation, generally had the lowest SE and met the homogeneity of variance and normality assumptions of regression. Back-transformational bias was corrected according to Baskerville (1972). Final parameter estimates and regression statistics are presented in Table 3.1. Biomass models were used to predict biomass components for each tree based on the 2002 measurements.

Predictive equations (Table 3.1) were all significant (p <0.0001) with coefficients of determination ranging from a low of 0.813 for redcedar foliage to a high of 0.981 for redcedar wood.

3.2.5 Statistical Analysis

Covariate analysis was used to determine whether density and fertility treatments significantly influenced within-tree biomass allocation patterns. Total tree biomass and component biomasses were tested using diameter-squared x height (d^2h), a measure of tree size and the most significant predictor variable, as the covariate. Both covariate and dependent variables were $\log_e$-transformed for the analysis. This approach was used to test for allocational differences that were independent of tree size (King *et al.* 1999, Naidu *et al.* 1998, Gower *et al.* 1993).

Table 3.1 Biomass prediction equations and model statistics (allometric model).

Biomass Components	n	β_o	β_1	SE	*p*	r^2
Western Red Redcedar:						
Total Tree	82	-2.018	0.728	0.023	<.0001	0.958
Wood	82	-3.569	0.838	0.013	<.0001	0.981
Bark	82	-4.092	0.636	0.013	<.0001	0.968
Foliage	82	-2.478	0.566	0.073	<.0001	0.813
Branches	82	-3.274	0.719	0.091	<.0001	0.847
Western Hemlock:						
Total Tree	41	-1.883	0.732	0.131	<.0001	0.939
Wood	41	-3.081	0.808	0.064	<.0001	0.975
Bark	41	-4.496	0.713	0.145	<.0001	0.930
Foliage	41	-2.872	0.642	0.275	<.0001	0.850
Branches	41	-3.139	0.701	0.280	<.0001	0.869

A general linear model approach was used to examine the cumulative effect of treatments on stand-level biomass allocation after 14 years of stand development on each site. A mixed-effects was model used for each site type with species, fertilization and density tested as fixed effects and blocks included as a random effect:

$$y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + (abc)_{ijk} + \varepsilon_{ijkl}$$

Where: y_{ijk} = Response of the *i*th species at the *j*th fertility level at the *k*th density level
μ = General Mean
a_i = Species Effect
b_j = Fertility Effect
c_k = Density Effect
ε_{ijkl} = Residual Error

Where interaction terms were significant, given significance of at least one constituent fixed effect, simple effects were compared by adjusting least-square means for Tukey's Honestly Significant Difference test. Where interactions were significant, density, fertilizer and species effects were examined together. Where interaction terms were not significant, simple effects were compared using Tukey's HSD test. For all tests a significance level of $p < 0.05$ was used. Using this approach, treatment effects were examined for stand biomass of wood, bark, branches and foliage; proportional biomass of wood, bark, branches and foliage and average tree biomass. Biomass variables were $\log_e$-transformed to homogenize variances. Total stand biomass was tested in a similar fashion but with the inclusion of terms for testing site influence and associated interactions.

Changes in the relative importance of density stress on the development of competition and biomass allocation within stands as site productivity increased was examined by regressing stand-level proportional biomasses and average tree size against establishment density for each species-site-fertility combination. A gradient of increasing site productivity was associated with increased site fertility status resulting from fertilization, or non-fertilization, combined with greater inherent nutrient supply on HA compared to CH sites. Average tree size was $\log_e$ -transformed for the analysis, to homogenize variances. Significance of the regressions and coefficients of determination were used to assess the presence and influence of competition on biomass structure of stands across a gradient of nutrient availability and growth potential from an extreme low on unfertilized CH sites to an extreme high on fertilized HA sites.

3.3 Results

Treatment means for stand biomass and biomass components are presented in Table 3.2. Average tree biomass and proportional stand biomass components are presented in Table 3.3. Analysis was performed on transformed variables but untransformed least-square means are presented in the statistical tables (Appendix 2).

3.3.1 Tree-Level Biomass Allocation in Redcedar

The covariate significantly ($p < 0.01$) predicted change in tree biomass and tree biomass components (Table A2.1). Tree biomass and biomass components were significantly related to the covariate (Table A2.2). Neither nutrient regime nor establishment density significantly influenced tree biomass or biomass components when adjusted for tree size.

These results support the hypothesis that biomass allocation in redcedar is not influenced by either fertilization or density stress.

3.3.2 Tree Biomass, Stand Biomass and Biomass Components

Tree biomass, stand biomass and biomass components were generally increased by fertilization and tended to be greater on HA compared to CH sites (Tables 3.2, 3.3, A2.3 – A3.12). The effect of establishment density on tree, stand and component biomasses was more complex but tended to be stronger on CH than on HA sites (Tables 3.2, 3.3, A2.3 – A3.12).

Significant interactions for site x species, site x fertilization, site x establishment density, species x fertilization and site x species x fertilization existed for total stand biomass (Tables 3.2 and A2.5). These interactions indicated that: hemlock stands on CH sites were least productive; fertilized hemlock stands on HA sites were most productive; unfertilized redcedar stands were equally productive on both CH and HA sites; fertilized stands on CH sites, fertilized redcedar on HA and unfertilized hemlock on HA stands were all equally productive; fertilization increased the productivity of both species but increased hemlock productivity more than that of redcedar and; productivity of stands established at 2500 and 1500 sph did not differ and were significantly greater than the 5000-sph treatment (Table A4.5).

On HA sites, average tree biomass and component biomasses (wood, bark, branches and foliage) were greater for hemlock than for redcedar (Tables 3.2, 3.3, A2.4, A2.6, A2.9 and A2.12). Fertilization increased average tree and component biomasses on HA sites, compared to unfertilized stands (Tables 3.2, 3.3, A2.4, A2.6, A2.9 and A2.12). Increasing establishment density did not significantly affect average tree biomass or foliage and wood biomass components on HA sites, but significantly increased bark and twig biomasses of stands. Bark and twig biomasses were significantly higher at 2500 sph and 1500 sph than at 500-sph on HA sites but there was no significant difference between the 1500 and 2500 sph treatments (Tables 3.2, 3.3, A2.4, A2.6, A2.9 and A2.12).

Table 3.2 Means of stand biomass and biomass components with standard errors in brackets.

Species	Fert.	Planting Density (Stems/ha)	Stem Wood (t/ha)	Stem Bark (t/ha)	Branches (t/ha)	Foliage (t/ha)	Stand (t/ha)
CH Sites:							
Cw	F0	500	2.12(0.68)	0.35(0.09)	1.33(0.38)	1.10(0.25)	4.92(1.41)
Cw	F0	1500	3.41(1.47)	0.66(0.22)	2.37(0.87)	2.25(0.63)	8.71(3.25)
Cw	F0	2500	3.66(0.73)	0.78(0.13)	2.68(0.49)	2.74(0.43)	9.83(1.81)
Cw	F1	500	5.04(1.03)	0.69(0.11)	2.85(0.51)	2.03(0.28)	10.66(1.92)
Cw	F1	1500	11.86(3.61)	1.77(0.43)	7.05(1.88)	5.35(1.15)	26.22(7.08)
Cw	F1	2500	10.56(4.77)	1.75(0.68)	6.68(2.78)	5.56(1.98)	24.74(10.35)
Hw	F0	500	0.78(0.24)	0.12(0.03)	0.43(0.12)	0.41(0.10)	1.75(0.49)
Hw	F0	1500	1.39(0.52)	0.23(0.08)	0.84(0.28)	0.86(0.26)	3.35(1.15)
Hw	F0	2500	0.72(0.18)	0.13(0.03)	0.49(0.11)	0.54(0.12)	1.89(0.44)
Hw	F1	500	6.96(2.37)	0.84(0.26)	2.99(0.92)	2.53(0.72)	13.18(4.17)
Hw	F1	1500	9.44(3.57)	1.25(0.44)	4.52(1.58)	4.06(1.35)	19.31(6.92)
Hw	F1	2500	14.52(7.86)	1.94(0.93)	7.00(3.30)	6.31(2.73)	29.83(14.68)
HA Sites:							
Cw	F0	500	2.79(1.40)	0.42(0.18)	1.66(0.76)	1.28(0.50)	6.18(2.84)
Cw	F0	1500	4.89(1.99)	0.86(0.28)	3.21(1.16)	2.82(0.83)	11.85(4.32)
Cw	F0	2500	6.17(6.18)	1.07(0.89)	3.99(3.61)	3.46(2.62)	14.74(13.44)
Cw	F1	500	5.31(2.03)	0.70(0.22)	2.94(1.00)	2.03(0.56)	10.99(3.76)
Cw	F1	1500	18.31(6.97)	2.42(0.73)	10.12(3.41)	6.99(1.89)	37.87(12.87)
Cw	F1	2500	22.74(6.64)	3.18(0.74)	13.02(3.36)	9.42(1.94)	48.59(12.65)
Hw	F0	500	6.32(3.97)	0.76(0.44)	2.71(1.54)	2.30(1.22)	11.95(7.00)
Hw	F0	1500	15.05(11.04)	1.86(1.24)	6.65(4.39)	5.73(3.53)	29.09(19.82)
Hw	F0	2500	21.06(19.38)	2.61(2.23)	9.34(7.92)	8.06(6.48)	40.80(35.50)
Hw	F1	500	11.90(1.69)	1.34(0.18)	4.74(0.63)	3.84(0.49)	21.38(2.87)
Hw	F1	1500	45.69(7.95)	5.08(0.82)	17.94(2.88)	14.41(2.21)	81.24(13.36)
Hw	F1	2500	56.64(14.78)	6.48(1.52)	23.00(5.30)	18.84(4.02)	103.13(24.70)

Cw = Redcedar, Hw = Hemlock, Fert. = Fertilization; F0 = Unfertilized, F1-= Fertilized

Table 3.3 Means of biomass component proportion of total stand biomass and average tree biomass with standard errors in brackets.

Species	Fert.	Planting Density (sph)	Stem Wood (%)	Stem Bark (%)	Branches (%)	Foliage (%)	Tree Biomass (kg)
CH Sites:							
Cw	F0	500	42.57(2.07)	7.11(0.30)	27.00(0.10)	22.66(1.83)	10.10(2.98)
Cw	F0	1500	38.52(2.08)	7.72(0.34)	27.20(0.11)	26.43(2.14)	5.50(2.09)
Cw	F0	2500	37.16(0.62)	7.95(0.12)	27.28(0.04)	27.96(0.78)	3.99(0.71)
Cw	F1	500	47.08(1.22)	6.51(0.14)	26.79(0.05)	19.14(0.78)	22.66(4.18)
Cw	F1	1500	44.93(1.57)	6.78(0.20)	26.88(0.07)	20.62(1.14)	16.50(4.34)
Cw	F1	2500	41.91(2.48)	7.21(0.39)	27.03(0.13)	23.23(2.49)	10.09(4.12)
Hw	F0	500	44.34(1.24)	6.65(0.05)	24.39(0.28)	23.77(0.81)	3.89(0.96)
Hw	F0	1500	41.33(1.26)	6.77(0.05)	25.09(0.31)	25.78(0.92)	2.31(0.65)
Hw	F0	2500	38.15(0.62)	6.91(0.03)	25.93(0.17)	28.42(0.54)	0.89(0.13)
Hw	F1	500	52.38(1.78)	6.37(0.06)	22.75(0.33)	19.36(0.82)	29.07(9.15)
Hw	F1	1500	48.49(1.52)	6.49(0.06)	23.48(0.32)	21.25(0.85)	12.80(4.17)
Hw	F1	2500	47.92(2.10)	6.51(0.07)	23.60(0.42)	21.56(1.12)	12.20(5.92)
HA Sites:							
Cw	F0	500	44.16(2.98)	6.91(0.41)	26.93(0.14)	21.49(2.48)	13.39(5.93)
Cw	F0	1500	40.83(1.55)	7.36(0.24)	27.08(0.08)	24.17(1.48)	7.59(2.67)
Cw	F0	2500	39.45(3.60)	7.62(0.58)	27.17(0.19)	25.95(3.76)	6.29(5.28)
Cw	F1	500	47.77(2.42)	6.45(0.28)	26.76(0.11)	18.85(1.54)	24.34(9.00)
Cw	F1	1500	47.58(3.03)	6.47(0.36)	26.77(0.13)	18.95(2.00)	24.82(8.97)
Cw	F1	2500	46.39(2.17)	6.61(0.27)	26.82(0.10)	19.68(1.54)	20.16(5.55)
Hw	F0	500	51.58(2.85)	6.39(0.09)	22.91(0.53)	19.78(1.33)	25.40(14.59)
Hw	F0	1500	50.02(3.45)	6.45(0.12)	23.20(0.67)	20.55(1.73)	20.27(14.80)
Hw	F0	2500	48.54(4.94)	6.50(0.18)	23.52(1.02)	21.44(2.76)	17.99(15.46)
Hw	F1	500	55.61(0.908)	6.27(0.03)	22.19(0.15)	17.99(0.36)	52.55(8.78)
Hw	F1	1500	56.17(0.70)	6.25(0.02)	22.09(0.12)	17.77(0.27)	58.59(8.51)
Hw	F1	2500	54.69(1.28)	6.29(0.04)	22.34(0.22)	18.36(0.52)	45.08(10.49)

Cw = Redcedar, Hw = Hemlock, Fert. = Fertilization; F0 = Unfertilized, F1-= Fertilized

Significant species x fertilization and species x establishment density x fertilization interactions existed on CH sites for all biomass components and average tree biomass. These interactions indicated that for average tree biomass, stand foliage biomass and stand wood biomass indicated: increasing establishment density reduced average tree, stand foliage and stand wood biomasses; hemlock biomasses (average tree, stand foliage and stand wood) tended to be less than redcedar in unfertilized stands but equal in fertilized stands; that biomasses increased more in hemlock than in redcedar with fertilization and; that establishment density had a stronger influence on hemlock biomasses than on redcedar biomasses on unfertilized stands on CH sites (Tables A2.3, A2.7 and A2.11). For stand bark and branch biomasses, these interactions indicated that increasing stand density increased stand biomasses of bark and branches between the 500 and 1500-sph treatments but not between the 1500 and 2500-sph treatments (Tables A2.8 and A2.10). The results also indicated that redcedar stands had greater bark and branch biomasses than hemlock stands at a given density on unfertilized sites but fertilization increased biomasses more in hemlock than in redcedar and reduced species differences in branch and bark biomass on fertilized sites (Tables A2.8 and A2.10).

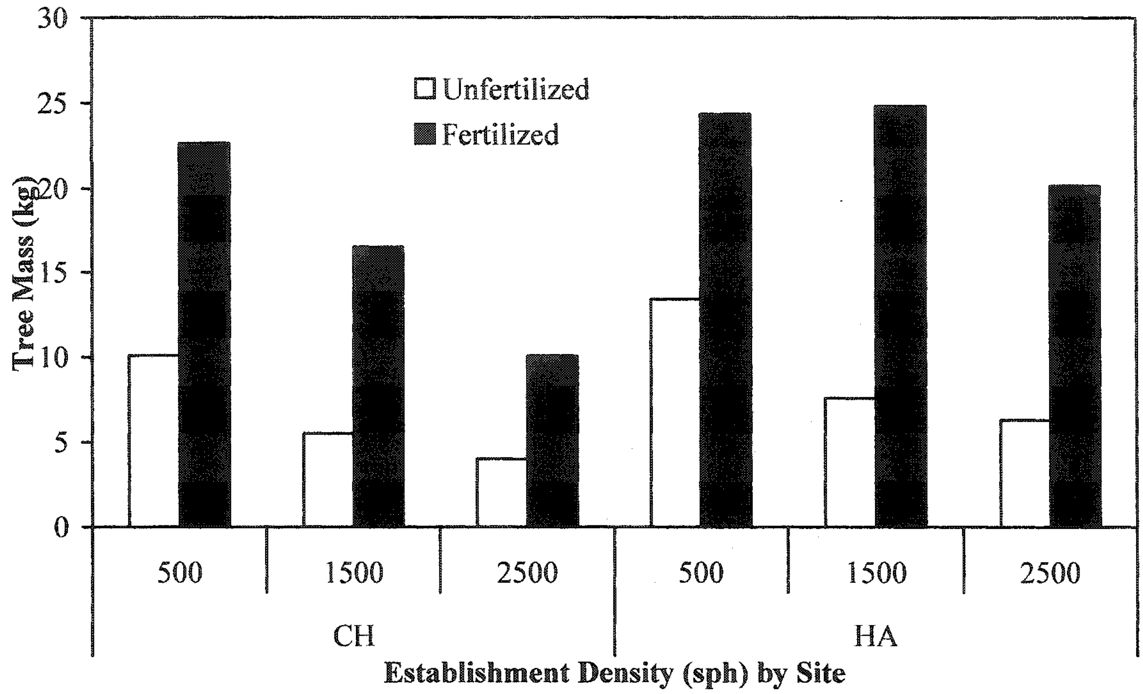
These results confirm the hypothesis that fertilization tends to increase stand and component biomasses. However, increasing establishment density did not always increase component biomasses: foliage and wood biomasses on unfertilized CH sites tended to decrease with increasing establishment density. This suggests that stand productivity could be limited by density stress on unfertilized CH sites. Results did not fully support the hypothesis that CH sites are less productive than HA sites: redcedar tended to be equally productive on both sites while hemlock was more productive on CH than on HA sites. Hemlock responded more strongly to fertilization than redcedar on CH sites, which did not support the hypothesis of no species effects.

3.3.3 Stand Biomass Proportions

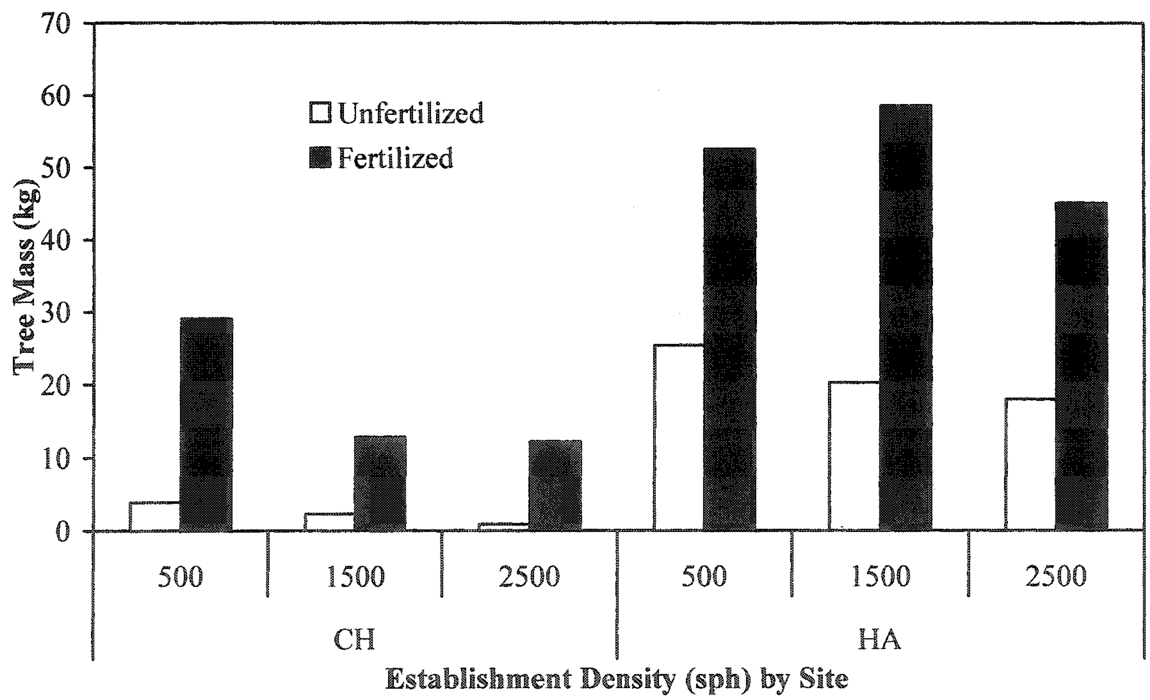
Fertilization generally led to proportionally less biomass in bark, foliage and branches and increased wood biomass. The effect of establishment density on stand biomass proportions was more variable but tended to be stronger on CH than on HA sites.

Significant species x fertilization interactions on CH sites indicated that fertilization reduced the proportion of bark biomass in redcedar more than in hemlock (Tables A2.13). Species x density interactions on CH sites indicated that increasing establishment density increased bark proportion more in redcedar than in hemlock and increased proportional branch biomass in hemlock but not in redcedar (Table A2.13).

Significant species x fertilization interactions on HA sites indicated that fertilization reduced bark biomass proportion in redcedar, while not affecting hemlock bark proportion, thereby reducing difference between the species (Table A2.14). A significant establishment density effect on HA sites indicated that the proportion of bark biomass increased with establishment density in stands but with significant differences existing only between the 500 and 2500-sph treatments (Table A2.14).

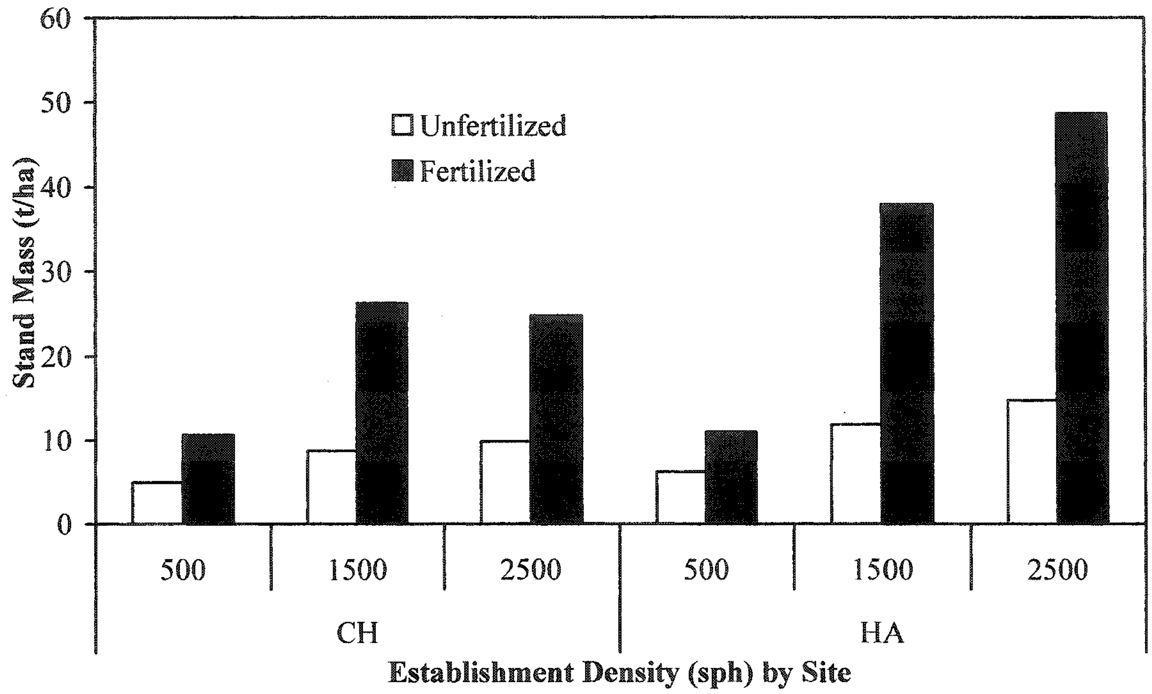


a)



b)

Figure 3.1. Average tree biomass of: a) western red redcedar and b) western hemlock.



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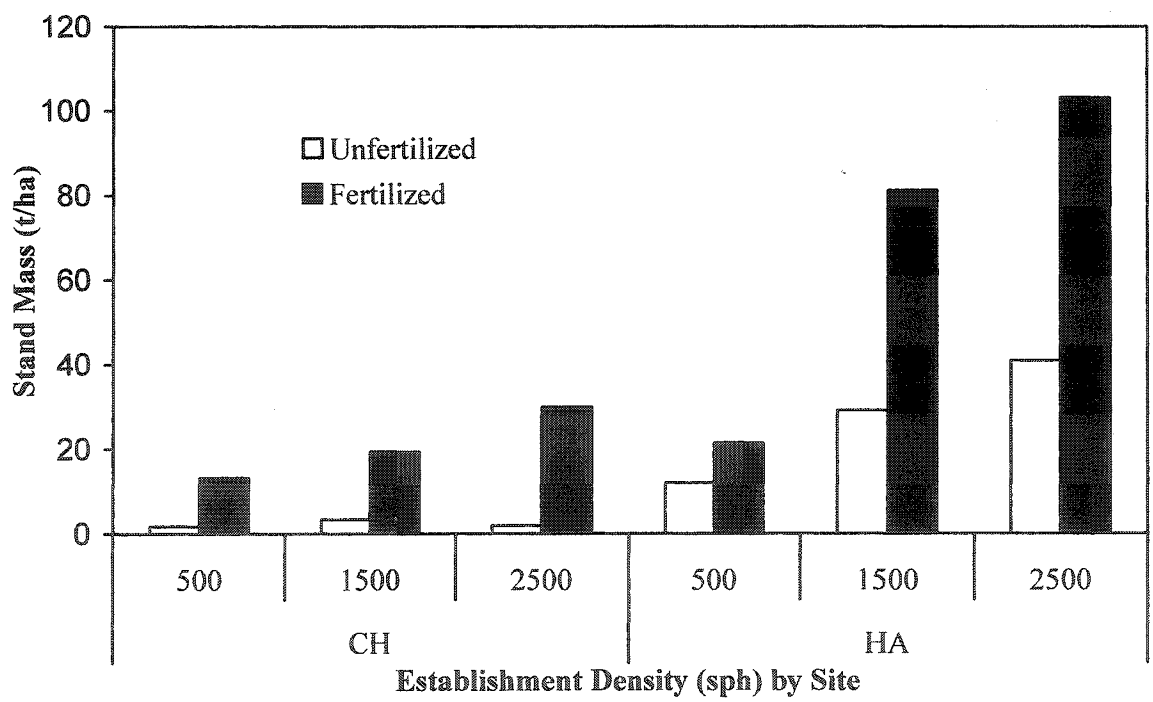
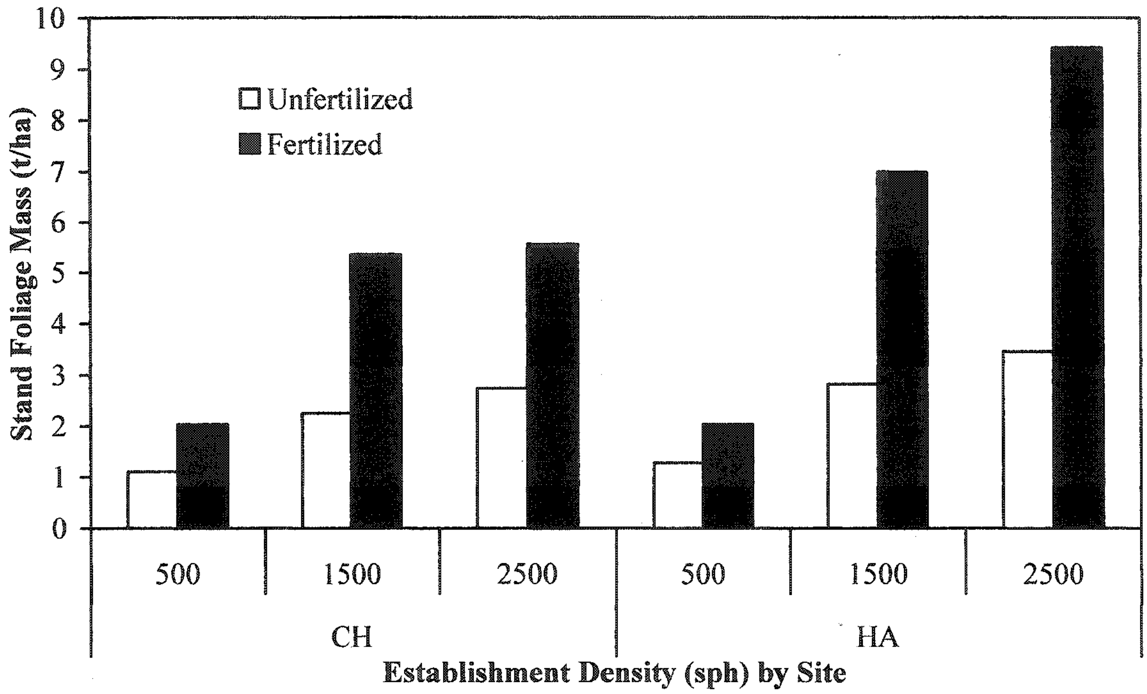
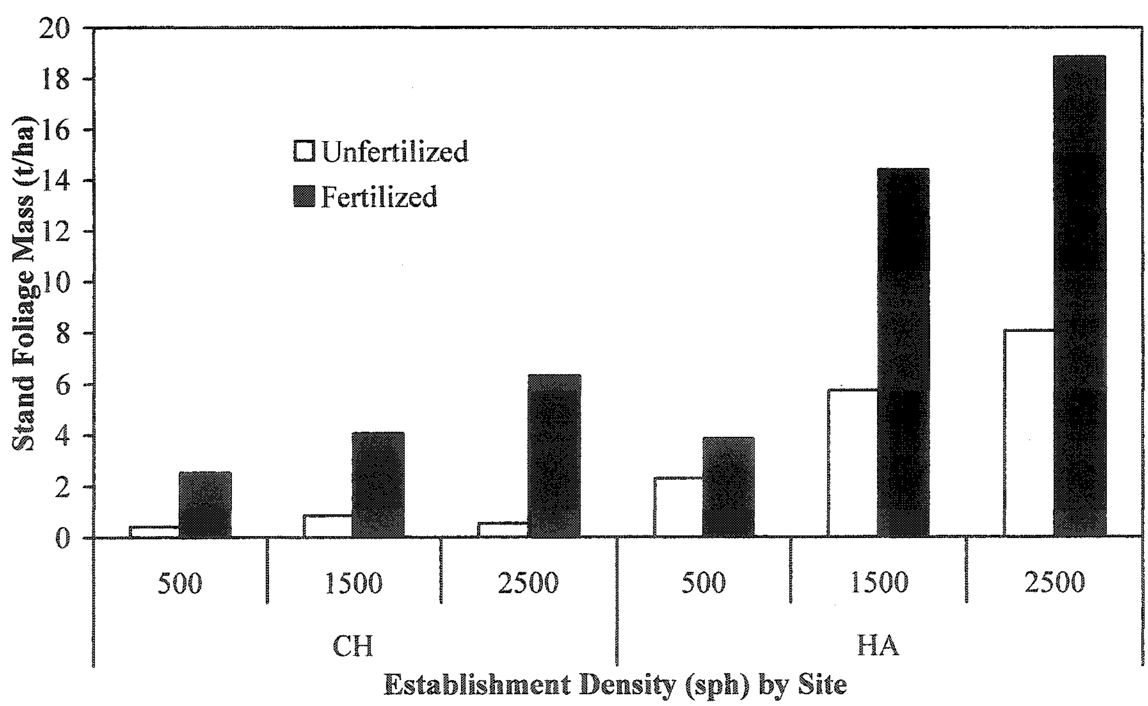


b)

Figure 3.2. Average stand biomass of: a) western red redcedar and b) western hemlock.

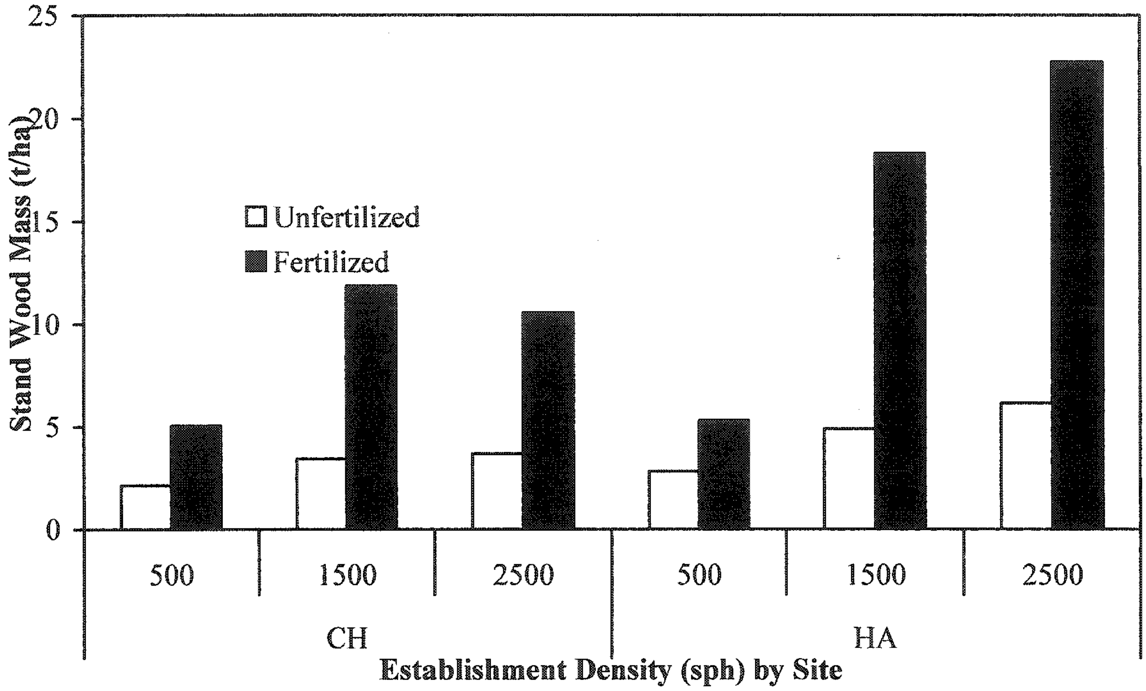


a)

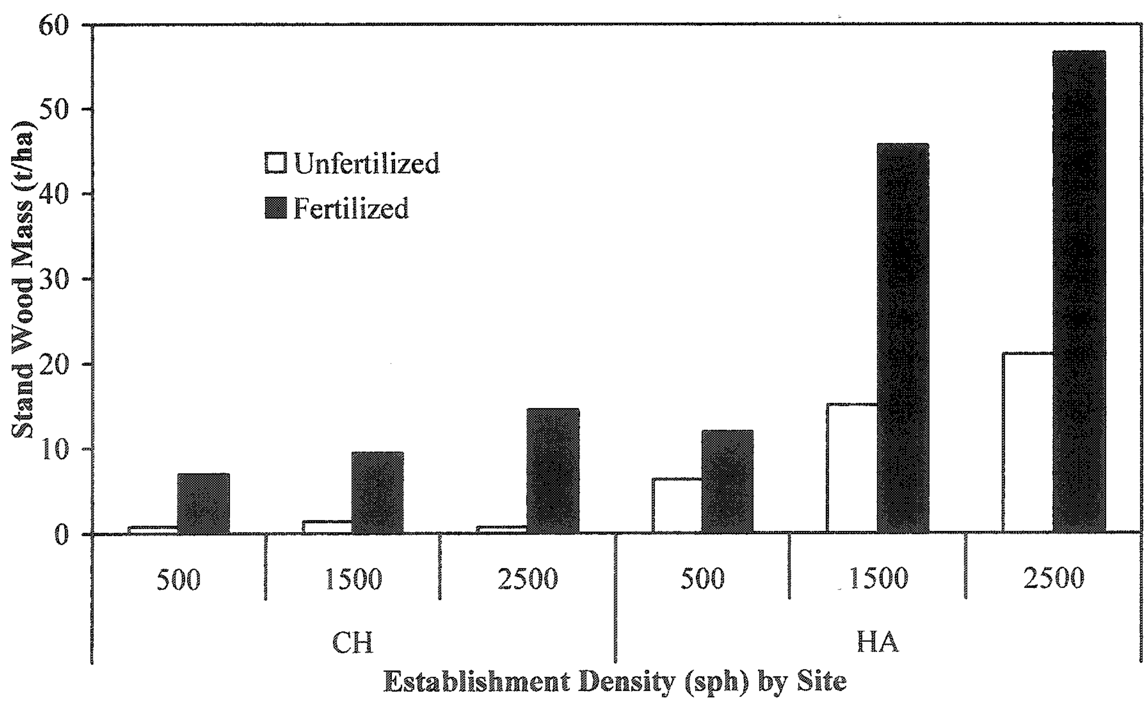


b)

Figure 3.3. Average stand foliage biomass of: a) western red redcedar and b) western hemlock.

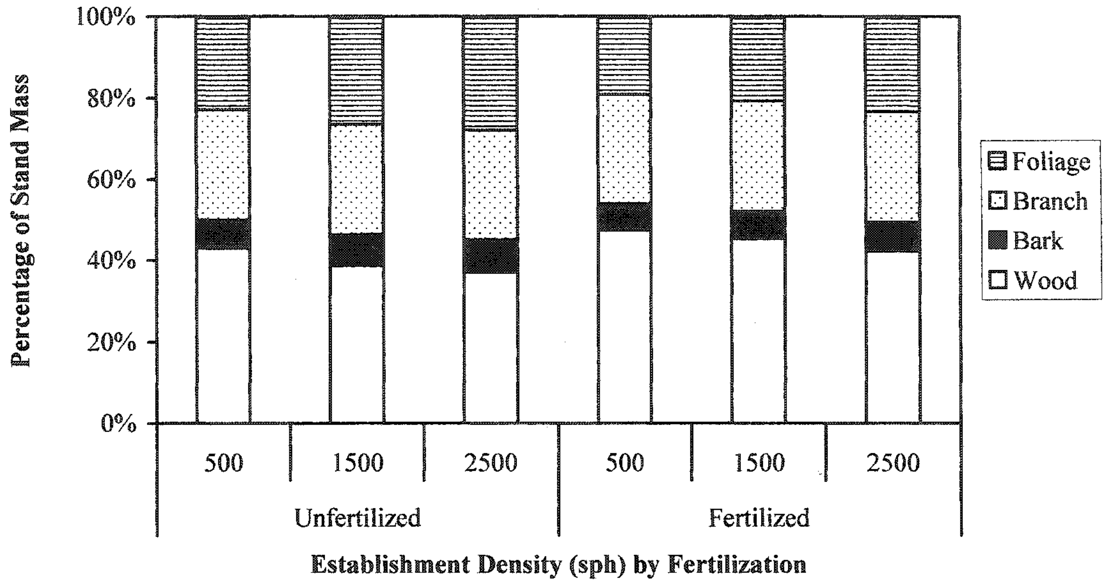


a)

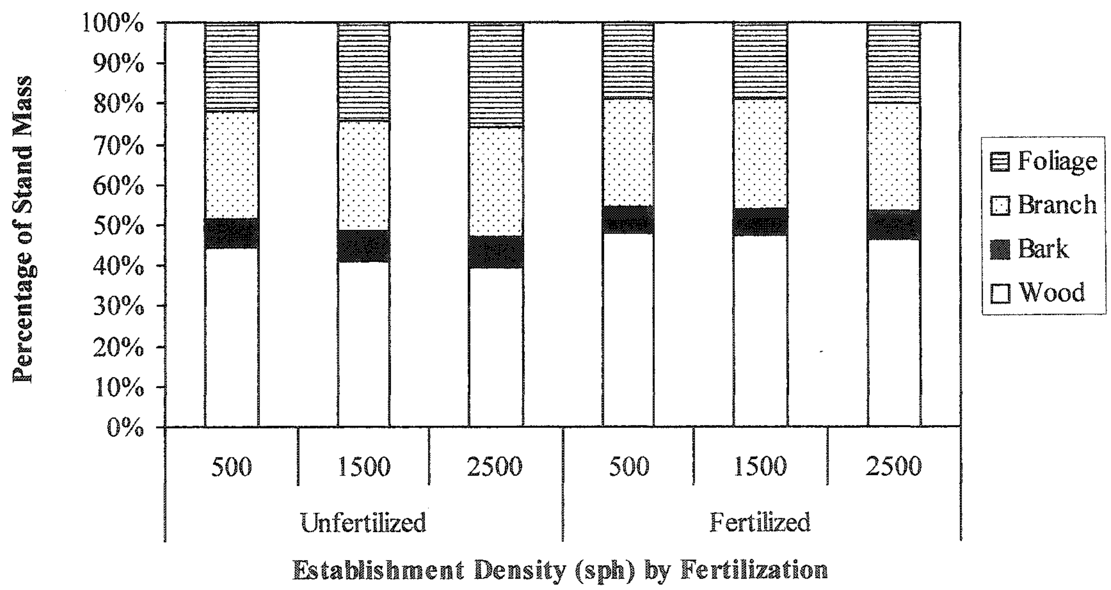


b)

Figure 3.4. Average stand wood biomass of: a) western red redcedar and b) western hemlock.

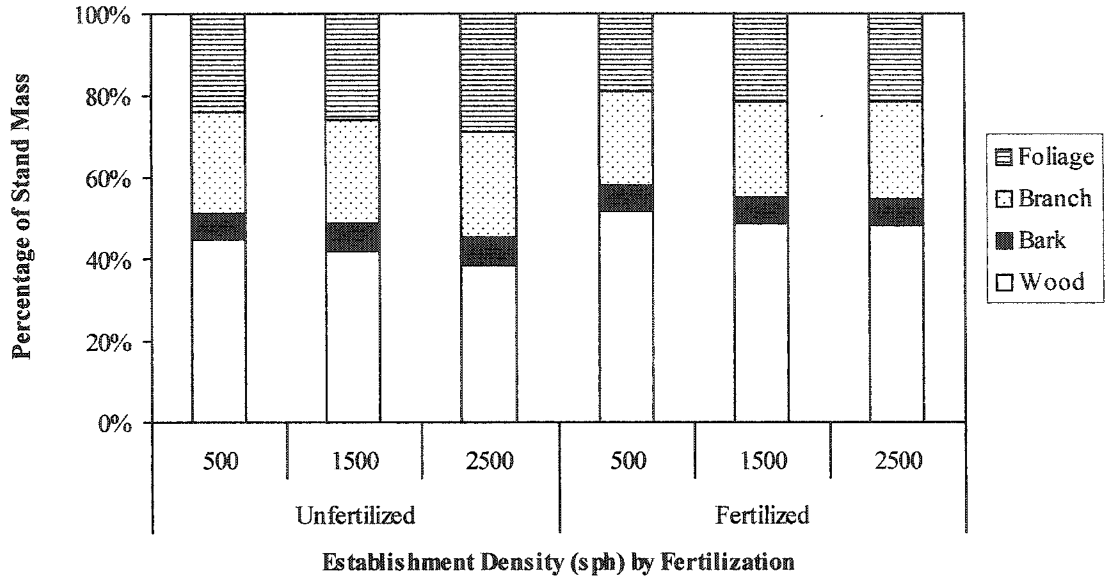


a)

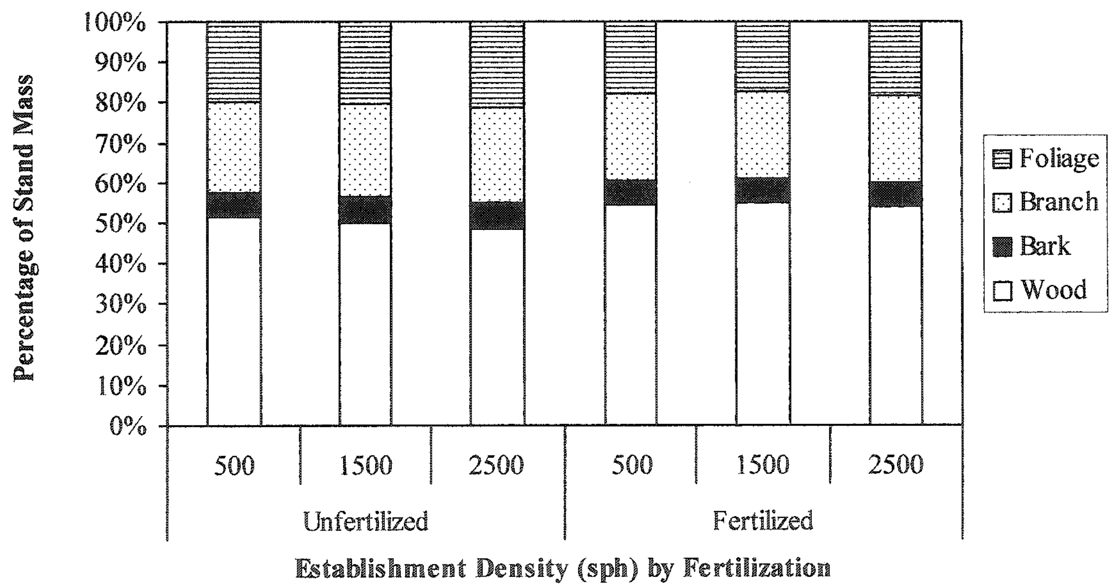


b)

Figure 3.5. Stand biomass allocation for western redcedar stands on: a) CH and b) HA sites.



a)



b)

Figure 3.6. Stand biomass allocation for western hemlock stands on: a) CH and b) HA sites.

Significant species x fertilization interactions for stand wood proportion on CH sites indicated that wood proportion tended be greater in hemlock than in redcedar stands. Hemlock stands also responded more strongly to fertilization and increased proportional wood biomass more than fertilized redcedar stands (Table A2.16). Increasing establishment density significantly reduced the wood biomass proportion of stands on CH sites with significant differences existing between each density level (Table A2.16).

On HA sites, hemlock stands had significantly greater proportional wood biomass than redcedar stands. Fertilization significantly increased stand wood biomass proportion of HA sites, compared to unfertilized stands. Increasing establishment density reduced stand wood biomass proportion on HA sites, but significant differences only existed between the 500 and 2500-sph treatments (Table A2.16).

Significant species x establishment density, species x fertilization, establishment density x fertilization and species x establishment density x fertilization interactions were present for branch biomass proportions on CH sites. Proportional branch biomass was always greater in redcedar than in hemlock and was not influenced by either fertilization or establishment density. In hemlock, proportional branch biomass was lower on fertilized sites and increased with tree density; this increase was more pronounced on non-fertilized sites (Table A2.17).

On HA sites, a species x fertilization interaction indicated that branch biomass proportion was significantly increased by fertilization in hemlock stands but was unaffected by fertilization in redcedar stands (Table A2.15).

Foliage biomass proportion was reduced by increasing establishment density on both CH and HA stands. On CH sites, significant differences existed between each density level, while significant differences existed only between the 500 and 2500-sph treatments on HA sites. Fertilization significantly reduced foliage biomass proportion on CH sites, compared to unfertilized stands. Significant species x fertilization interactions existed on HA sites. These interactions indicated that unfertilized redcedar stands had greater foliage biomass proportion than unfertilized hemlock stands. Redcedar responded more strongly to fertilization than hemlock and fertilization eliminated species differences in foliage biomass proportion (Table A2.18).

These results support the hypothesis that fertilization would increase stand biomass proportion in wood and decrease biomass proportion in foliage. The results also support the hypothesis that increasing establishment density would increase stand biomass proportion in foliage and decrease biomass proportion in wood. Contrary to the hypothesis of no species differences, hemlock tended to have greater biomass proportion in wood while redcedar tended to have greater biomass proportions in bark and branches and, on HA sites, in foliage.

3.3.4 Competition, Site Productivity and Fertilization

Stand biomasses increased with fertilization and were greater on HA than on CH sites for hemlock. Redcedar stand biomass did not significantly vary with site but were increased by fertilization. Therefore, it may be inferred that the combination of fertilization and site produced a productivity gradient for hemlock, from least to greatest, in the order: unfertilized CH, fertilized CH; unfertilized HA, fertilized HA. In the case of redcedar, the productivity gradient, from least to greatest was: unfertilized CH and HA; fertilized CH and HA. As productivity increased, negative relationships between tree size and establishment density became less pronounced, in terms of regression significance and magnitude of r^2 values (Table A3.18). Similar trends of stronger relationships with declining productivity were also noted between establishment density and component biomass proportions, although direction of the relationship varied with component. Therefore, it may be inferred that competition and consequent influence on biomass partitioning within stands increased with declining productivity. Symmetric competition is suggested by the declining significance of negative relationships between establishment density and tree size as site productivity increased.

Hemlock had a higher correlation between establishment density and tree biomass (0.864) than redcedar (0.613) on unfertilized CH sites. The relationship between tree size and establishment density weakened with increasing productivity, becoming non-significant for redcedar on fertilized HA sites, while hemlock only showed significant relationships on CH sites. Proportions for biomass component showed similar patterns. It may be inferred that hemlock experienced greater intra-specific competition and commensurate influence on biomass allocation patterns within stands at lower site fertility status. The presence and influence of competition on stand structure, in terms of biomass partitioning patterns, declined with increasing site productivity for both species.

These results confirm the hypothesis that competition would decrease with conditions of increasing productivity and presumably soil resource availability. That competition increased with decreasing soil resource availability suggests that the dominant mode of competition on these sites was resource-depletion or symmetric, rather than resource pre-emption or asymmetric, in nature.

3.4 Discussion

The results regarding size-independent treatment effects on tree-level biomass allocation are in agreement with existing literature, where fertilization effects on biomass allocation last less than seven years after treatment (Brix 1981, Barclay *et al.* 1986, Gower *et al.* 1993, Gillespie *et al.* 1994, Mitchell *et al.* 1996, Albaugh *et. al.*1998, Yang 1998, King *et al.* 1999) or do not occur (King *et al.* 1999, Retzlaff *et al.* 2001). Tree-level allocation results also are in accord with previous studies that have found no effect of establishment density on size-independent allocation patterns (Nilsson 1994, Makinen 1996). Changes in biomass component allometry may only occur with competition for light over time, as differences in allometry have been noted between individuals of different competitive status or in young stands of very high stocking of over 18 000 sph (Nilsson and Albrektson 1993, Naidu *et al.* 1998, Vanninnen and Makela 2000). Both redcedar and hemlock are very shade tolerant (Mailly 1998, Drever and Lertzmann 2001) and may be comparatively resistant to competition-induced changes in biomass allometry.

Allocation of biomass to tree components varied as tree size increased. Highest priority biomass allocation to wood and least priority to foliage as tree size increases is congruent with that shown for loblolly pine after five years of annual irrigation and fertilization (Retzlaff *et al.* 2001) but contradicts that found for individual Douglas-fir trees nine years after fertilization (Barclay *et al.* 1986), where allocation to foliage and branches had a higher priority than that to wood and bark. The net effect of treatments on stand-level component biomass proportions resulted from combined effects on tree size and the tree size distributions that developed. Species differences may have manifested as different growth responses to treatments and possible inherent tendencies to form stands with different size distributions. The effects of fertilization and establishment density on average redcedar and hemlock growth on CH and HA sites has been documented by this study and Chapter 2, however, the influence of these factors, singly and in combination, on the mix of tree sizes that result has not yet been investigated. The degree to which competition may develop and the dominant mode of competition present could significantly affect resulting stand structures (Newton 1990, Newton and Jolliffe 1993, Schwinning and Weiner 1998).

The generally greater growth of hemlock compared to redcedar on HA sites and the greater response of hemlock to fertilization on CH sites likely resulted from a combination of rooting habit and nutrient use efficiency. Hemlock roots at a more shallow depth than redcedar, generally at the same level of salal (Bennett *et al.* 2002, Wang *et al.* 2002), which may result in greater suppression of hemlock growth by salal on CH sites. However, hemlock root systems are physically closer to the surface-applied fertilizer and may take advantage of it more fully. Hemlock also has been shown to have greater N use efficiency than redcedar under laboratory conditions (Brown *et al.* 1996a, 1996b) and may have used the additional nutrients more efficiently and produced relatively more growth than redcedar. However, fertilization has not resulted in elevated current foliar N concentrations in either redcedar or hemlock on CH sites (Chapter 2) so this effect has either dissipated, did not occur, or may also be occurring with P, the foliar concentration of which remains elevated on fertilized sites and is more closely linked to redcedar and hemlock growth than is foliar N concentration (Chapter 2). Phosphorus and N use efficiency by redcedar and hemlock under field conditions are not well documented.

Increasing establishment density tended to increase stand and component biomasses, consistent with greater filling of available growing space by higher density stands. The exception to this was foliage biomass, which did not increase with density on HA sites and decreased with increasing density on CH sites. As tree numbers increased, the reduction in foliage biomass per tree was not compensated for by increased tree numbers. The negative impact of density on foliage biomass has been demonstrated in thinning trials, where thinning has typically resulted in more foliage per tree but less per ha, although the gap between thinned and non-thinned stands closed with age (Barclay *et al.* 1986, Mitchell *et al.* 1996). The comparatively low foliage biomass on these sites may be the result of a high water table and a reduced ability for trees to support foliage due to soil moisture conditions (Gower *et al.* 1993). Non-trial trees of both species growing on raised microsites near access roads appeared to have larger crowns containing more foliage (personal observation). High levels of stand growth and biomass accumulation are related to stands being able to establish and maintain high amounts of foliage biomass per ha (Espinosa Bancalari and Perry 1987, Vose and Allen 1988). The tendency for increasing density early in stand development to not increase stand foliage biomass on HA sites and to actually decrease it on CH sites suggests that density may be negatively affecting stand production on both sites but particularly the CH sites. Stand nutrient demand is likely to increase until canopy closure is attained (Miller 1995) so a determination of whether foliage carrying capacity has been attained on these sites would increase our ability to interpret the results. Further investigations of the role of soil moisture regimes on the development of stand foliage and the influence and interaction of site factors with cultural manipulations on foliage development and efficiency are also necessary to more fully understand stand productivity on these sites.

The greater impact of establishment density on hemlock biomass accumulation was likely the result of individual hemlock saplings having to compete with both salal, due to overlap in rooting depths of these species, and with other individuals in the stand, whereas redcedar did not have to compete as strongly with salal due to its greater rooting depth (Fraser *et al.* 1995, Bennett *et al.*2002, Wang *et al.* 2002). By reducing tree size, increasing establishment density shifted allocation away from stem wood into non-wood components. Interactions between species, fertilization and establishment densities for biomass proportions reflects the tendency for hemlock to respond more to fertilization and density stress on CH sites (see above) and its ability to attain greater size than redcedar across all treatment combinations on HA sites.

These results disagree with existing literature, which shows that fertilization increased stand-level proportional branch biomass (Barclay *et al.* 1986, King *et al.* 1999) but agree in regards to fertilization either not affecting or reducing proportional foliage biomass (Barclay *et al.* 1986, King *et al.* 1999). In accord with results presented here, increasing stand density has been found to decrease proportional stem wood biomass while increasing proportional stand biomass of bark and foliage, but disagree in that a decrease in proportional branch biomass occurred with increasing density (Newton and Jolliffe 1993).

Competition and its influence on biomass structure of stands were shown to decrease as site productivity was increased by fertilization. This result supports theories and findings which suggest that net above- and belowground competition is unaffected by site productivity (Tilman 1988, Wilson and Tilman 1993) rather than those which suggest that competition increases with site productivity (Goldberg and Barton 1992, Grime 2001). In their meta-analysis of competition experiments with plants, Goldberg and Barton (1992) found that competition increased along naturally occurring soil resource gradients but competition tended not to be affected when resource supply increased were induced through fertilization. The reason for this difference in response was obscure (Goldberg and Barton 1992). The results of this study showing decreased competition associated with fertilization on more nutrient -poor CH sites and a general lack of competition on the relatively more nutrient-rich HA sites disagree with the findings of Goldberg and Barton (1992). Alternatively, competition may not have developed as strongly on more productive HA sites because carrying capacity for forest growth has not yet been reached or has not been met for as long as on less productive sites or because the level of herbivory (which was not accounted for) was different (Gurevitch *et al.* 2000). Maximum stand productivity has been shown to be reached when foliage carrying capacity for the site has been reached and self-thinning begins (Ford 1982). An examination of whether maximum foliage biomass has been attained on these sites would assist in determining whether site carrying capacity has been reached. Investigations of the influence of fertility on competition with populations of herbaceous plants have indicated that intensity of competition, in terms of slopes in size-density relations, is most severe at lower soil nutrient availability levels but develops more quickly at higher soil nutrient availability levels (Morris and Myerscough 1991, Wilson and Tilman 1993). Competition for light and soil resources has been shown to operate in opposition with the prominence of either mode determined by resource availability. Thus, under conditions of relatively greater soil resource availability, plant biomass and height development are stimulated and competition for light develops more strongly than competition for soil nutrients. Conversely, under nutrient limiting conditions, plant stand biomass and height are inhibited by strong competition for soil resources but light competition tends not to develop as strongly. The sum of both above and belowground competition showed no variation over site fertility levels although the relative prominence of each changes (Wilson and Tilman 1993). Although not tested, slopes of the size-density and biomass proportion-density relationships were fairly uniform, when relationships were statistically significant. This indicates similar intensity of competition where competition did develop. Competition tended to develop on sites of lower productivity and reduce average tree size, suggesting that competition for soil resources, or symmetric competition, was likely dominant. Competition for light, or asymmetric competition, may also have developed but further analysis of size distributions is necessary in order to confirm this (Newton and Jolliffe 1993).

3.5 Conclusion

The results of this trial supported the following hypotheses: CH sites were less productive than HA sites; competition was more pronounced on CH sites; fertilization increased biomass development, increased stand-level wood proportion and may have reduced competition and its effects on biomass structure, although the effect of competition-modifying herbivory were not accounted for; and increasing establishment density increased stand level foliage proportion. However, increasing establishment density did not always increase biomass development: foliage biomass on CH sites decreased and foliage biomass on HA sites did not change as establishment density increased. On CH sites, hemlock was more strongly influenced by both fertilization and density stress than was redcedar. Competition developed more strongly in hemlock stands under lower productivity conditions than in redcedar stands.

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Chapter 4

Foliar and Resource Use Efficiencies in Juvenile Western Redcedar and Western Hemlock Plantations

4.1 Introduction

Fertilization with N and P has been shown to increase forest stand growth and has the potential to greatly increase fibre yield (Harrington and Wierman 1990, Valinger 1993, McWilliams and Therien 1996, Mitchell *et al.* 1996). Fertilization of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red redcedar (*Thuja plicata* Donn.) stands is increasingly common in coastal British Columbia. Establishment of plantations with sufficiently high density is necessary in order to capture site growth capability in the establishing stand and to shade out competitors (Oliver and Larson 1996). Inter-tree competition, however, affects growth processes, stand structural development and timber quality (Waring *et al.* 1981, Ford 1982, Ballard and Long 1988, Velazquez-Martinez 1992, Dicus and Dean 2001). An understanding of the mechanisms by which fertilization and establishment density influence stand growth processes is desirable in order to more effectively manage western hemlock and western red redcedar stands in coastal British Columbia.

Forest growth can be described as a function of resource supply, the proportion of resources captured by trees and the efficiency with which trees use resources to fix carbon dioxide (Binkley *et al.* 2004). Fertilization has been shown to increase soil resource supply (Bradley *et al.* 2000, Bennett *et al.* 2002). Fertilization has also been shown to increase foliar efficiency (growth per unit of foliage mass or leaf area) in loblolly pine, Scots pine and Douglas-fir (Brix 1983, Valinger 1983, Albaugh *et al.* 1998), although efficiency per unit of leaf area may decline asymptotically with increasing stand leaf area in Douglas-fir and loblolly pine stands (Velazquez-Martinez 1992, Vose and Allen 1988). However, increases in foliar efficiency due to fertilization tend to decline to levels equal or below those of unfertilized controls within 7 to 9 years after treatment (Brix 1983, Barclay *et al.*1986, Valinger 1993, Mitchell *et al.* 1996).

Increasing stand density results in increased stand growth as a consequence of increased amount of foliage in close-canopied stands (Ford 1982, Espinosa Bancalari and Perry 1987, Vose and Allen 1988, Velazquez-Martinez *et al.* 1992). However, foliar efficiency (growth per unit of foliage) tends to decline with increasing amount of foliage in a stand, which offsets the growth effect of greater foliage mass (Waring *et al.* 1981, Ford 1982, Velzquez-Martinez *et al.* 1992). Reduction of stand density through thinning increased foliar efficiency of Douglas-fir stands for longer periods than fertilization, although the effect was slower to develop (Brix 1983, Mitchell *et al.* 1996). As trees increase in size, an increase in resource availability, especially light, is likely necessary to prevent reduction in foliar efficiency (Maguire *et al.* 1998). Stand growth and mass accumulation results in smaller trees using growing space (based on growth per unit sapwood basal area, crown projection or crown volume) more efficiently than larger trees, although stand structure also influences the most efficient tree size (O'Hara 1988, Larocque and Marshall 1994, Sterba and Amateis 1998, Vanninen and Makela 2000).

Nutrient use efficiency (growth per unit concentration or content of a nutrient) is largely a function of species but can be influenced by fertilization and density stress.

Nutrient use efficiency tends to decline with increasing soil nutrient availability and with fertilizer application (Barclay and Brix 1985, Prescott *et al.* 1989, Elliott and White 1993, Elliott and White 1994, Mitchell *et al.*1996). The tendency for nutrient use efficiency to decline with nutrient availability may be a result of photosynthetic rates tending to initially be positively correlated with nutrient concentrations at lower levels but plateau at higher concentrations (Reich and Schoettle 1988, Brown *et al.* 1996a, 1996b). Nutrient use efficiency may be reduced by competition but this varies with species (Elliott and White 1993, Dicus and Dean 2001, Robinson *et al.* 2001). Nutrient use efficiency varies with species and reflects different physiological investment strategies and response to external conditions (Prescott *et al.* 1989, Gower *et al.* 1993, Bothwell *et al.*2001, Dicus and Dean 2001, Ripullone *et al.* 2003). Differences in investment strategy may allow superior growth of one species versus another under conditions of low nutrient availability (Bothwell *et al.* 2001). Foliar N use efficiency declined with increasing N concentrations in hemlock and western red redcedar but tended to be higher for hemlock than for redcedar at lower N concentrations (Brown *et al.* 1996a, 1996b). Fertilization resulted in increased absorbed-light use efficiency in Douglas-fir stands and it has been suggested that light use efficiency of stem wood production increases exponentially with light absorption while other stand components only increase linearly (Balster and Marshall 2000).

The influence of fertilization and density stress on foliar, nutrient use and light use efficiencies will be examined for western red redcedar and western hemlock in a 14-year-old silviculture trial on northern Vancouver Island that was fertilized 10 years previously. In this study, foliar and resource use efficiencies were examined to determine whether increased growth in fertilized stands 10 years after treatment could be attributed to increases in these rates and whether competition was influencing them. Results of these studies led to the hypotheses that: 1) foliar and nutrient use efficiencies would not increase with either fertilization or increasing stand establishment density; 2) foliar efficiency would decrease with increasing tree size; 3) stand growth capacity would be closely and linearly related to stand foliage mass; 4) hemlock would have greater nutrient use efficiency than redcedar; 5) light interception by stands would increase with fertilization and establishment density; 6) light use efficiency would increase with fertilization and decrease with increasing establishment density and; 7) efficiency of stem wood production would exponentially increase with light absorption by stands while efficiency of foliage and total stand mass production would increase linearly with light absorption.

4.2 Materials and Methods

4.2.1 Study Sites

The study site was located on northern Vancouver Island, British Columbia, Canada, between Port Hardy and Port McNeill (50° 60'N, 127° 35' W) in the Submontane Very Wet Maritime variant of the Coastal Western Hemlock Biogeoclimatic, or CWHvm1, zone (Green and Klinka 1994). The study site was approximately 50m ASL in undulating terrain with frequent rocky knolls and wetlands located in depressions. Surface materials consist of unconsolidated glacial moraine and fluvial outwash deposits that range from over 1m in depth to shallow with exposed bedrock. Mineral soils ranged from silty clay loams to fine sand with high coarse fragment content. Organic soils of wetland or upland origin are also common within the study site.

The area receives approximately 1900 mm of precipitation annually, most of which falls as rain. Growing season soil moisture deficits typically do not occur (Lewis 1982).

Average daily mean temperature ranges from 3.3° C in January to 14.1° C in August. A relatively high percentage of the annual solar radiation is received as diffuse radiation (McKay and Morris 1985), reflecting overcast conditions throughout the year and frequent summer fog. Direct sunlight exposure ranges from 1.5 h/day in December to 6.4 h/day in July. Global solar radiation incident of a horizontal surface averages 10.212 MJ/m^2 per day and ranges from a low of 2.043 MJ/m^2 per day in December to 18.935 MJ/m^2 per day in July (McKay and Morris 1985).

Two common CWHvm1 forest types were examined at the study site. Hemlock Amabilis Fir (HA) types are occupied by stands composed of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) while Redcedar Hemlock (CH) types are occupied by stand composed of western red redcedar (*Thuja plicata* Donn) and western hemlock. Both forest types are typically found on well to imperfectly drained Duric Humo-Ferric Podzols and are considered zonal sites (Lewis 1982, Green and Klinka 1994). HA sites typically occur on areas that have historically been subject to stand-replacing wind throw events (Lewis 1982). HA stands are mid-seral and have a dense, even-aged structure with uniform canopies. Due to the dense canopy cover, HA stands have poorly developed understory vegetation layers. Surface organic layers in HA stands are comparatively thin (5 – 10 cm) and friable. CH stands likely represent a climatic climax state, with an uneven-aged structure and open, irregular canopies. CH stands typically have well developed understory plant communities dominated by dense salal (*Gaultheria shallon* Pursh) growth. Surface organic layers in CH stands are thicker (10 – 45 cm) and more compact than on HA sites. Soil nutrient availability is lower on CH sites than on HA sites (Prescott *et al* 1996).

The study site was clear-cut logged in 1986, broadcast burned and planted with western hemlock and western red redcedar in 1987.

4.2.2 Treatments

Ninety-six treatment plots, each containing 64 sample trees were established in 1987. Plot size and tree spacing varied with density. Treatments consisted of a fully crossed factorial combination with two levels of fertility (fertilized and non-fertilized) and three levels of density (500, 1500 and 2500 stems per ha). Trees in the 500-sph plots were spaced 4.5 m apart, resulting in a central (core) measurement area of 36 x 36 m and a total plot size of 54 x 54m, including a buffer zone. The 1500 sph treatment had a tree spacing of 2.6 m, a core measurement area of 21 x 21 m and a total area plot size of 32 x 3 m. Between tree spacing was 2 m in the 2500-sph treatments, with a 16 x 16 m core measurement area and total plot size of 36 x 36 m.

Fertilized plots were received a 60 g dressing of Nutricoat™ controlled release fertilizer at time of planting. The fertilizer was raked into a 15cm radius areas around each seedling, provided 10 g of N, 2.5 g of P and 5 g of K to each seedling. Total application rated per ha varied with density. All fertilized plots were refertilized before the beginning of the growing season early spring of 1993 with a broadcast application of 225 kg of N and 100 kg of P per ha.

The 2 x 3 combination of fertilizer/no-fertilizer by densities was duplicated for each of redcedar and hemlock on both CH and HA sites. Each fertilization-density-species combination was randomly assigned within four blocks on each site, with a single treatment level replicate per block. Thus, a total of 48 plots examined 12 treatments with 4 replications per treatment level.

Height and diameter of each sample tree within core measurement areas were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997 and 2002. Height was recorded to the nearest cm. Diameter was measured in mm at the root collar for the years 1988 – 1997. Diameter was measured at 1.3 m above the root collar (breast height) in 1997 and 2002.

4.2.3 Mass Prediction Equations

Regression equations were developed to predict individual tree total mass and mass of foliage. Saplings were destructively sampled after growth had ceased in the fall of 2001 and 2002. Saplings were selected to represent the existing size range within treatment levels based on diameter at breast height. Both redcedar and hemlock were sampled from across a range of treatment levels on both sites. Sample trees were selected using a two-stage process. In the first stage, several sample trees were initially selected using a random procedure within each treatment level. Diameter at breast height was measured for all neighbouring trees within a 4.3 m radius of randomly selected trees to establish a size range for the treatment level. In the second stage, sample trees were selected to span the size range determined in the first stage. Sample trees were selected to be free of significant stem and crown damage. Sample trees were felled and their height and diameter at breast height determined. The sample trees were then cut into 1 m segments and branches removed by severing at the point of branch contact with the stem section. Total fresh mass of the stem section and the branches was then determined to the nearest 50 g. A 3 cm wide disk was subsampled from each stem section. These subsamples were removed approximately 30 cm from the bottom of each stem section such that they were located within the tree beginning 30 cm from the root collar and then at 100 cm intervals up the stem, with an additional section extracted where the stem narrowed to a diameter of 1 cm. The portion of the stem above this point was designated the terminal and was analyzed separately as a branch. Two or three undamaged branches were randomly sub sampled from each section. In some cases, no branches could be sampled from the bottom stem section, as no living branches were present. Dead branches were discarded and not included in calculations. Stem disks and branch sub samples were removed to a lab facility in Port McNeill for further analysis. Total and foliage dry mass for each tree were determined based on dry mass conversion factors calculated from the sub samples.

Initial analysis of sample tree data in 2001 indicated greater variability in component masses of redcedar compared to hemlock. Consequently, a total of 84 redcedar and 41 hemlock saplings were destructively sampled.

Predictive equations for total and foliage mass were developed based on tree diameter and height as predictive variables. The variable (d^2h), or diameter squared multiplied by height, was used as the predictor variable in an allometric model of the form:

$$\log_e Y_{ij} = \log_e \beta_{0i} + \log_e \beta_{1i} X_j + \log_e \varepsilon_{ij} \qquad [1]$$

Where Y_{ij} is the oven dry mass (g) of the ith component (i is total tree mass or foliage mass) of the jth sample tree (j ranging from 1 to 84 for redcedar and 1 to 41 for hemlock); X_j is (d^2h) of the jth sample tree; $\log_e \beta_{0i}$ and loge β_{1i} are parameters estimated by ordinary least squares regression on $\log_e$-transformed data for the ith component and $\log_e \varepsilon_{ij}$ is the residual term for the ith component. Assumptions of normality and homogeneity of variance were tested using the Shapiro-Wilks test and examination of residual plots. Model-fitting was conducted using the Statistical Analysis System (SAS), Version 8.2. Back-transformational bias was corrected according to Baskerville (1972). Final parameter estimates and regression statistics are presented in Table 3.1. Mass models were used to predict mass components for each tree based on the 2002 and 1997 measurements.

Table 4.1 Mass prediction equations and model statistics.

Mass Components	n	b_o	b_1	SE	p	r^2
Western Red Redcedar:						
Total Tree	82	-2.018	0.728	0.023	<.0001	0.958
Foliage	82	-2.478	0.566	0.073	<.0001	0.813
Western Hemlock:						
Total Tree	41	-1.883	0.732	0.131	<.0001	0.939
Foliage	41	-2.872	0.642	0.275	<.0001	0.850

4.2.4 Foliar Nutrient Concentration Determination

Samples of current-year foliage were collected from the upper crowns of trees within each plot. Approximately 500g of fresh foliage was collected from about 60 trees in each plot and combined into one composite sample per plot. Composite samples were dried to constant weight at 70 °C and ground. Nutrient concentration was determined following sulphuric-acid hydrogen-peroxide digestion (Parkinson and Allen 1975). Nitrogen and P concentrations were determined colorimetrically on a Technicon auto-analyzer. K, Ca, Mg, Mn and Al concentrations were determined by atomic absorption specrography. Cu, Zn, and

Fe concentrations were determined through dry-ashing and subsequent analysis with atomic absorption spectography. Boron concentration was determined colorimetrically with the azomithine-H method. Total S concentration was determined using a LECO Sulfur Analyzer. Available sulphate-sulphur concentration was determined using 0.01 N HCl extraction and determined colorimetrically in an HI-Bismuth reducible distillate. All analyses were conducted at Pacific Soils Analysis Incorporated of Richmond, British Columbia.

4.2.5 Estimation of IPAR

Light environment was quantified using digital analysis of hemispheric photographs. Six hemispheric images were obtained from randomly located locations within each plot planted to redcedar on CH sites, for a total of 144 images. Images were taken 1.3m above ground during uniformly overcast conditions during the day, or during clear sky conditions at dawn and dusk, in late October of 2002. Digital images were obtained with a Nikon Coolpix 990 digital camera and Nikon FC-E8 hemispheric lens and were analyzed using WinSCANOPY, a commercial software program (Regent Instruments, Quebec City). Average photosynthetically active photon flux density (PPFD) during the growing season both above and below the tree canopy was determined, based on local solar radiation data from Port Hardy Airport (McKay and Morris 1985, Canadian Climate Program 1982). The proportional amount of photosynthetically active radiation intercepted or scattered by the tree canopy (IPAR) was determined for each photographic location from these measurements and averaged for each plot.

4.2.6 Determination of Resource Use Efficiencies

Total mass and foliage mass were calculated per ha for each experimental unit using the mass estimation equations derived above. Total mass and foliage mass were determined using predictive equations for each tree for 1997 and 2002 and summed to give plot totals for each of these years, which were then converted to per ha estimates. Stand-level foliage growth efficiency was determined as unit mass rate (Hunt 1990):

$$E = ((W_2 - W_1) / 5) \times ((\ln(F_2) - \ln(F_1)) / F_2 - F_1) \qquad [2]$$

Where:
E = Foliar Efficiency (kg/kg foliage/yr)
W_1 = Total Mass in 1997
W_2 = Total Mass in 2002
F_1 = Foliage Mass in 1997
F_2 = Foliage Mass in 2002

To determine tree-level foliar efficiency, trees from all four replicates per treatment level were pooled and sorted by dbh in 1997 (the beginning of the growth analysis period). Following sorting by size, the pooled tree data were divided into groups to form consecutive size-rank classes. Foliar efficiency was determined for the trees in each size-rank class at each treatment level. Analysis of variance examining tree-level E used 5 consecutive size-rank classes. Regression analysis of E vs. size class used 10 size-rank classes. This method allowed E to be compared based on relative position of individual trees within the stand, rather than on absolute size, which changed with treatment.

Nutrient use efficiencies were determined as:

$$\text{NUE} = ((W_2 - W_1) / 5) / (\text{Percent Nutrient Concentration}) \qquad [3]$$

Where: NUE = Nutrient use efficiency of a given nutrient (t/ha/ %content / yr)
W_1 = Total Mass in 1997
W_2 = Total Mass in 2002

Based on the screening in Chapter 2, N, P, K, S, Ca, Mg, Zn and B efficiencies were examined.

Light use efficiency for redcedar stands on CH sites were determined in a similar fashion to nutrient use efficiency:

$$LUE = ((W_2 - W_1) / 5)/(\% \text{ IPAR}) \quad [4]$$

Where: LUE = Light use efficiency (t/ha/% IPAR)
W_1 = Total Mass in 1997
W_2 = Total Mass in 2002
% IPAR = % of incident PAR absorbed/scattered by the stand

4.2.7 Statistical Analysis

A general linear model approach was used to examine the effects of treatments on annual average stand mass growth rate, stand-level foliage growth efficiency, nutrient use efficiency, IPAR and light use efficiency. A mixed-effects model (PROC Mixed in SAS, Version 8.2) was used for each site type with species, fertilization and density tested as fixed effects and blocks included as a random effect:

$$y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + (abc)_{ijk} + \varepsilon_{ijkl}$$

Where: y_{ijk} = Response of the *i*th species at the *j*th fertility level at the *k*th density level
μ = General Mean
a_i = Species Effect
b_j = Fertility Effect
c_k = Density Effect
ε_{ijkl} = Residual Error

Analysis of light use efficiency did not include a species effect, as only redcedar stands were examined. Where interaction terms were significant, given significance of at least one constituent fixed effect, simple effects were compared by adjusting least-square means for Tukey's Honestly Significant Difference test. Where interactions were significant, density, fertilizer and species effects were examined together. Where interaction terms were not significant, simple effects were compared using Tukey's HSD test. For all tests a significance level of $p < 0.05$ was. Variables were $\log_e$-transformed to homogenize variances for the analysis, where necessary. IPAR was arcsine-transformed for the analysis.

Tree-level foliar efficiency was examined using analysis of variance (PROC GLM in SAS, Version 8.2) according to the following model:

$$y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + (abc)_{ijk} + \varepsilon_{ijkl}$$

Where: y_{ijk} = Response of the ith species at the jth fertility level at the kth density level
μ = General Mean
a_i = Size Effect
b_j = Fertility Effect
c_k = Density Effect
ε_{ijkl} = Residual Error

Effects of fertilization, density and size-rank class on E were tested for each species-site combination. Although the number of trees used to determine E for each size-rank class tended to be unequal, the amount of variation between classes within an analysis tended to be small. Given the large number of replicates per size-rank class, on average 47 trees, the generally small variation in replication number and the desire to compare treatment combinations equally, cell means were not weighted (Littell *et al.* 2002, O'Hara 1988). Where interaction terms were significant ($p < 0.05$), simple effects were compared by adjusting least-square means for Tukey's Honestly Significant Difference test, given the significance of at least one constituent fixed effect. The response variable was $\log_e$-transformed for the analysis, to homogenize variance.

Ordinary least-squares regression analysis (OLS) was used to examine the relationship between tree-level E and size rank class for each site-species-fertilization-size-density combination. The relationship between total 1997 – 2002 average annual stand mass growth rate and estimated 2002 foliage mass was examined for each site-species combination using OLS. Non-linear regression was used to examine the relationship between percent IPAR in redcedar stands on CH sites and 1997 – 2002 total mass growth rate, wood mass and foliage mass using an exponential growth function:

$$y = (b)\, e^{(c \times \%IPAR)} \qquad [5]$$

Where: y = 1997 – 2002 component mass growth rate (t/ha/yr)
% IPAR = Percent of incident PAR absorbed or scattered by the stand
b and c = Parameters

4.3 Results

Treatment means for stand-level E, nutrient use efficiencies and 1997 - 2002 stand dry mass growth rates are presented in Table 4.2. Tree-level E for each site-species combination are presented in Table 4.3. Results showing outcomes of F-tests and least-square means are found in Appendix 3. Only results of significant F-tests are described.

4.3.1 Annual Dry Mass Growth Rate and Stand-Level Foliar Efficiency

A significant species x fertilizer interaction for annual dry mass growth rate on CH sites indicated fertilization increased growth of both hemlock and redcedar stands but that hemlock responded more strongly to fertilization than did redcedar on CH sites (Tables 4.2 and A3.1). Thus, fertilization reduced species differences in annual mass growth rate. Fertilization also increased annual dry mass growth rate on HA sites, compared to unfertilized stands (Tables 4.2 and A3.1). On CH sites, the increase in growth rates associated with fertilization was 391% compared to non-fertilized stands and on HA sites the increase was 153%.

Stand-level dry mass growth rates were less in the 500-sph than the 1500 or 2500-sph densities, which were similar on both sites (Tables 4.2 and A3.1). On HA sites, annual mass growth rate of hemlock stands was significantly (196%) greater than that of redcedar. Species x establishment density, species x fertilization and species x fertilization interactions were present on CH sites (Tables 4.2 and A3.2). These interactions indicated that: *E* of redcedar stands was unaffected by fertilization but *E* of hemlock stands was reduced by fertilization; increasing density tended to increase *E* in unfertilized hemlock stands but decreased *E* in fertilized hemlock stands, and; redcedar response to density did not change with fertilization. No significant treatment or species effects on *E* were present on HA sites (Table A3.3).

These results do not fully support the hypotheses of this study: fertilization only reduced foliar efficiency in hemlock, and *E* was greater in hemlock than in redcedar, but only on CH sites and not on HA sites. Density stress only affected hemlock, and its effects varied with fertility status. Thus species and treatment responses varied according to site and fertility status.

Table 4.2. Means of stand-level foliar and nutrient use efficiencies, standard errors in brackets.

Species	Fert.	Planting Density (Stems/ha)	Dry Mass Growth Rate (t/ha/yr)	*E* (kg/kg/ha/yr)	N Use Efficiency (t/ha/%/yr)	P Use Efficiency (t/ha/%/yr)	K Use Efficiency (t/ha/%/yr)
CH Sites:							
Cw	F0	500	0.73(0.22)	1.04(0.13)	0.68(0.19)	4.12(1.33)	1.08(0.26)
Cw	F0	1500	1.21(0.42)	0.82(0.08)	1.25(0.40)	7.64(2.76)	2.13(0.67)
Cw	F0	2500	1.33(0.30)	0.69(0.07)	1.48(0.40)	8.71(2.24)	2.51(0.52)
Cw	F1	500	1.42(0.24)	1.04(0.06)	1.25(0.14)	5.88(0.94)	2.57(0.32)
Cw	F1	1500	3.06(0.80)	0.78(0.05)	2.78(0.63)	13.32(3.11)	5.72(1.46)
Cw	F1	2500	3.10(1.23)	0.79(0.08)	2.98(1.23)	15.19(6.40)	6.46(2.82)
Hw	F0	500	0.24(0.06)	0.94(0.150)	0.32(0.08)	2.13(0.51)	0.37(0.09)
Hw	F0	1500	0.50(0.14)	1.04(0.215)	0.63(0.12)	4.27(1.72)	0.67(0.16)
Hw	F0	2500	0.32(0.09)	1.01(0.097)	0.39(0.11)	2.71(1.39)	0.45(0.14)
Hw	F1	500	1.68(0.53)	1.02(0.07)	2.08(0.58)	6.28(2.10)	2.30(0.72)
Hw	F1	1500	2.41(0.93)	0.88(0.15)	3.05(1.22)	8.84(3.91)	3.28(1.12)
Hw	F1	2500	3.46(1.79)	0.77(0.06)	4.50(1.91)	13.71(6.61)	4.93(2.89)
HA Sites:							
Cw	F0	500	0.78(0.30)	0.88(0.05)	0.77(0.30)	4.97(2.32)	1.44(0.62)
Cw	F0	1500	1.55(0.52)	0.78(0.04)	1.66(0.52)	10.06(2.90)	3.15(1.25)
Cw	F0	2500	1.89(1.56)	0.69(0.12)	1.90(1.38)	11.63(8.91)	3.64(2.49)
Cw	F1	500	1.37(0.44)	0.97(0.09)	1.26(0.42)	6.89(1.90)	2.90(1.13)
Cw	F1	1500	4.58(1.63)	0.91(0.15)	4.18(1.20)	22.22(6.48)	9.63(3.47)
Cw	F1	2500	5.83(1.35)	0.88(0.07)	5.12(1.03)	27.78(8.12)	10.07(2.07)
Hw	F0	500	1.42(0.79)	0.92(0.04)	1.73(0.98)	12.49(8.30)	1.88(1.10)
Hw	F0	1500	3.36(2.35)	0.82(0.13)	3.64(1.84)	33.73(24.03)	4.34(2.92)
Hw	F0	2500	4.80(4.03)	0.87(0.18)	5.39(3.71)	53.72(44.25)	7.26(6.64)
Hw	F1	500	2.45(0.35)	0.95(0.02)	2.89(0.44)	9.19(1.64)	3.53(0.54)
Hw	F1	1500	9.38(1.74)	0.93(0.05)	8.95(1.06)	35.89(5.09)	13.86(2.65)
Hw	F1	2500	11.57(2.16)	0.90(0.13)	10.16(1.12)	44.38(14.52)	17.17(5.11)

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Table 4.2 (cont.) Means and standard errors of stand-level foliar and nutrient use efficiencies.

Species	Fert.	Planting Density (Stems/ha)	Ca Use Efficiency (t/ha/%/yr)	S Use Efficiency (t/ha/%/yr)	Mg Use Efficiency (t/ha/%/yr)	Zn Use Efficiency (t/ha/ppm/yr)	B Use Efficiency (t/ha/ppm/yr)
CH Sites:							
Cw	F0	500	1.43(0.54)	7.30(1.89)	4.64(1.55)	0.06(0.02)	0.08(0.02)
Cw	F0	1500	2.08(0.78)	13.86(3.79)	7.95(2.45)	0.10(0.02)	0.12(0.05)
Cw	F0	2500	2.51(0.53)	15.14(3.04)	8.23(1.76)	0.11(0.03)	0.14(0.03)
Cw	F1	500	2.20(0.46)	14.65(2.82)	9.23(1.40)	0.08(0.02)	0.14(0.01)
Cw	F1	1500	5.21(1.64)	35.17(9.83)	19.86(5.64)	0.23(0.05)	0.30(0.08)
Cw	F1	2500	4.40(1.74)	33.61(12.04)	19.12(8.20)	0.23(0.10)	0.31(0.12)
Hw	F0	500	1.15(0.44)	3.05(0.61)	2.10(0.48)	0.02(0.01)	0.01(0.00)
Hw	F0	1500	2.38(0.63)	6.04(1.64)	4.36(1.18)	0.06(0.01)	0.02(0.01)
Hw	F0	2500	1.43(0.43)	3.74(1.44)	2.84(0.74)	0.03(0.01)	0.01(0.00)
Hw	F1	500	9.36(3.99)	20.70(6.63)	12.61(4.29)	0.16(0.06)	0.07(0.03)
Hw	F1	1500	16.77(9.54)	30.17(11.42)	16.56(7.13)	0.25(0.13)	0.11(0.05)
Hw	F1	2500	17.67(6.30)	41.45(22.80)	22.77(13.16)	0.30(0.18)	0.16(0.10)
HA Sites:							
Cw	F0	500	1.17(0.46)	8.17(3.01)	5.82(2.61)	0.05(0.01)	0.07(0.03)
Cw	F0	1500	2.47(0.93)	16.56(3.88)	11.07(3.77)	0.11(0.03)	0.15(0.04)
Cw	F0	2500	3.07(2.49)	19.96(13.62)	12.97(12.03)	0.15(0.13)	0.19(0.15)
Cw	F1	500	1.91(0.67)	14.56(4.17)	10.09(3.99)	0.09(0.03)	0.11(0.02)
Cw	F1	1500	5.83(1.56)	47.98(16.37)	35.48(12.41)	0.29(0.09)	0.36(0.09)
Cw	F1	2500	9.11(3.02)	63.04(11.72)	41.23(10.91)	0.34(0.06)	0.46(0.09)
Hw	F0	500	7.87(4.90)	14.42(7.04)	12.13(7.04)	0.13(0.07)	0.07(0.04)
Hw	F0	1500	17.65(14.05)	33.21(19.96)	28.44(23.36)	0.30(0.22)	0.17(0.13)
Hw	F0	2500	22.64(19.12)	44.90(30.14)	37.12(29.21)	0.46(0.37)	0.30(0.30)
Hw	F1	500	17.28(2.614)	30.20(5.29)	19.76(1.90)	0.24(0.06)	0.13(0.05)
Hw	F1	1500	46.86(7.037)	96.66(13.59)	69.82(14.42)	0.75(0.20)	0.52(0.09)
Hw	F1	2500	56.32(10.097)	108.28(20.37)	76.65(16.65)	0.94(0.25)	0.78(0.21)

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Table 4.3. Means of tree-level foliar efficiency, standard errors in brackets.

Fertilization	Planting Density (Stems/ha)	Size Class (Ascending)	Cw CH Sites (kg/kg/yr)	Hw CH Sites (kg/kg/yr)	Cw HA Sites (kg/kg/yr)	Hw HA Sites (kg/kg/yr)
F0	500	1	1.02(0.37)	1.57(0.71)	1.10(0.42)	1.23(0.40)
F0	500	2	0.93(0.27)	1.26(0.37)	0.87(0.26)	0.95(0.25)
F0	500	3	1.03(0.24)	1.06(0.33)	0.83(0.18)	0.88(0.20)
F0	500	4	1.06(0.19)	0.96(0.32)	0.84(0.19)	0.92(0.18)
F0	500	5	1.12(0.18)	0.83(0.26)	0.90(0.21)	0.90(0.18)
F0	1500	1	0.96(0.36)	1.42(0.50)	0.85(0.32)	1.00(0.46)
F0	1500	2	0.83(0.20)	1.30(0.35)	0.70(0.22)	0.91(0.25)
F0	1500	3	0.80(0.20)	1.00(0.39)	0.73(0.21)	0.79(0.20)
F0	1500	4	0.77(0.17)	1.00(0.34)	0.81(0.16)	0.80(0.18)
F0	1500	5	0.84(0.19)	0.87(0.31)	0.84(0.17)	0.86(0.18)
F0	2500	1	0.67(0.29)	1.58(0.56)	1.15(0.33)	1.23(0.49)
F0	2500	2	0.64(0.20)	1.41(0.56)	0.74(0.29)	1.01(0.34)
F0	2500	3	0.65(0.18)	1.25(0.39)	0.72(0.21)	0.85(0.22)
F0	2500	4	0.68(0.18)	1.24(0.35)	0.72(0.20)	0.83(0.18)
F0	2500	5	0.72(0.15)	0.94(0.35)	0.83(0.19)	0.85(0.18)
F1	500	1	0.97(0.27)	1.06(0.34)	0.90(0.30)	1.01(0.22)
F1	500	2	1.03(0.20)	1.05(0.25)	0.86(0.23)	0.91(0.19)
F1	500	3	0.99(0.26)	1.00(0.16)	0.94(0.25)	0.92(0.16)
F1	500	4	1.02(0.24)	1.00(0.22)	0.94(0.21)	0.96(0.15)
F1	500	5	1.05(0.23)	1.01(0.13)	1.02(0.26)	0.92(0.14)
F1	1500	1	0.62(0.21)	0.80(0.45)	0.69(0.23)	0.91(0.19)
F1	1500	2	0.74(0.18)	0.88(0.27)	0.77(0.21)	0.90(0.19)
F1	1500	3	0.77(0.17)	0.99(0.25)	0.88(0.23)	0.95(0.15)
F1	1500	4	0.79(0.17)	0.90(0.24)	0.95(0.23)	0.93(0.13)
F1	1500	5	0.81(0.16)	0.81(0.21)	1.04(0.26)	0.94(0.13)
F1	2500	1	0.78(0.29)	0.85(0.29)	0.78(0.38)	0.98(0.25)
F1	2500	2	0.73(0.18)	0.72(0.23)	0.80(0.24)	0.87(0.22)
F1	2500	3	0.73(0.16)	0.79(0.24)	0.81(0.20)	0.87(0.15)
F1	2500	4	0.79(0.20)	0.79(0.22)	0.81(0.20)	0.84(0.13)
F1	2500	5	0.82(0.2)	0.73(0.19)	0.94(0.22)	0.86(0.14)

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Table 4.4 Statistics for regressions of tree-level foliar efficiency as related to tree size.

Site	Species	Fertilization	Establishment Density	b_1	p	r^2
CH	Cw	F0	500	-0.023	0.0169	0.523
			1500	0.003	0.7165	n.s.
			2500	0.024	0.0237	0.429
CH	Cw	F1	500	0.007	0.3195	n.s.
			1500	0.032	0.0001	0.837
			2500	0.026	0.0002	0.869
HA	Cw	F0	500	0.001	0.8824	n.s.
			1500	0.007	0.6780	n.s.
			2500	-0.037	0.1160	n.s.
HA	Cw	F1	500	0.016	0.0090	0.544
			1500	0.043	0.0006	0.762
			2500	0.018	0.0167	0.473
CH	Hw	F0	500	-0.111	0.0002	0.852
			1500	-0.201	0.0008	0.745
			2500	-0.400	0.0031	0.647
CH	Hw	F1	500	-0.010	0.1650	n.s.
			1500	0.002	0.9230	n.s.
			2500	-0.011	0.3399	n.s.
HA	Hw	F0	500	-0.032	0.0189	0.458
			1500	-0.020	0.0906	n.s.
			2500	-0.023	0.0169	0.522
HA	Hw	F1	500	-0.010	0.1197	n.s.
			1500	0.004	0.4667	n.s.
			2500	-0.015	0.0132	0.502

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

4.3.2 Tree-Level Foliar Efficiency

Significant establishment density x size and size x establishment density x fertilization interactions were present for tree-level *E* in redcedar stands on CH sites (Tables 4.3 and A3.4). These interactions indicated that in redcedar stands on CH sites: tree-level *E* decreased more strongly with increasing establishment density on unfertilized compared to fertilized sites and; *E* increased with tree size.

Significant establishment density x fertilization and fertilization x size interactions existed for *E* in hemlock stands on CH sites (Tables 4.3 and A3.5). These interactions indicated that in hemlock stands on CH sites: increasing establishment density reduced tree-level *E* but did so more in fertilized than in unfertilized treatments and; *E* decreased with tree size in both fertilized and unfertilized treatments.

Significant establishment density x size and fertilization x size interactions were present for *E* in redcedar stands on HA sites (Tables 4.3 and A3.6). These interactions indicated that, in redcedar stands on HA sites, tree-level *E* was not affected by size at the 500-sph establishment density but increased with tree size in the 1500 and 2500-sph treatments. Tree-level *E* also increased with tree size but increases with size were greater in fertilized than in unfertilized areas in redcedar stands on HA sites.

Significant establishment density x fertilization and fertilization x size interactions were present in hemlock stands on HA sites (Tables 4.3 and A3.7). These interactions indicated that tree-level *E* decreased with increasing density in 1500 and 2500-sph treatment but not in 500-sph treatments. Decreases in tree-level hemlock *E* with increasing density occurred in fertilized stands but not in unfertilized stands on HA sites. Tree-level *E* decreased with size in unfertilized hemlock stands on HA sites but was unaffected by size in fertilized treatments.

Regression analyses of tree-level *E* with size class for each species-site-fertility-density combination are presented in Table 4.4. Where regressions were significant, foliar efficiency of individual redcedar trees tended to increase with tree size. The exception to this trend was unfertilized redcedar planted at 500-sph on CH sites, where *E* decreased with tree size. With hemlock, *E* always decreased with increasing tree size, where regressions were significant. In six out of the 24 regressions, single data points had Studentized residual values exceeding 2.5 and were removed from the regression. In all cases, these outliers represented the smallest rank-size class and had *E* values much greater than the other data points.

Generally, increasing establishment density reduced *E* and this effect was stronger on CH than on HA sites. Fertilization reduced the influence of tree size on *E* for both redcedar and hemlock on HA sites, compared to unfertilized treatments.

These results generally fail to support the hypotheses of this study, with the exception of fertilization. As hypothesized, fertilization did not affect *E* in most instances except fertilized hemlock on CH, where fertilization actually reduced *E*. Tree size did not uniformly influence *E*, as the effects of tree size on *E* were opposite for the two species and were influenced by fertilization. Increasing establishment density decreased *E* but its effects varied with species and fertility status.

4.3.3 Light Interception and Light Use Efficiency

Both fertilization and increasing establishment density increased the amount of PAR intercepted by stands (Tables 4.5 and A3.18). Fertilization increased absorption by 222% relative to unfertilized redcedar stands on CH sites. The 500-sph treatment had significantly lower IPAR compared to the 1500 and 2500-sph treatments, between which no difference existed.

Light use efficiency decreased significantly with each level of increased establishment density (Table A3.18). Fertilization did not affect light use efficiency.

Table 4.5. IPAR and light use efficiency for CH sites.

Fertilized	Planting Density (Stems/ha)	Intercepted PAR (IPAR) (% Incident PAR)	Light Use Efficiency (t/ha/% IPAR)
No	500	15.93(7.979)	0.10(0.031)
No	1500	23.79(11.468)	0.03(0.006)
No	2500	34.182(2.062)	0.02(0.004)
Yes	500	36.07(11.726)	0.09(0.021)
Yes	1500	60.428(12.842)	0.032(0.002)
Yes	2500	62.31(12.946)	0.02(0.005)

These results confirmed the hypothesis that fertilization and increasing establishment density would increase stand interception of light and that density stress would decrease light use efficiency. However, the results did not support the hypothesis that fertilization would increase light use efficiency.

4.3.4 Nutrient Use Efficiencies

Nutrient use efficiencies for all nutrients examined were generally greater in redcedar than in hemlock on CH sites and greater in hemlock than in redcedar on HA sites (Tables 4.2, A3.8 – A3.18). The exception to this trend was Ca use efficiency, which was greater in hemlock on both sites. No significant species effects were present for B use on HA sites.

Fertilization increased the use efficiency of all nutrients examined on both sites and for both species. Species x fertilization interactions were present for the use efficiency of N, K, Ca, Mg, Zn and B on CH sites and P on both sites. Fertilization increased N use efficiencies of both species on CH sites but increased it more in hemlock than in redcedar and increased the difference between the two species. Fertilization increased the use efficiencies of P, S, Mg and Zn more in hemlock than in redcedar and eliminated species differences. On HA sites, fertilization did not increase P use efficiency in hemlock but did so in redcedar and eliminated species differences. Fertilization increased K and B use efficiency in hemlock more than in redcedar on CH sites but did not eliminate the tendency for redcedar to have greater use efficiency. Fertilization increased Ca use efficiency more in hemlock than in redcedar on CH sites and created a species difference where none existed on unfertilized sites.

Species x establishment density x fertilization interactions existed for N and Zn use efficiency on CH sites. Nitrogen and Zn use efficiency increased with establishment density in unfertilized redcedar stands. Use efficiencies in hemlock were less than in redcedar and were unaffected by density on unfertilized CH sites. Fertilization increased N and Zn use efficiencies but the increase was greater at higher establishment densities and in hemlock than in redcedar.

These results generally did not support the hypotheses. Fertilization tended to increase nutrient use efficiencies, rather than decrease them as was expected.

4.3.5 Foliage – Growth Rate Relationships

Regressions describing relationships between 2002 stand foliage mass (t/ha) and average annual mass growth rate (t/ha/yr) for each site-species combination, including both fertilized and unfertilized stands at all three establishment densities, are presented in Table 4.6 and shown in Figures 4.1 and 4.2. In all cases a strong, positive and linear relationship existed between foliage mass and average annual mass growth rate. There were no indications of declining growth capacity per unit of foliage mass.

Table 4.6. Statistics for regressions of average annual stand growth rate vs. stand foliage mass.

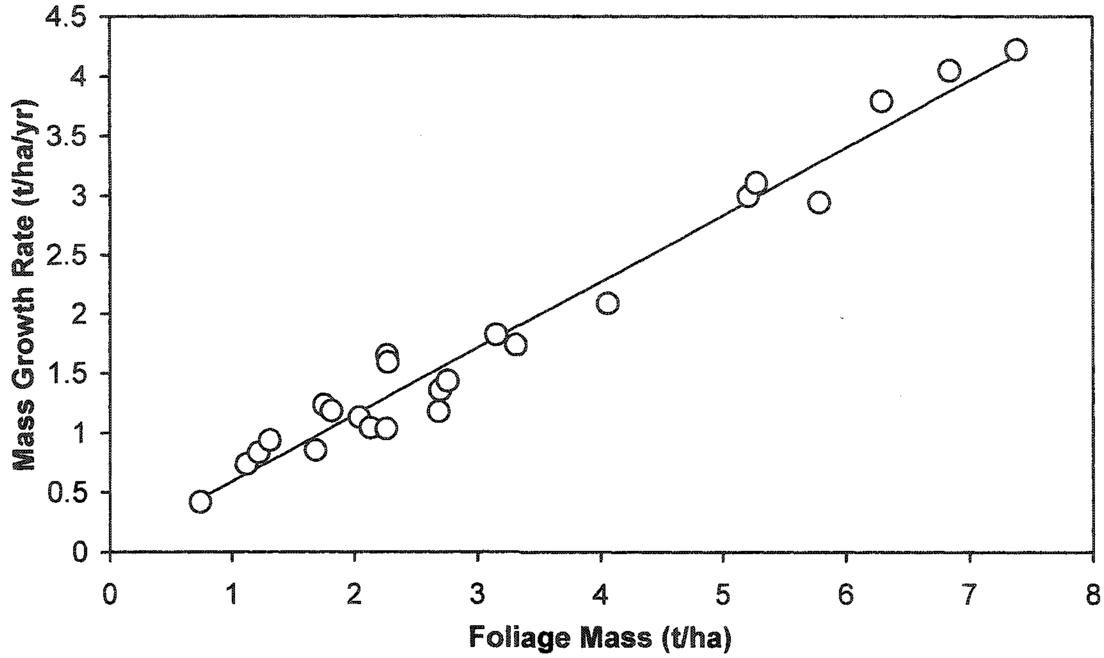
Site	Species	b_1	p	r^2
CH	Cw	0.562	<.0001	0.967
HA	Cw	0.646	<.0001	0.983
CH	Hw	0.577	<.0001	0.984
HA	Hw	0.625	<.0001	0.988

Table 4.7. Statistics for regressions of average annual mass growth rate vs. IPAR for Cw on CH sites.

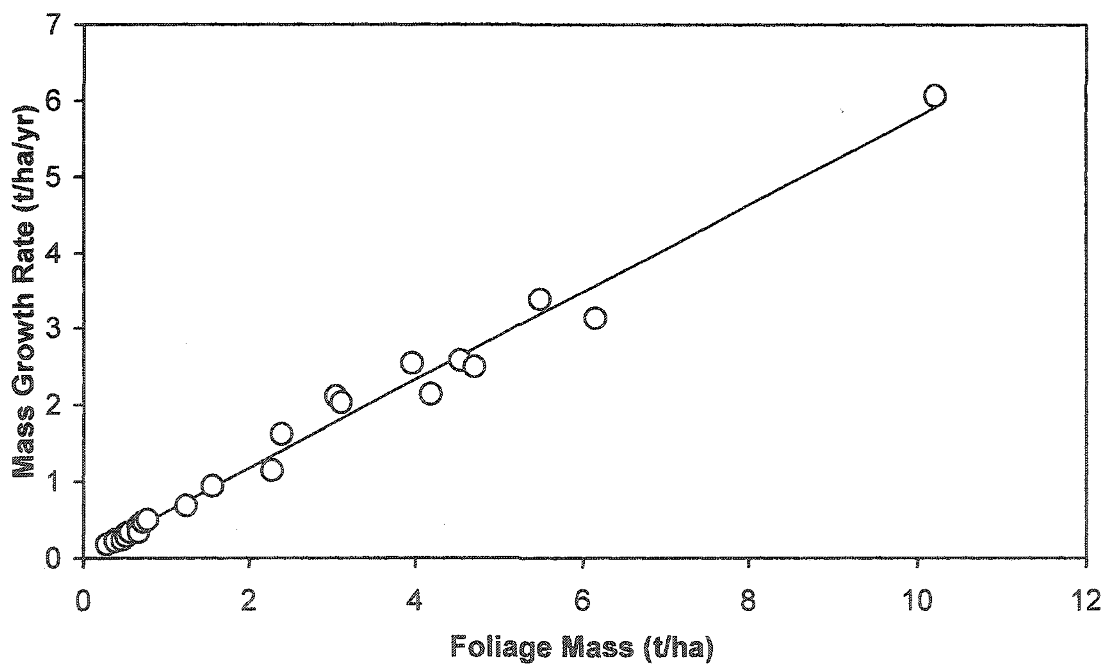
Mass Component	b	SE (b)	c	SE (c)	F	p
Total Mass (t/ha/yr)	0.538	0.0558	0.027	0.0017	615.26	<.0001
Wood Mass (t/ha/yr)	0.222	0.0254	0.030	0.0018	562.39	<.0001
Foliage Mass (t/ha/yr)	0.133	0.0148	0.022	0.0019	416.82	<.0001

Regressions describing the relationship between IPAR and annual mass growth rate (t/ha/yr) of stands are found in Table 4.7 and shown in Figures 4.3 to 4.5. The non-linear regressions were significant and had high F values. The relationships indicated an increasing rate of annual growth for all three mass components as IPAR increased.

The results of this study support the hypothesis that stand growth rates were related to foliage mass in a linear fashion. The linear relationships between foliage mass and annual growth rates indicates that canopy carrying capacity has likely not yet been reached on the more productive fertilized and HA sites, and that continued, or increasing, levels of growth may be anticipated, unless nutrient supplies limit further canopy expansion. Maximum intra-specific competition is associated with attainment of site foliage carrying capacity (Ford 1982). Therefore, density stress and resulting competition may increase on these sites until foliage carrying capacity is attained. These results do not confirm the hypothesis that light use efficiency would exponentially increase for stem wood growth but increase linearly for other components with increased light absorption. Rather, foliage, wood and total mass growth rates all increased exponentially with increasing stand light absorption.

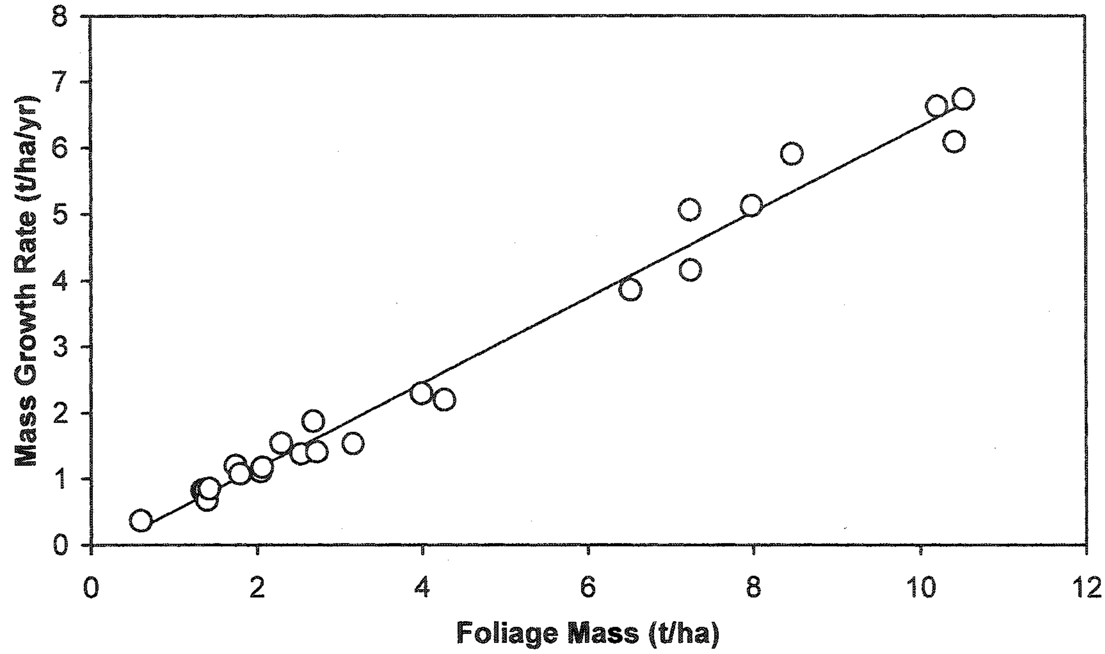


a) Western redcedar

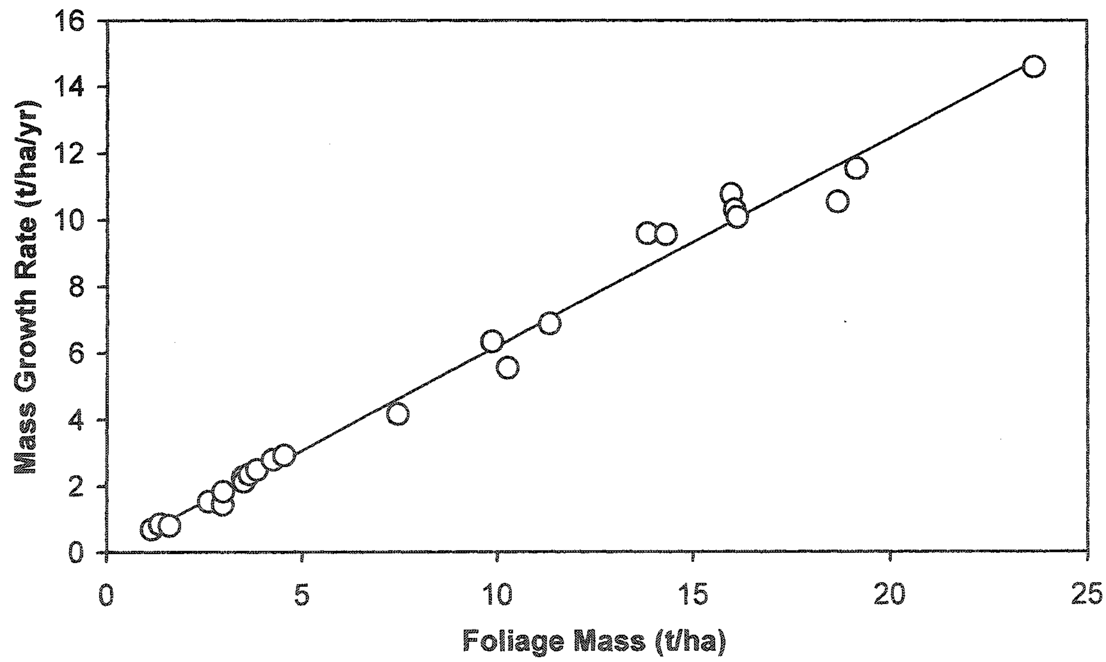


b) Western hemlock

Figure 4.1 Average annual stand mass growth rates on CH sites as a function of stand foliage mass.



a) Western redcedar



b) Western hemlock

Figure 4.2 Average annual stand mass growth rates on HA sites as a function of stand foliage mass.

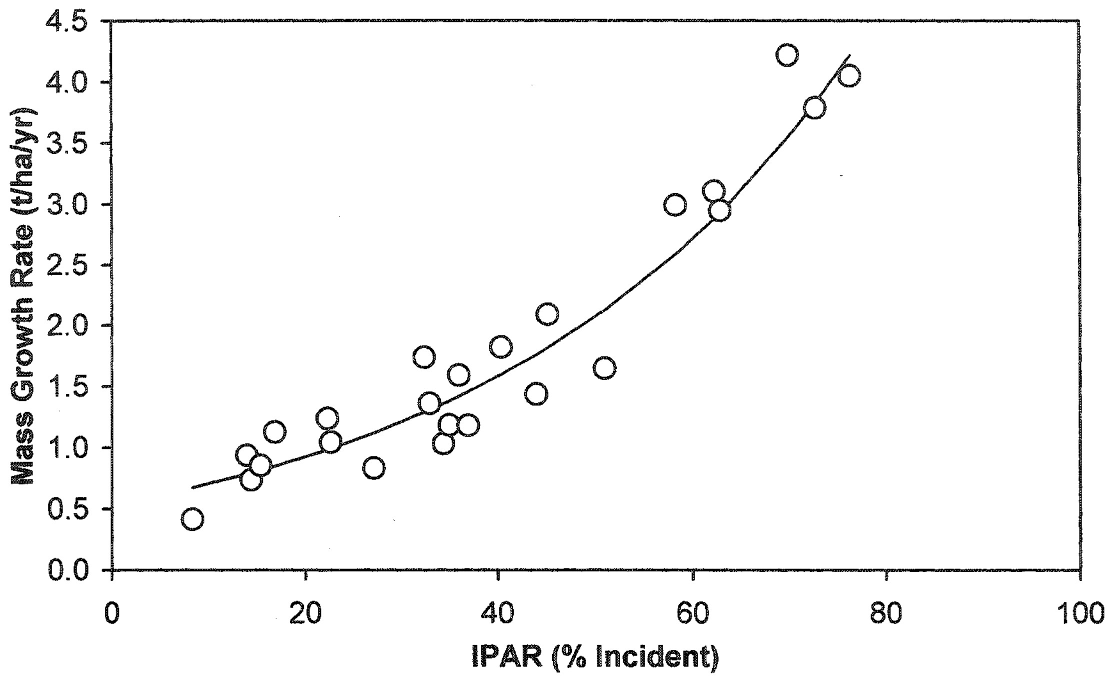


Figure 4.3 Average annual stand dry mass growth rate with increasing IPAR.

Figure 4.4 Average annual stand foliage mass growth rate increasing IPAR.

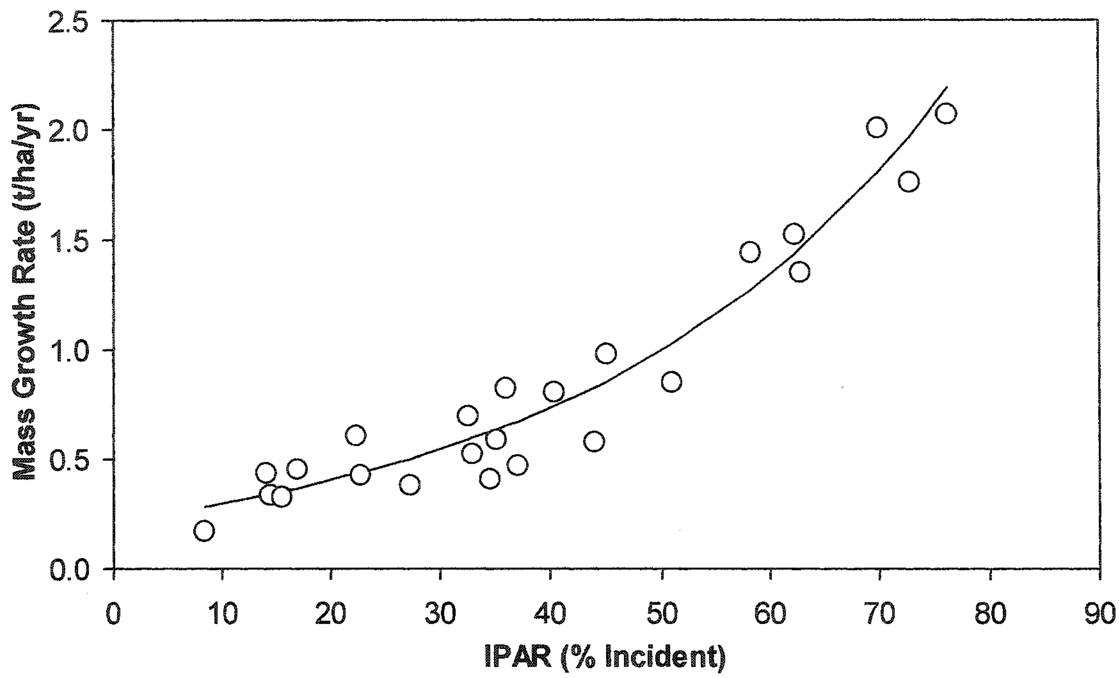


Figure 4.5 Average annual stand wood mass growth rate with increasing IPAR.

4.4 Discussion

Fertilization increased nutrient use efficiency of all nutrients examined on both sites. This was unexpected as other studies have shown that fertilization tends to decrease nutrient use efficiencies because net photosynthetic capacity per unit of foliar nutrient tended to decline as foliar nutrient concentrations increased (Barclay and Brix 1985, Elliott and White 1993, Elliott and White 1994, Brown *et al.* 1996a, 1996b, Mitchell *et al.* 1996). Nitrogen use efficiency of both hemlock and redcedar has been shown to increase up to a whole plant concentration of approximately 11 – 12 mg per g and then remain constant (Brown *et al.* 1996a). Whole-plant nutrient concentrations in stands in this study may not have reached the point of diminishing returns and thus nutrient use efficiency may have continued to increase when foliar nutrient concentrations were increased by fertilization (Chapter 2). This relationship may exist for nutrients other than N and P, as addition of urea fertilizer has been shown to increase solubility and leaching of Al, Cu, Fe, Mn and Zn in forest soil horizons and increase foliar nutrient concentrations of nutrients not applied in fertilizer (Chapter 2, Otchere-Boateng and Ballard 1981). The foliar concentration of one nutrient may also affect the use efficiency of another (Reich and Schoettle 1988), which creates complex conditions when many nutrients are considered.

Hemlock showed greater nutrient use efficiency than redcedar on HA sites, while redcedar tended to have greater use efficiencies on CH sites. However, fertilization on CH sites tended to increase hemlock use efficiencies to the point of equalling or exceeding those of redcedar. Redcedar had greater nutrient use efficiency on the more nutrient-poor CH site, which is surprising, given that hemlock has been shown under laboratory conditions to have greater N use efficiency, particularly under conditions of low N supply (Brown *et al.* 1996a, 1996b). Physical conditions, such as the tendency for soils on CH sites to be saturated for longer in the year than on HA sites, or the greater influence of salal on nutrient availability to hemlock and its possible allelopathic activity (Prescott *et al.* 1996) may have negatively influenced nutrient use efficiencies in hemlock. Differences in nutrient use efficiency between species have been attributed to differences in priority allocation to physiological processes and responses to environmental conditions (Gower *et al.* 1989, Bothwell *et al.* 2001, Dicus and Dean 2001, Ripullone *et al.* 2003).

The generally positive influence of increasing establishment density on nutrient use efficiency reflects the greater amount of available growing space filled by denser stands. The tendency for there to be no difference in use efficiency between the 1500 and 2500-sph treatments may indicate the developing influence of competition. Increased density and intra-specific competition has been shown to decrease nutrient use efficiencies (Dicus and Dean 2001).

Foliar efficiency was examined at both stand and tree levels. No species or treatment effects were significant for stand-level *E* on HA sites. On CH sites, both increasing establishment density and fertilization reduced stand-level *E*. Tree-level foliar efficiency decreased with increasing establishment density on both CH and HA sites, although there tended to be no significant differences between the 1500 and 2500-sph treatments. Increasing stand density has been noted to reduce foliar efficiency at both stand and tree levels (Waring *et al.* 1981, Ford 1982, Brix 1983, Velzquez-Martinez *et al.* 1992, Sterba and Amateis 1998, Woodall *et al.*2003). Fertilization increased tree-level *E* in redcedar stands on HA sites. This increase in *E* ten growing seasons after the last fertilizer application is unexpected but possibly the result of elevated nutrient supply levels following fertilization. Why redcedar, but not hemlock, may be able to take advantage of elevated nutrient supply levels on HA sites is unclear, but may be related to the deeper rooting depth of redcedar (Bennett *et al.* 2002, Wang *et al.* 2002). Fertilized stands have been noted to have initially increased *E*, up to seven years post-treatment, but then to experience declines in *E* to levels equal to or below unfertilized stands (Brix 1983, Valinger 1993, Mitchell *et al.* 1996,). Stand-level foliar efficiency of hemlock was greater than that of redcedar and reflected the effects of fertilization more strongly than redcedar, while *E* of redcedar stands was reduced more by increasing establishment density than that of hemlock.

The regression analysis of foliar efficiency by size-rank class and interactions present in the analyses of variance of tree-level *E* indicate complex relationships between fertilization, size, and density for each species-site combination. Tree-level *E* was influenced by tree size in all four species-site combinations. Redcedar *E* tended to increase with tree size, with the exception of unfertilized CH sites planted to 500-sph. Foliar efficiency in hemlock always decreased with tree size, where the effect was present. The large *E* values of the smallest sized trees may reflect a change in strategy from expansive growth to stress tolerance as these trees assume a subordinate competitive position (Grime 2001). Foliar and crown efficiency has generally been shown to decrease with tree size, although the most efficient tree size depends on stand structure and the nature of competition (O'Hara 1988, Larocque and Marshall 1994, Maguire *et al.* 1998, Sterba and Amateis 1998, Vanninen and Makela 2000).

Why unfertilized redcedar at 500 sph on CH sites should show a trend more similar to hemlock than redcedar under other conditions is unknown but may be due to relatively greater influence of salal on nutrient availability. Low-density stands are more open and the salal more abundant because it's less shaded. Under these conditions the relative advantage redcedar has over hemlock of rooting deeper than the salal (Bennett *et al.*2002, Wang *et al.* 2002) may be negated. The lack of any clear relationship between *E* and tree size in redcedar stands at 1500-sph on CH stands may reflect a transitional status between the negative relationship between *E* and tree size in 500-sph stands and the more general condition of a positive trend between tree size and *E* in redcedar. Development of the positive relationship between tree size and *E* in redcedar appears to have been promoted by increasing establishment density on both sites and by fertilization on HA sites. Increasing establishment density resulted in a greater tendency for *E* to be influenced by tree size on unfertilized compared to fertilized redcedar stands on CH sites. The relationship between tree size and *E* was less complex for hemlock than for redcedar. Fertilization tended to reduce the relationship between tree size and foliar efficiency while increasing density tended to promote it.

The presence of size influence on foliar efficiency in redcedar and hemlock may indicate the development of competition under different conditions of density and nutrient availability. The general species difference in size effect on E may have implications for stand development in that smaller trees in hemlock stands may be at less of a competitive disadvantage compared to larger trees due to their greater E. This would likely result in lower differentiation in hemlock stands. The opposite condition would possibly be true in redcedar stands, which would tend to differentiate more rapidly due to the competitive advantage of larger trees, in term of E. Chapter 5 results confirm that size hierarchies are more strongly developed in redcedar than in hemlock stands.

The strong positive relationship between stand foliage mass and average mass growth rate for all four site-species combinations indicates that foliage mass was an important determinant stand growth. The consistent positive linear relationship between stand foliage mass and mass growth rate, with no plateau effect or indication of declining growth per additional unit of foliage mass, indicates that stands on more productive site or fertilization combinations have not yet reached carrying capacity for foliage mass. Additional foliage mass expansion and commensurate increases in average mass growth rate are likely and may be promoted by further applications of fertilizer. That foliage carrying capacity has not yet been reached under more productive conditions also suggests that competition is not yet fully developed in these stands. The close relationship between total stand foliage mass and total stand growth has been demonstrated in other studies (Ford 1982, Espinosa Bancalari and Perry 1987, Vose and Allen 1988, Velazquez-Martinez *et al.* 1992), as has been the development of intra-specific competition with canopy closure and the attainment of maximum canopy size (Ford 1982).

Light interception increased with establishment density and fertilization. Light use efficiency was decreased by increasing establishment density and was not affected by fertilization. Fertilization has been shown in other studies to increase intercepted light use efficiency (Balster and Marshall 2000). Self-shading by canopy components has been considered responsible for reductions in canopy efficiency with canopy size (Waring *et al.* 1981, Ford 1982, Brix 1983, Russell *et al.* 1989, Velazquez-Martinez *et al.* 1992). Average annual growth rate of stem wood, foliage and total stand mass increased exponentially with light absorption. Exponential increases in stem wood growth rate with increasing PAR interception by stands have been noted before and it has been hypothesized that differences in nutrient availability or environmental conditions may preferentially shift carbon allocation to stem wood, compared to total mass and other mass components (Balster and Marshall 2000). The results of this study contradict this theory in that an exponential increase in mass growth rate with increasing PAR absorption was observed not only for stem wood but for foliage and total mass as well. The cause of this exponential rather than linear increase in mass growth rate remains obscure but may be due to the increased nutrient use efficiencies, for many nutrients, not just those added in fertilizer, observed in fertilized stands.

4.5 Conclusion

Fertilization has resulted in increased nutrient use efficiency and this is likely its only structural-functional legacy in these stands that would continue to increase growth.

Foliar efficiency varied with tree size in both redcedar and hemlock but with different patterns for each species. There was a generally positive relationship between tree size and *E* in redcedar and a negative relationship with tree size in hemlock. This difference in pattern implies that redcedar stands may differentiate more readily and inherently be more structurally diverse than hemlock stands, due to the competitive advantage that larger trees have, in terms of *E*. Hemlock stands, on the other hand, may be more structurally uniform due to the higher *E* of smaller trees, although this is speculative.

Site foliage carrying capacity has likely not yet been reached on the site type and fertilization combinations that are most productive for vegetation growth.

Mass component growth rates of stem wood, foliage and total stand mass increased exponentially with intercepted PAR, although the reason for this is obscure.

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Chapter 5

Size Hierarchy Development in Juvenile Western Redcedar and Western Hemlock Stands

5.1 Introduction

Our understanding of the influence of fertilization, and more generally soil resource supply, on stand development continues to evolve. Fertilization was once regarded as being able to increase tree growth over the short term and truncate the period of stand development, rather than increasing the vegetation potential of sites (Miller 1981). More recently, fertilization has been shown to increase site nutrient supply (Bradley *et al.* 2000, Bennett *et al.* 2003), tree growth (Bennett *et al.* 2003) and canopy efficiency (Balster and Marshall 2000) 8 to 13 years after treatment. Our understanding of the influence of fertilization and site fertility on stand development is limited by our understanding of the more general topic of the effect of soil resource supply on competition. Conflicting theories exist regarding the role of fertility in competition processes. It has been suggested that competition is of greater magnitude on sites with greater resource supply (Goldberg and Barton 1992, Grime 2001). Alternatively, greater soil resource supply may not affect competition (Tilman 1988), possibly because decreased competition for soil resources on more productive sites is offset by increased competition for light (Wilson and Tilman 1993) or because levels of herbivory may change with site growth potential, effectively altering competitive relations (Gurevitch *et al.* 2000). The addition of fertilizer to artificially enhance soil nutrient supply has tended not to increase the magnitude of competition in plant communities (Goldberg and Barton 1992). To understand the influence of fertilization on stand development, we need to better understand the influence of soil resource supply on competition, the subsequent influence of competition on stand structure, and the influence of structure on growth.

Size hierarchies describe concentration of biomass within populations (Weiner and Solbrig 1984, Weiner and Thomas 1986) and offer insight into inter-plant relations and factors influencing stand development (Newton 1990, Sarkkola *et al.* 2003). Generally, variable growth rates associated with conditions in the regeneration niche, and the varying genetic potential of individuals, will produce some size variation and differences in exponential growth within a developing population (Weiner and Thomas 1986, Schwinning and Weiner 1998). There is a tendency for this inequity in size to increase with time, as trees compete due to their increasing size and site occupancy by the stand, until smaller trees die and self-thinning begins (Weiner and Thomas 1986). However, competition influences and modifies size distribution (Westoby 1982). Symmetric competition is two-sided with resource capture ability proportionally related to tree size (Weiner 1990). Relative growth rate (RGR) is either uncorrelated or negatively correlated with tree size in symmetric competition (Weiner 1990). Asymmetric competition is one-sided with resource capture ability disproportionably greater for larger individuals (Weiner 1990). Relative growth rate may be positively correlated with tree size in asymmetric competition (Weiner 1990, Laroque and Marshall 1993, Stoll *et al.* 1994). Factors that increase asymmetric competition, typically associated with pre-emption of light, are hypothesized to increase differences in size between individuals and lead to more strongly developed size hierarchies, with a greater proportion of biomass concentrated in fewer individuals (Weiner 1986, Weiner and Solbrig 1984, Weiner 1990). Conversely, symmetric competition, typically for soil resources, is thought to produce more weakly developed hierarchies with more uniformly sized individuals composing the population (Schwinning and Weiner 1998 Weiner *et al.* 1997). Competition between trees within stands typically includes both symmetric and asymmetric elements because competition exists concurrently for both light and soil resources. Site conditions, stand structure and stand age determine which mode is dominant (Newton 1990, Weiner 1990, Nambiar and Sands 1993, Newton and Jolliffe 1993). Intensity of competition, in terms of the steepness of slopes in yield-density relationships, for belowground resources is negatively correlated with that for aboveground resources in herbaceous ecosystems: increased competition for light is associated with decreased competition for soil nutrients and vice versa (Wilson and Tilman 1993). Heterogeneously distributed soil resources, particularly soil-available phosphorus, may lead to a masking of symmetric competition and the appearance of asymmetric competition, although evidence for this is contradictory (Schwinning and Weiner 1998, Blair 2001, Facelli *et al.* 2002).

The influence of density and environmental factors on the development of size hierarchies in trees is unclear. Competition has been shown to increase size inequity within populations of trees (Knox *et al.* 1989, Newton 1990, Laroque and Marshall 1993) and non-woody species (Weiner 1985, Schmitt *et al.* 1986, Weiner 1986), although response varies among species (Lieffers and Titus 1989). However, the role of site factors, such as soil moisture and nutrient supply are not clear. Increased availability of soil moisture has been shown to increase competition and enhance the development of size inequality within tree stands and populations of non-tree plants through increased growth rates (Wichmann 2001, Briones *et al.* 1998, Weiner 1985). However, the influence of soil nutrient availability on size hierarchies is complex. Peatland drainage of boreal sites, which presumably enhances nutrient supply in the root zone through increased mineralization rates, reduced size inequity within stands, by increasing the growth rate of smaller trees relative to that of larger trees (MacDonald and Yin 1999). Drainage initially increased size inequality within stands across southern Finland, however, size inequality later remained stable and it was concluded that although the importance of asymmetric competition increased with drainage, a symmetric component was still present (Sarkkola *et al.* 2003). In this latter case, though, size diversity rather than size inequity, *per se*, was examined (Sarkkola *et al.* 2003). Irrigation and fertilization, both separately and in combination, did not influence size hierarchy development in stands, relative to untreated controls, although the growth rate of small trees was increased by combined fertilization and irrigation relative to that of larger trees (Nilsson *et al.* 2002). The lack of influence of resource supply on competition and size hierarchy development could have resulted from an increase in site carrying capacity or 'stockability' in this experiment (Nilsson *et al.* 2002, DeBell *et al.* 1989). Size hierarchies tend to decline with stand age in regenerating stands on poor sites, consistent with an increase in significance of symmetric competition (Newton 1990).

Size inequality measures have been inconsistently presented in the literature. It has been argued that size hierarchies are described in the most biologically meaningful manner with the Gini coefficient or coefficient of variation (Weiner and Solbrig 1984, Knox *et al.* 1989). Measures of size distribution, such as Weibull parameters (Sarkkola *et al.* 2003) and skewness (Knox *et al.* 1989) have been used to describe size hierarchy, although their interpretation is tendentious (Weiner and Solbrig 1984, Weiner and Thomas 1986, Knox *et* *al.* 1989). A combination of a measure of strict size inequity accompanied by a measure of size distribution (Newton 1990) likely gives the clearest picture of mode of competition and consequent changes in stand structure.

This study examined the influence of soil fertility (qualitative nutrient supply levels associated with site and fertilization) on development of size hierarchies and the comparative growth rates of different sized individuals within these hierarchies. The study was conducted in 14-year-old stand of western redcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), last fertilized 10 year previously. The study was established at three densities with and without fertilization, on nutrient-poor (CH) and nutrient-rich (HA) sites on northern Vancouver Island. Specific questions were: 1) does fertilization influence size hierarchy development; 2) does size hierarchy development vary between two species; 3) does increasing density stress influence size hierarchy development; and 4) are fertilizer and species effects on size hierarchy development consistent across two sites of different inherent fertility. Based on results from previous studies, it was hypothesized that size hierarchy development would not be influenced by fertilization or species; would not increase with stand density; and would be consistent on both sites.

5.2 Materials and Methods

5.2.1 Study Sites

The study site was located on northern Vancouver Island, British Columbia, Canada, between Port Hardy and Port McNeill (50° 60'N, 127° 35' W) in the Submontane Very Wet Maritime variant of the Coastal Western Hemlock Biogeoclimatic, or CWHvm1, zone

(Green and Klinka 1994). The study site was approximately 50m ASL in undulating terrain with frequent rocky knolls and wetlands located in depressions. Surface materials consist of unconsolidated glacial moraine and fluvial outwash deposits that range from blankets over 1m in depth to shallow veneers with exposed bedrock. Mineral soils ranged from silty clay loams to fine sand with high coarse fragment content. Organic soils of wetland or upland origin are also common within the study site.

The area receives approximately 1900 mm of precipitation annually, most of which falls as rain. Growing season soil moisture deficits typically do not occur (Lewis 1982). Average daily mean temperature ranges from 3.3° C in January to 14.1° C in August. A relatively high percentage of the annual solar radiation is received as diffuse radiation (McKay and Morris 1985), reflecting overcast conditions throughout the year and frequent summer fog. Direct sunlight exposure ranges from 1.5 h/day in December to 6.4 h/day in July. Global solar radiation incident of a horizontal surface averages 10.212 MJ/m^2 per day and ranges from a low of 2.043 MJ/m^2 per day in December to 18.935 MJ/m^2 per day in July (McKay and Morris 1985).

Two common CWHvm1 forest types were examined at the study site. Hemlock Amabilis Fir (HA) types are occupied by stands composed of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) while Redcedar Hemlock (CH) types are occupied by stand composed of western red redcedar (*Thuja plicata* Donn) and western hemlock. Both forest types are typically found on well to imperfectly drained Duric Humo-Ferric Podzols and are considered zonal sites (Lewis 1982, Green and Klinka 1994). HA sites typically occur on areas that have historically been subject to stand-replacing wind throw events (Lewis 1982). HA stands are mid-seral and have a dense, even-aged structure with uniform canopies. Due to the dense canopy cover, HA stands have poorly developed understory vegetation layers. Surface organic layers in HA stands are comparatively thin (5 – 10 cm) and friable. CH stands likely represent a climatic climax state, with an uneven-aged structure and open, irregular canopies. CH stands typically have well developed understory plant communities dominated by dense salal (*Gaultheria shallon* Pursh) growth. Surface organic layers in CH stands are thicker (10 – 45 cm) and more compact than on HA sites. Soil nutrient availability is lower on CH sites than on HA sites (Prescott *et al* 1996).

The study site was clear-cut logged in 1986, broadcast burned and planted with western hemlock and western redcedar in 1987.

5.2.2 Treatments

Ninety-six treatment plots, each containing 64 sample trees were established in 1987. Plot size and tree spacing varied with density. Treatments consisted of a fully crossed factorial combination with two levels of fertility (fertilized and non-fertilized) and three levels of density (500, 1500 and 2500 stems per ha). Trees in the 500 sph plots were spaced 4.5 m apart, resulting in a central (core) measurement area of 36 x 36 m and a total plot size of 54 x 54 m, including a buffer zone. Buffer zones were planted at the same spacing as the core areas they surrounded. The 1500 sph treatment had a tree spacing of 2.6 m; a core measurement area of 21 x 21 m and a total area plot size of 36 x 36 m. Between-tree spacing was 2 m in the 2500-sph treatments; with a 16 x 16m core measurement area and total plot size of 32 x 32 m.

Fertilized plots received a 60 g dressing of Nutricoat™ controlled release fertilizer at time of planting. The fertilizer was raked into a 15 cm radius area around each seedling and provided 10 g of N, 2.5 g of P and 5 g of K to each seedling. Total application rate per ha varied with density. All fertilized plots were refertilized before the beginning of the growing season in early spring of 1993 with a broadcast application of 225 kg of N and 100 kg of P per ha.

The 2 x 3 combination of fertilized/unfertilized by density was duplicated for both redcedar and hemlock on both CH and HA sites. Each fertilization-density-species combination was randomly assigned within four blocks on each site, with a single treatment level replicate per block. Thus, a total of 48 plots examined 12 treatments with 4 replications per treatment level.

Height and diameter of each sample tree in core measurement areas were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997 and 2002. Height was recorded to the nearest cm. Diameter was measured in mm at the root collar for the years 1988 – 1997. Diameter was measured at 1.3 m above the root collar (breast height) in 1997 and 2002.

5.2.3 Biomass Determination

Regression equations were developed to predict individual tree total biomass and biomass of foliage, branch, bark and wood components. Individual saplings were destructively sampled after growth had ceased in the fall of 2001 and 2002. Saplings were selected to span the existing size range within treatment levels based on measurements at breast height. Both redcedar and hemlock were sampled from across a range of treatments on both site types. Sample trees were selected using a two-stage process. In the first stage, several sample trees were initially selected using a random procedure within each treatment level. Diameter at breast height was measured for all neighbouring trees within a 4.3 m radius of randomly selected trees to establish a size range for the treatment level. In the second stage, sample trees were selected to span the size range determined in the first stage. Sample trees were selected to be free of significant stem and crown damage. Sample trees were felled and their height and diameter at breast height were measured. Stems were then cut into 1 m segments and branches removed by severing at the point of branch contact with the stem section. Total fresh biomass of the stem section and the branches was then determined to the nearest 50 g. A 3-cm-wide disk was subsampled from each stem section. These subsamples were removed approximately 30 cm from the bottom of each stem section, then at 100-cm intervals up the stem, with an additional section extracted where the stem narrowed to a diameter of 1 cm. The portion of the stem above this point was designated the terminal and analyzed separately as a branch. Two or three undamaged branches were randomly subsampled from each section. In some cases, there were no living branches on the bottom stem section, and dead branches were not included in calculations. Stem disks and branch subsamples were taken to a laboratory facility in Port McNeill for further analysis.

Dry biomass conversion factors were determined for stem wood, stem bark, foliage and branch components (twig) for each section of each sample tree. In the lab, bark was manually stripped from each stem section and branches were dissected into 10 – 15 cm segments. Fresh biomass of each of the components was determined to the nearest 0.01 g. Bark, stem wood components and dissected branches were dried at 70 ^{0}C in a drying oven for 72 hours, or until they ceased to lose biomass. Foliage was separated from woody portions of branches through manual agitation and stripping. Dry biomass of bark, wood, foliage and twig components was measured to the nearest 0.01 g. Dry biomass conversion factors for each section were determined as follows:

$$\textit{proportional dry biomass (foliage or twig)} = \frac{\textit{dry biomass of foliage or twig}}{\textit{fresh biomass of branch}}$$

$$\textit{proportional dry biomass (wood or bark)} = \frac{\textit{dry biomass of wood or bark}}{\textit{fresh biomass of stem section}}$$

Foliage and twig conversion factors were averaged for each section. Total component dry biomass was determined for each section by multiplying fresh biomass of the stem and branches by respective conversion factors. Total section dry biomass was determined by summing all components. Total tree dry biomass was determined by summing values for each section.

Initial analysis of sample tree data in 2001 indicated greater variability among component biomasses in redcedar compared to hemlock. Consequently, a total of 84 redcedar sampling were destructively sampled and a total of 41 hemlock.

5.2.4 Biomass Prediction Equations

Predictive equations from total biomass were developed based on tree diameter and height as predictive variables. Both diameter at breast height squared (d^2) and height multiplied by d^2 (d^2h) were investigated as predictor variables. Two regression models commonly used in biomass estimation were examined: a second degree polynomial model using weighted least squares (1) and an allometric model ordinary least squared regression on logarithmically transformed data (2):

$$Y_j = \beta_{0i} + \beta_1 X_{1j} + \beta_{2i} X_{2j} + \varepsilon_j \qquad [1]$$

Where Y_j is the oven dry biomass (g) of the jth sample tree (j ranging from 1 to 84 for redcedar and 1 to 41 for hemlock); $X_{1j\ and}\ X_{2j}$ were d^2 and $(d^2)^2$ or d^2h and $(d^2h)^2$, respectively for the jth sample tree and β_0, β_1, and β_2 were parameters estimated by weighted least squares. Two weights were attempted, the inverse of the predictor variable ($1/\ d^2$ and $1/\ d^2h$) and the inverse of the predictor variable squared ($1/\ d^4$ and $1/(\ d^2h)^2$). These weights were selected based on the pattern of variability in the predictor variables (variances proportional to the weight used).

The allometric model tested was:

$$\log_e Y_j = \log_e \beta_{0i} + \log_e \beta_1 X_j + \log_e \varepsilon_j \qquad [2]$$

where $\log_e \beta_0$ and $\log_e \beta_1$ are parameters estimated by ordinary least squares regression on $\log_e$-transformed data for tree biomass and $\log_e \varepsilon_j$ is the residual term.

Predictive models were assessed based on the proportion of biomass variation explained (r^2), the standard error or estimate for the regression (SEE) residual plots, and a positive test for normality using the Shapiro-Wilks test. Model fitting was conducted using the Statistical Analysis System (SAS), Version 8.2.

Results indicated that the allometric model [1] using d^2h as the predictor variable explained the greatest biomass variation tended to have the lowest SEE and met the homogeneity of variance and normality assumptions of regression. Back-transformational bias was corrected according to Baskerville (1972). Final parameter estimates, correction values and regression statistics are presented in Table 5.1. Predictive models were used to predict tree biomass based on the 2002 measurements. Stand-level biomass was determined by summing tree biomasses for each plot and converting the sum to a per ha value.

Table 5.1 Tree biomass prediction equations and model statistics (allometric model).

Species	*n*	b_o	b_1	*SE*	*p*	r^2
Redcedar	82	-2.018	0.728	0.023	<.0001	0.958
Hemlock	41	-1.883	0.732	0.131	<.0001	0.939

5.2.5 *Quantification of Growth and Size Hierarchy Development*

Size hierarchies within tree size and biomass frequency distributions were quantified with the Gini coefficient (G; Weiner and Solbrig 1984), a dimensionless index ranging in value from a minimum of 0.0 (absolute equality of a size variable within a frequency distribution) to a maximum of 1.0 (absolute size inequality). The Gini coefficient was determined as:

$$G = \left(\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|\right) / \ 2n(n-1)(M)$$

Where: G = Gini Coefficient
M = Sample Mean of Size Variable or Biomass Component
n = Number of Sample Observations
x_i, x_j = ith and jth individuals

Stem volume index was calculated using the volume of a cone into which tree height and diameter at breast height values were substituted for each tree. Volume index was used as an indicator of tree size during stand development. Gini coefficient values were determined for tree height and stem volume index for each measurement year and for tree biomass in

2002. The direction of size hierarchy development, or asymmetry, was assessed using the grouped skewness coefficient (g_1; Sokal and Rohlf 1995) determined for volume index in each measurement year. Size hierarchies were thus assessed with two measures: the magnitude of hierarchy development was determined with the Gini coefficient and its tendency towards smaller or larger individuals determined with the skewness coefficient.

Relative growth rate and absolute growth rate (RGR, AGR; Hunt 1990) for stem volume index were calculated as:

$$RGR = [\log_e (X_n) - \log_e (X_{n-1})] / (t_n - t_{n-1})$$

$$AGR = (X_n - X_{n-1}) / (t_n - t_{n-1})$$

Where: RGR = Relative Growth Rate of X
AGR = Absolute Growth Rate of X
X = Volume Index
t = Measurement Year

RGR was calculated based on plot averages for volume index and for 10 basal area size classes drawn from pooled observations for each treatment level. Size classes were delineated by pooling all plot observations for each treatment level, sorting in ascending order by size and dividing to achieve classes with an approximately equal number of individuals. Absolute growth rate between measurement years was determined based on plot averages of volume index. Both RGR and AGR were calculated for growth periods between measurement years: 1988 – 1989; 1989 – 1990; 1990 – 1992; 1992 – 1994; 1994 – 1997; and 1997 – 2000.

5.2.6 *Statistical Analysis*

A general linear model approach was used to examine the cumulative effect of treatments on stand structural inequality, asymmetry and growth after 14 years of stand development on each site. A mixed-effects was model used for each site type with species, fertilization and density tested and fixed effects and blocks included as a random effect:

$$y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (ac)_{ik} + (bc)_{jk} + (abc)_{ijk} + \varepsilon_{ijkl}$$

Where: y_{ijk} = Response of the *i*th species at the *j*th fertility level at the *k*th density level
μ = General Mean
a_i = Species Effect
b_j = Fertility Effect
c_k = Density Effect
ε_{ijkl} = Residual Error

Where interaction terms were significant, given significance of at least one constituent fixed effect, simple effects were compared by adjusting least-square means for Tukey's Honestly Significant Difference test. Where interactions were significant, density, fertilizer and species effects were examined together. Where interaction terms were not significant, simple effects were compared using Tukey's HSD test. A significance level of $p < 0.01$ was used for detecting the presence of main effects and interactions, while a significance level of $p < 0.05$ was used in mean separation tests. The different significance levels were used to ensure that mean separation tests reflected significant interaction terms. Using this approach, treatment effects were examined for *G* determined for the following variables in 2002: tree height; stem volume index, total tree biomass and biomass skewness. Total stand biomass was tested in a similar fashion but with the inclusion of terms for testing site effects and associated interactions.

Pearson correlation coefficients were calculated for determining the relationship between initial stem volume index at the beginning of a growth interval, RGR and AGR. Correlation coefficients were determined based on plot averages for volume index.

Relationships between G for tree biomass and total biological stocking (total stand biomass, t/ha) were examined using non-linear regression. Separate regressions of G as dependent variable and total stand biomass as predictor variable were calculated for each site-species combination with data pooled across all six fertilization-density combinations. Negative exponential regressions were fit using the form:

$$y = ax^{-b}$$

Where: $y = G$ (tree biomass)
x = Stand Biomass (t/ha)
a and b = Parameters

5.3 Results

Treatment means for structural inequality of height and tree biomass and skewness of tree biomass are presented in Table 5.2. Pearson correlation coefficients describing the relationships between absolute growth rate, relative growth rate and initial tree size at the beginning of respective growth periods are presented in Tables 5.3 and 5.4. Results showing outcomes of F-tests for significant treatment and species effects and least-square means are found in Appendix 4. Only results of significant F-tests are described. Development of structural inequality in tree height, total size (volume index) and skewness of tree size through stand life to 2002 are found in Figures 5.1 to 5.4. Relative growth rate (RGR), in terms of change in volume index, is described by size groupings for each of the six growth periods examined in Figures A4.1 to A4.24.

5.3.1 Effect of Treatment and Species on Size Hierarchy Development

Western redcedar showed greater structural inequity of tree biomass, stem volume index and height than did hemlock on HA sites (Tables 5.2, A4.1, A4.2 and A4.3). Hemlock stands showed greater inequality of height distribution and stem volume index on CH sites than did redcedar (Tables 5.2, A4.1 and A4.3). Both species developed stands showing positive or right-handed skewness in individual tree biomass (Table 5.2). Species differences in skewness were not detected on CH sites but redcedar was significantly more right-skewed than hemlock on HA sites. Establishment density did not produce any noticeable effect on within-stand inequality of height or tree biomass development within stands or on the skewness of tree biomass within stands (Tables 5.2, A4.1, A4.2 and A4.3).

Fertilization reduced the development of tree biomass, stem volume index and height inequality within stands on both CH and HA sites (Tables 5.2, A4.1, A4.2 and A4.3). Fertilization also reduced the amount of biomass skewness that developed within stands on both CH and HA sites (Tables 5.2 and A4.4).

A species x fertilization interaction for biomass inequality was present on CH sites (Tables 5.2 and A4.2). This interaction indicated that biomass inequality was initially greater within hemlock stands but hemlock responded to fertilization more strongly than redcedar. The result was that fertilization both reduced biomass inequity within stands and eliminated species differences in biomass inequity between redcedar and hemlock stands.

Table 5.2. Means and standard errors (in brackets) of Gini coefficient (*G)* measures of within-stand structural inequality of height, tree biomass, stem volume index and skewness (g_1) of tree size in 2002.

Species	Fertilization	Planting Density (Stems/ha)	Height (G)	Tree Biomass (G)	Volume Index (G)	Stand Biomass (t/ha)	Tree Biomass (g_1)
CH Sites:							
Cw	F0	500	0.16(0.01)	0.40(0.02)	0.51(0.03)	4.92(1.41)	1.19(0.27)
Cw	F0	1500	0.15(0.02)	0.38(0.01)	0.48(0.01)	8.71(3.25)	0.86(0.32)
Cw	F0	2500	0.16(0.04)	0.41(0.07)	0.52(0.08)	9.83(1.81)	1.63(0.54)
Cw	F1	500	0.10(0.02)	0.27(0.04)	0.34(0.05)	10.66(1.92)	0.37(0.17)
Cw	F1	1500	0.10(0.02)	0.28(0.05)	0.36(0.06)	26.22(7.08)	0.66(0.50)
Cw	F1	2500	0.13(0.04)	0.36(0.09)	0.46(0.10)	24.74(10.35)	1.27(0.69)
Hw	F0	500	0.22(0.02)	0.53(0.01)	0.64(0.03)	1.75(0.49)	1.94(0.75)
Hw	F0	1500	0.19(0.03)	0.44(0.06)	0.55(0.07)	3.35(1.15)	1.28(0.57)
Hw	F0	2500	0.21(0.02)	0.54(0.05)	0.64(0.06)	1.89(0.44)	1.41(0.40)
Hw	F1	500	0.12(0.01)	0.27(0.03)	0.36(0.04)	13.18(4.17)	0.92(0.42)
Hw	F1	1500	0.15(0.03)	0.34(0.07)	0.43(0.08)	19.31(6.92)	0.75(0.27)
Hw	F1	2500	0.14(0.02)	0.31(0.04)	0.39(0.05)	29.83(14.68)	0.53(0.25)
HA Sites:							
Cw	F0	500	0.17(0.05)	0.41(0.08)	0.51(0.08)	6.18(2.84)	1.11(0.27)
Cw	F0	1500	0.17(0.04)	0.41(0.08)	0.51(0.10)	11.85(4.32)	1.09(0.51)
Cw	F0	2500	0.23(0.08)	0.49(0.11)	0.59(0.12)	14.74(13.44)	1.44(0.62)
Cw	F1	500	0.11(0.04)	0.32(0.07)	0.42(0.08)	10.99(3.76)	0.99(0.45)
Cw	F1	1500	0.09(0.02)	0.29(0.02)	0.37(0.02)	37.87(12.87)	0.44(0.13)
Cw	F1	2500	0.11(0.01)	0.30(0.03)	0.39(0.03)	48.59(12.65)	0.65(0.28)
Hw	F0	500	0.14(0.03)	0.33(0.07)	0.42(0.09)	11.95(7.00)	0.87(0.85)
Hw	F0	1500	0.15(0.07)	0.33(0.12)	0.42(0.13)	29.09(19.82)	0.62(0.39)
Hw	F0	2500	0.14(0.06)	0.31(0.13)	0.40(0.16)	40.80(35.50)	0.91(1.03)
Hw	F1	500	0.09(0.01)	0.22(0.04)	0.29(0.05)	21.38(2.87)	0.15(0.34)
Hw	F1	1500	0.07(0.01)	0.20(0.04)	0.26(0.05)	81.24(13.361)	0.04(0.52)
Hw	F1	2500	0.07(0.02)	0.22(0.02)	0.29(0.03)	103.13(24.70)	0.39(0.53)

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Table 5.3. Pearson correlation coefficients for relative volume index growth rate as related to initial size at beginning of the growth period; significant correlations ($p<0.05$) shown with an asterisk.

Species	Fertilization	Planting Density (Stems/ha)	1997 – 2002	1994 – 1997	1992 – 1994	1990 – 1992	1989 – 1990	1988 – 1989
CH Sites:								
Cw	F0	500	-0.3501*	0.0590	-0.0969	-0.0375	0.0932	-0.1803*
Cw	F0	1500	-0.4206*	0.0380	-0.1881*	0.0567	0.0573	-0.0715
Cw	F0	2500	-0.3366*	0.1780	-0.2247*	-0.1209	0.1212	-0.0586
Cw	F1	500	-0.4326*	-0.3220*	-0.4713*	-0.0185	-0.0506	-0.1377*
Cw	F1	1500	-0.2218*	-0.0196	-0.4346*	-0.1436*	-0.0822	-0.2511*
Cw	F1	2500	-0.3696*	0.0095	-0.4235*	0.2226*	0.1081	-0.1116
Hw	F0	500	-0.4122*	-0.0337	0.0037	0.1088	0.0777	0.0931
Hw	F0	1500	-0.4250*	-0.1395*	-0.2874*	-0.0269	0.1526*	0.1212
Hw	F0	2500	-0.4658*	-0.1154	-0.1790*	0.0776	0.1235*	-0.1837*
Hw	F1	500	-0.3365*	-0.4668*	-0.2735*	0.0936	-0.1884*	-0.1897*
Hw	F1	1500	-0.2462*	0.1205	-0.2472*	-0.0949	-0.0890	-0.1432*
Hw	F1	2500	-0.3099*	-0.1014	-0.4399*	0.1048	-0.0646	-0.3695*
HA Sites:								
Cw	F0	500	-0.4134*	0.1132	0.0237	0.1196	0.2981*	-0.0578
Cw	F0	1500	-0.3582*	0.1430*	-0.0859	0.1123	0.1682*	-0.1212
Cw	F0	2500	-0.4039*	0.1398*	0.1717	0.4156*	0.4035*	0.0859
Cw	F1	500	-0.3358*	-0.2042*	-0.3625*	-0.0859	-0.0172	-0.1137
Cw	F1	1500	-0.0949	-0.2682*	-0.4070*	-0.2297*	0.1739*	-0.0667
Cw	F1	2500	-0.2473*	0.1784*	-0.4594*	-0.0073	0.0836	-0.3604*
Hw	F0	500	-0.4550*	0.0084	0.0801	-0.0272	-0.0464	-0.1097
Hw	F0	1500	-0.3555*	-0.0731	0.1783*	0.0541	0.0100	-0.1752*
Hw	F0	2500	-0.4559*	0.0959	0.2158*	0.2850*	0.1002	-0.1536*
Hw	F1	500	-0.4273*	-0.3533*	-0.3290*	-0.1570*	-0.1996*	-0.3452*
Hw	F1	1500	-0.2762*	-0.4318*	-0.3141*	-0.2353*	-0.1284*	-0.3100*
Hw	F1	2500	-0.4520*	-0.4077*	-0.1770*	-0.1470*	-0.2171*	-0.3037*

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Table 5.4. Pearson correlation coefficients for absolute volume index growth rate as related to initial size at beginning of the growth period; significant correlations ($p<0.05$) shown with an asterisk.

Species	Fertilization	Planting Density (Stems/ha)	1997 – 2002	1994 – 1997	1992 – 1994	1990 – 1992	1989 – 1990	1988 – 1989
CH Sites:								
Cw	F0	500	0.9315*	0.8434*	0.8636*	0.7934*	0.7734*	0.3254*
Cw	F0	1500	0.9210*	0.8758*	0.8858*	0.8603*	0.8485*	0.4834*
Cw	F0	2500	0.8923*	0.8712*	0.8275*	0.6926*	0.8241*	0.4443*
Cw	F1	500	0.7934*	0.8135*	0.8641*	0.7927*	0.7323*	0.5178*
Cw	F1	1500	0.8874*	0.8284*	0.8178*	0.7882*	0.8421*	0.5626*
Cw	F1	2500	0.8662*	0.8484*	0.8574*	0.8316*	0.7449*	0.5902*
Hw	F0	500	0.8533*	0.7737*	0.7794*	0.8037*	0.8564*	0.8236*
Hw	F0	1500	0.5918*	0.7322*	0.6236*	0.7752*	0.8196*	0.7685*
Hw	F0	2500	0.6028*	0.5211*	0.7632*	0.7176*	0.8284*	0.3718*
Hw	F1	500	0.8971*	0.7222*	0.8367*	0.6424*	0.7350*	0.7168*
Hw	F1	1500	0.7281*	0.8257*	0.7750*	0.6767*	0.7797*	0.7358*
Hw	F1	2500	0.8467*	0.7073*	0.7986*	0.6655*	0.7739*	0.6321*
HA Sites:								
Cw	F0	500	0.9031*	0.9185*	0.9038*	0.8268*	0.8230*	0.4542*
Cw	F0	1500	0.8750*	0.8648*	0.7896*	0.8359*	0.8176*	0.4124*
Cw	F0	2500	0.8980*	0.8598*	0.9269*	0.8872*	0.7298*	0.5618*
Cw	F1	500	0.8716*	0.8161*	0.7901*	0.7469*	0.6536*	0.5591*
Cw	F1	1500	0.8520*	0.8405*	0.8368*	0.8403*	0.8401*	0.5472*
Cw	F1	2500	0.8442*	0.8667*	0.8348*	0.8428*	0.6299*	0.2224*
Hw	F0	500	0.9011*	0.8336*	0.7694*	0.8034*	0.8735*	0.7068*
Hw	F0	1500	0.9211*	0.7971*	0.7747*	0.8125*	0.8262*	0.7273*
Hw	F0	2500	0.9111*	0.7506*	0.8263*	0.8314*	0.8502*	0.7085*
Hw	F1	500	0.8563*	0.7863*	0.6396*	0.6546*	0.7399*	0.5466*
Hw	F1	1500	0.8639*	0.7952*	0.7274*	0.7341*	0.7773*	0.6296*
Hw	F1	2500	0.8692*	0.7704*	0.7889*	0.6990*	0.7136*	0.5395*

Cw = Western Redcedar, Hw = Western Hemlock; F0 = Non=fertilized, F1 = Fertilized

Density levels were combined within site-species-fertility combinations for graphical presentation of size hierarchy development over time, given the lack of density effect on *G* values (Figures 4.1 and 4.2). Two general patterns of height and size (volume index) hierarchy development can be discerned over the course of stand development to date. The most common pattern among the species-site-fertilization combinations, referred to as Type I pattern, consisted of a rapid increase in structural inequality followed by a stable period with only moderate or slight changes in *G*. Stands on CH sites and redcedar stands on HA sites showed Type I size hierarchy development patterns. The increase in *G* for height and volume index tended to occur between stand establishment and 1992. Fertilization tended to reduce the magnitude *G* attained at the end of this period and produced a decline in *G* between 1992 and 1994, which correlates well with the second fertilizer application in spring of 1993. The second pattern, Type II, displayed constant or decreasing *G* over the course of stand development. Hemlock stands on HA sites showed the Type II pattern. Fertilization increased the rate of decline in *G* in the Type II pattern.

Skewness of volume index (Figures 4.3 and 4.4) showed a period of instability from stand establishment until about 1992 on CH sites. After 1992, volume index skewness showed a steady decline in fertilized hemlock on CH sites. Volume index initially declined

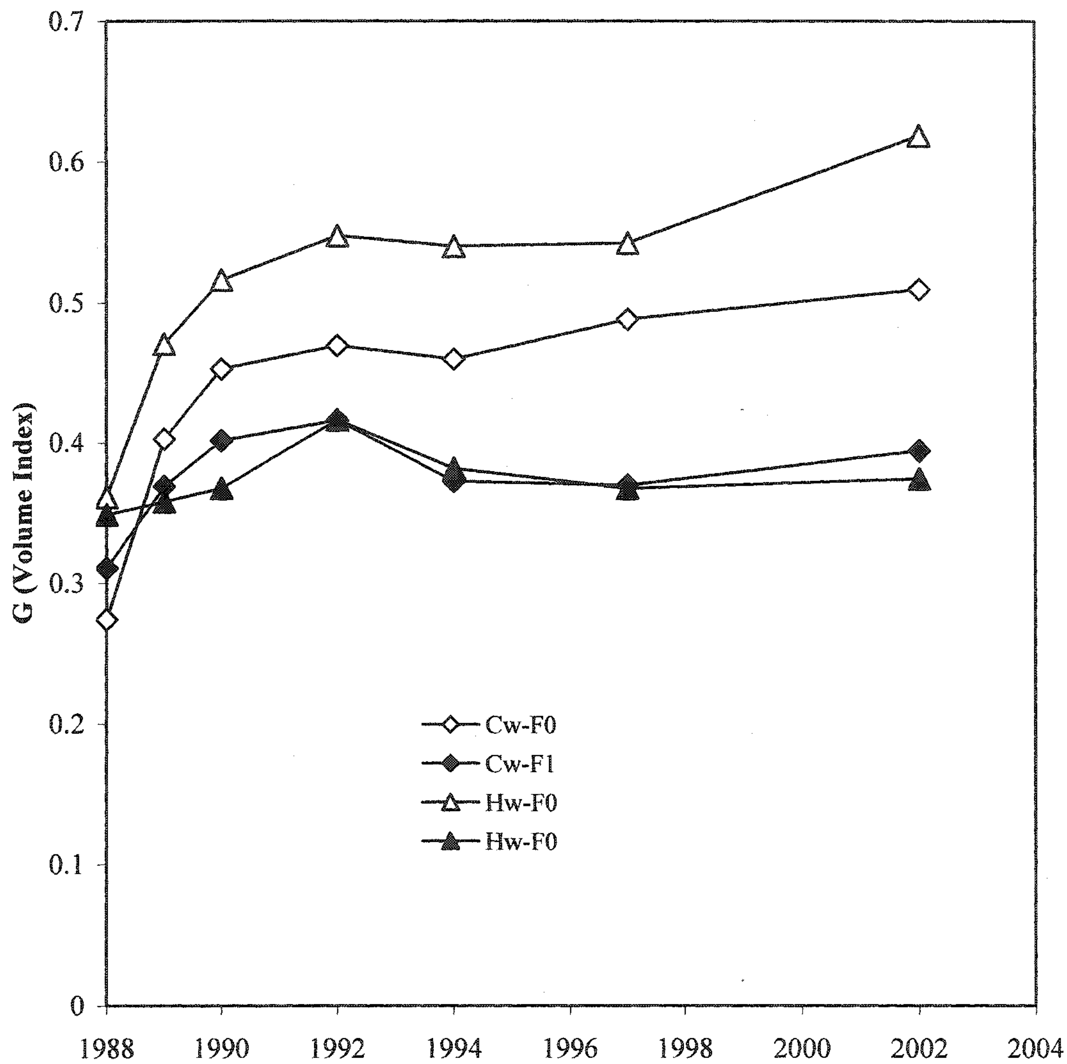


Figure 5.1. Within-stand development of volume index inequality (*G* or Gini index) on CH sites.

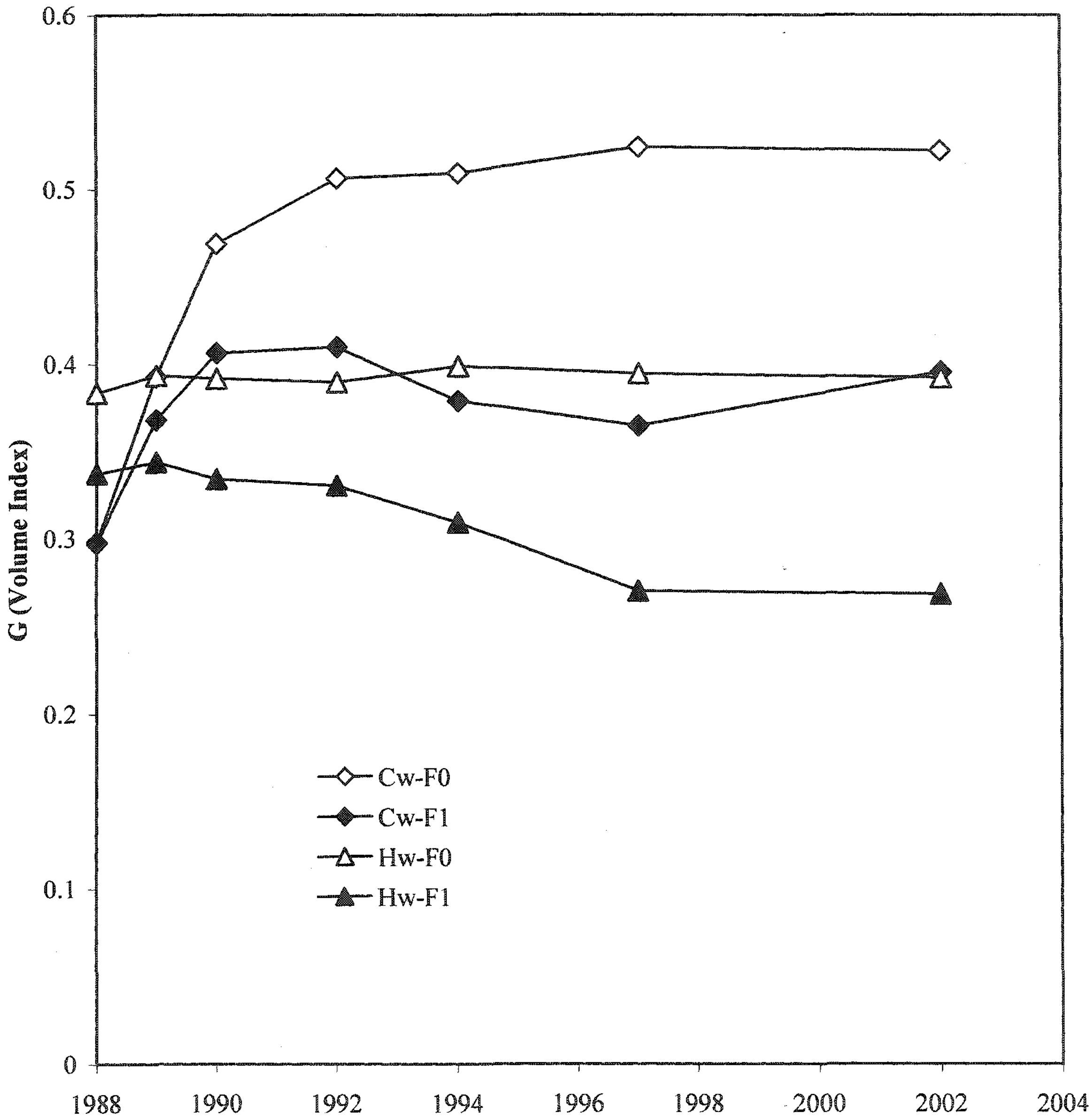


Figure 5.2. Within-stand development of volume index inequality (*G* or Gini index) on HA sites.

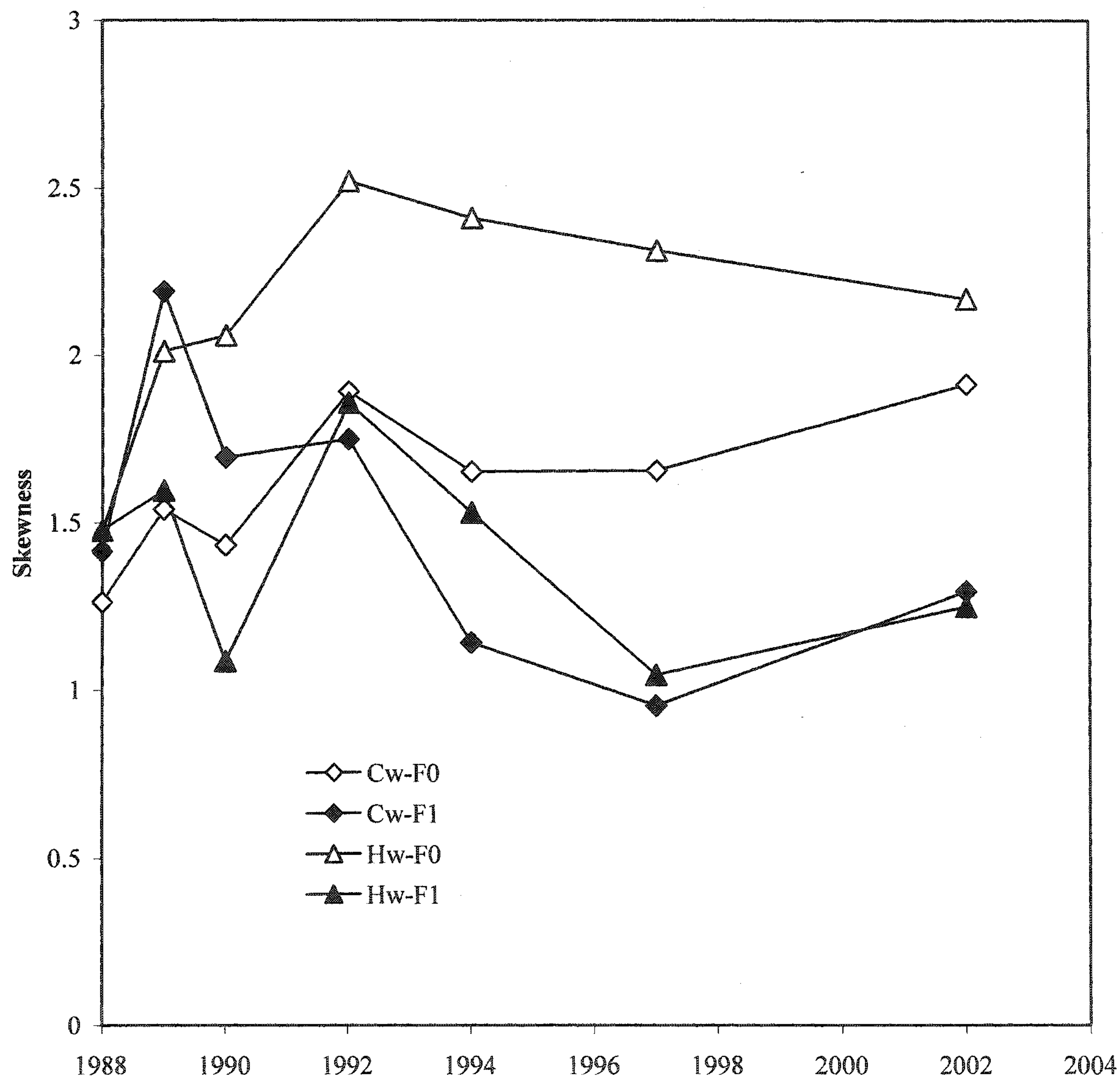


Figure 5.3. Skewness (g_I) development of volume index on CH sites.

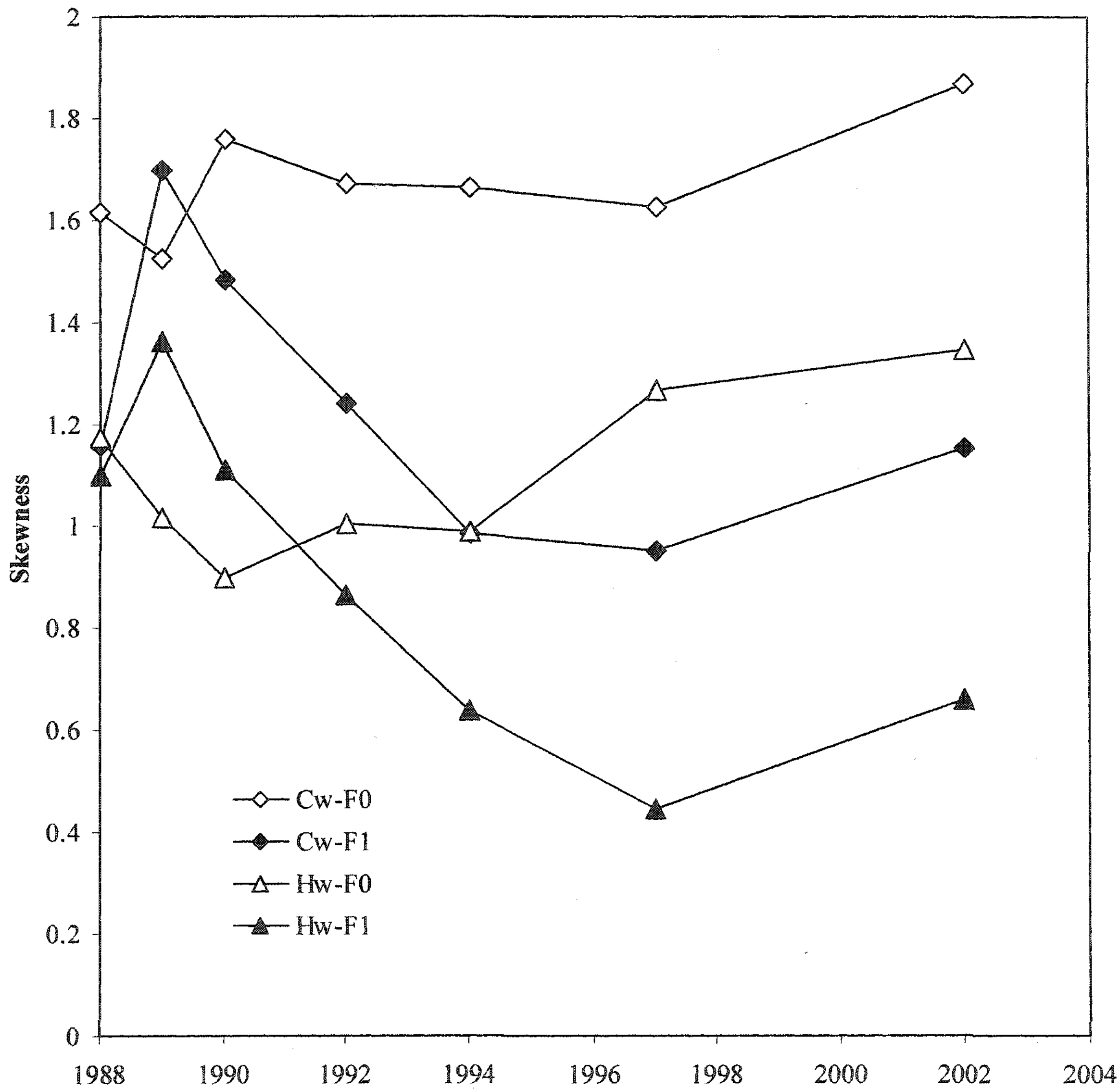


Figure 5.4. Skewness (g_1) development of volume index on HA sites.

but then increased between 1997 and 2002 in both fertilized and unfertilized redcedar stands and in fertilized hemlock stands.

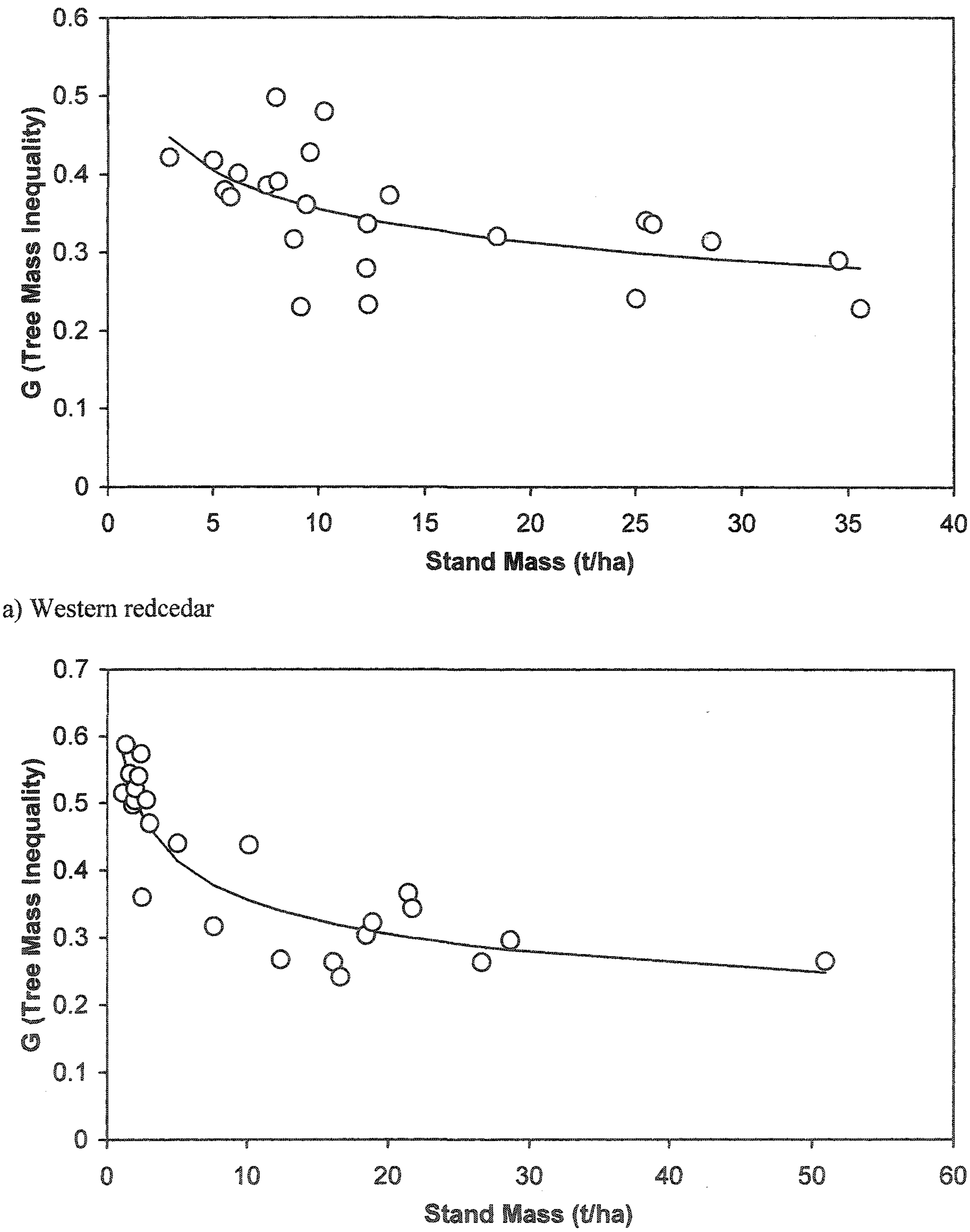
On HA sites, VI skewness declined between 1989 and 1997 but increased between 1997 and 2002. In unfertilized stands, VI skewness initially declined but then increased between 1997 and 2002.

Relationships between absolute biological density (stand biomass, t/ha) and within-stand tree biomass inequality (Figures 5.5 and 5.6) indicated a similar non-linear trend of rapid decline in G as stand biomass initially increased over the range of lower stand biomasses, followed by a trend for G to slowly decline or remain constant as total stand biomass increased (Table A4.6). Size hierarchies remained relatively unchanged over most of the range of stand biomasses for all site-species combinations. Hemlock tended to fit this relationship better than redcedar, although all regressions were significant ($p < 0.0001$).

5.3.2 Total Stand Biomass

Stands on HA sites produced 260% more total tree biomass after 14 years of growth than did stands on CH sites (Table A4.5). Fertilization increased stand biomass 369% compared to unfertilized stands. Stand biomass increased with establishment density. Stands established at 1500 and 2500 sph produced more biomass than stands established at 500-sph.

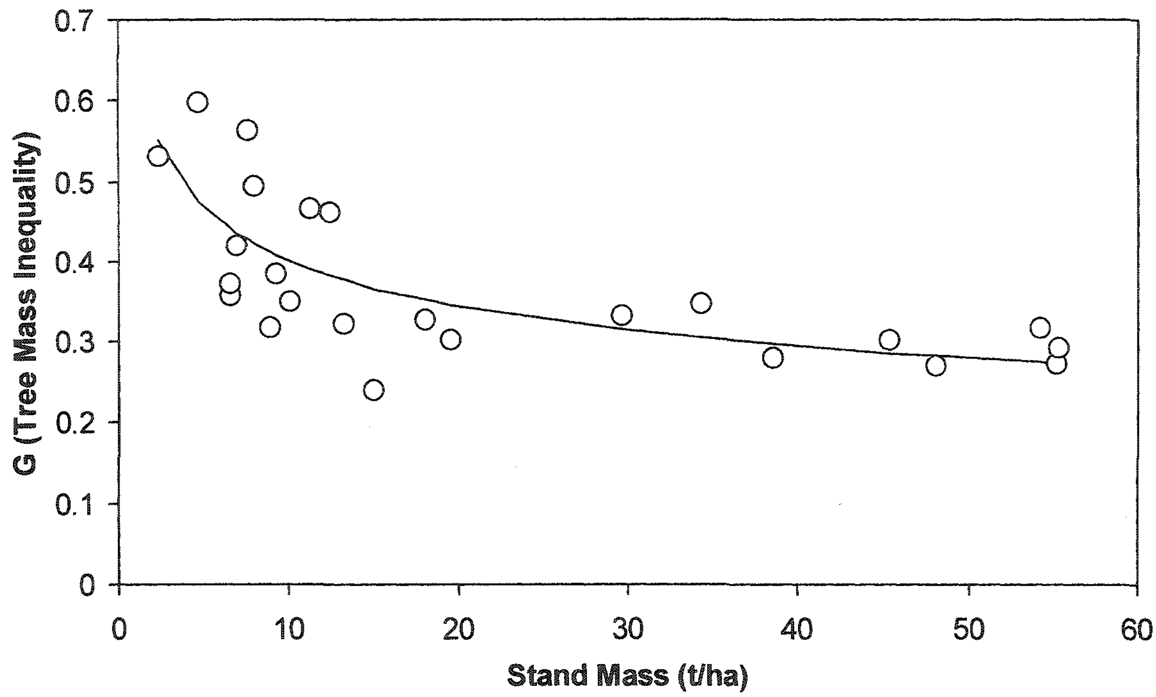
The following interactions were present for total stand biomass: site x species; species x fertilization; and site x species x fertilization (Table A4.5). These interactions indicated that: hemlock stands on CH sites were least productive; fertilized hemlock stands on HA sites were most productive; unfertilized redcedar stands were equally productive on



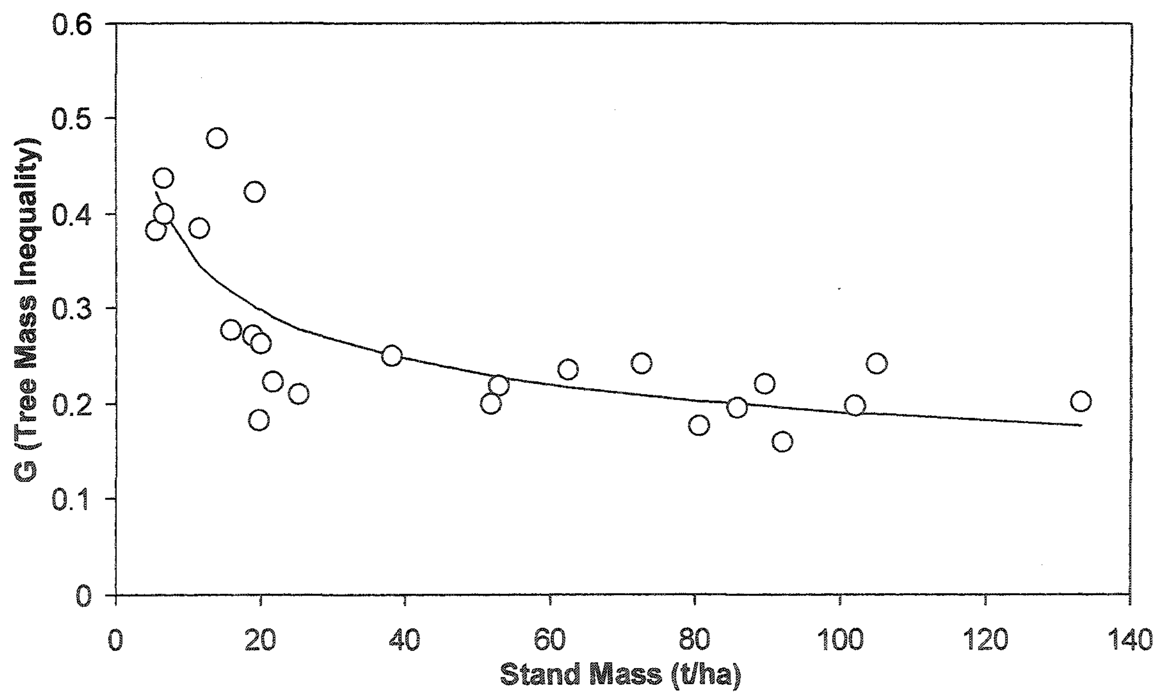
a) Western redcedar

b) Western hemlock

Figure 5.5. Size inequality (biomass) of western redcedar and western hemlock on CH sites as related to total stand biomass.



a) Western redcedar



b) Western hemlock

Figure 5.6. Size inequality (biomass) of western redcedar and western hemlock on HA sites as related to total stand biomass.

both CH and HA sites; fertilized stands on CH sites, fertilized redcedar on HA and unfertilized hemlock on HA stands were all equally productive and; fertilization increased the productivity of both species but increased hemlock productivity more than that of redcedar (Table A4.5).

5.3.2 Relationship Between Tree Size and Growth

Relative growth rate (RGR) has tended to be inversely related to tree size for these sites and species since stand establishment, where correlations were significant. This relationship has strengthened with stand development, in terms of significance and magnitude of the inverse relationship. A transient period of significant positive relation between RGR and tree size existed on: HA sites in the 1990 – 1994 interval in unfertilized hemlock and the 1989 - 1992 interval in redcedar stands; and in CH stands between 1989 – 1992. The development of a positive relationship between tree size and RGR was not significant as frequently on CH sites as on HA sites. Periods of positive relationship between RGR and tree size were associated with periods of rapidly increasing *G* values. This relationship between RGR and tree size changed to a significant inverse relationship in the 1997 – 2002 period for all species-site combinations.

Fertilization tended to establish, or strengthen, the inverse relationship between tree size and RGR earlier in stand development (Figures A3.1 – A3.24 in Appendix 3), compared to unfertilized stands. Fertilized stands showed a more strongly developed negative relationship between RGR and tree size, or no relationship, during the 1989 – 1992 period of increase in *G*. This pattern of declining RGR with increasing size became more common and more pronounced during the 1992 – 1994 period. Periods of inverse or non-relationship between tree size and RGR in fertilized stands up to 1992 coincided with lower increases in G during this period in these stands. Periods of strongly developed inverse relationship between RGR and tree size coincided with reduction in G during the 1992 – 1994 period. The inverse relationship between RGR and tree size become common across all species-site-fertilization combinations from 1994 – 2002.

Absolute growth rate (AGR) was positively related to tree size from stand establishment and the strength of the correlation increased with stand development.

5.4 Discussion

The hypotheses that fertilization and species would not influence size hierarchy development were not supported by the results of this study. Neither was the hypothesis that size hierarchy development would be consistent across two different site types supported by the results. Results did support the hypothesis that size hierarchy development would not be increased by density stress.

Size hierarchies have been noted to decrease with the onset of density-dependent mortality (Knox *et al.* 1989). The highest average annual mortality in this study did not exceed 1.2% and was generally under 0.5%. Increased mortality was not associated with increasing establishment density (Chapter 2). Therefore, density-dependent mortality does not explain the reduction in size hierarchy development associated with fertilization nor the general patterns of stable or decreasing size hierarchies observed in the Type I and II patterns.

Increase in size hierarchies over time in plant populations, including forest stands, has been attributed to greater relative growth of larger versus smaller individuals that commences with the onset of asymmetric competition (Weiner 1990, Laroque and Marshall 1993, Wichmann 2001). Increased RGR of smaller compared to larger trees has explained reduction in size variability in stands on drained sites and also a lack of increase in size variability in fertilized and irrigated stands compared to untreated controls (MacDonald and Yin 1999, Nilsson *et al.* 2002). The tendency for fertilization to increase the relative growth of smaller individuals relative to larger individuals was also likely the mechanism by which size hierarchies were reduced in this study. By contrast, increased soil moisture availability has been shown to increase size inequality within plant populations (Wichmann 2001, Briones *et al.* 1998). The previous observed tendency for size hierarchies to neither increase nor decrease significantly with an increase in both soil moisture and nutrient availability (Nilsson *et al.* 2002) may therefore have resulted from diametric effects of fertilization and irrigation on size hierarchy development. It may also be because Nilsson *et al.* (2002) only examined stem volume rather than total tree biomass inequality. Also, Nilsson *et al.* (2002) examined loblolly pine (*Pinus taeda* L.), which has been shown to increase biomass allocation to stem wood in suppressed canopy positions (Naidu *et al.* 1998) and thus tends not to show increased size variability in stem volume as stands began to differentiate.

Trees in poorer microsites with lower nutrient supply tend to grow slower and remain smaller compared to trees located in better microsites. Fertilization may have increased the growth of smaller trees by reducing differences in nutrient availability between microsites. This effect may have been amplified over time as the tendency for RGR to be negatively correlated with size increased over time.

Differences in size hierarchy development of the two species on CH and HA sites may also be explained in terms of growth. The species that showed the greatest growth on each site also had the least size hierarchy development. Hemlock showed a greater growth response to fertilization (hemlock on CH sites, Chapter 2), but it also showed a greater decline in size inequality. This may have resulted from fertilization having a stronger effect on average growth and on growth of small individuals, as described above. Redcedar may have an inherent tendency to form more structurally diverse stands, having greater size inequality, because of its stronger tendency to show a positive relationship between foliar efficiency and tree size (Chapter 4). Conversely, hemlock may have an inherent tendency to form more structurally uniform stands because of its stronger tendency to show a negative relationship between foliar efficiency and tree size (Chapter 4). This relationship between size and foliar efficiency may explain the Type II pattern of size hierarchy development on HA sites. The steady decline in size hierarchies in fertilized hemlock stands on HA may have resulted from the homogenizing of microsite quality, as described above. The failure of hemlock to develop the Type II pattern on CH sites may relate to the low ability of these sites to support hemlock growth, as well as high competition from salal, which has a rooting habit closely matching that of hemlock (Bennett 2001, Fraser *et al.* 1995, Messier 1993, Weetman *et al.* 1989). The general stability, or decrease, in size inequality, with stand development may be a characteristic of shade-tolerant species (Lundqvist 1994).

Conifers stands have been described as showing predictable patterns of stand development (Nilsson *et al.* 2002, Knox *et al.* 1989) but results of this study do not support this assertion. Redcedar and hemlock has similar structural development patterns (Type I) on CH sites but different patterns on HA sites (Type I for redcedar; Type II for hemlock). Fertilization reduced the degree of size inequality that developed within these two essential patterns. Both Type I (Nilsson *et al.* 2002) and Type II (Newton 1990) patterns of size hierarchy development have been observed elsewhere. Size inequality has been shown to increase with stand age and has been attributed to the development of asymmetric competition, which occurs after crown closure (Wichmann 2001, Larocque and Marshall 1993). Asymmetric competition and increasing size inequality may eventually develop in the stands studied here, however, the Type II pattern showing the most stable or consistently decreasing trend in size inequality was present in hemlock stands on HA sites. Crowns of hemlock stands on HA sites had been closed for several years by the time this study was conducted and these stands also showed the greatest total biomass development. Given the trend for a negative relationship between RGR and size that has developed in these stands and the slight trend for size inequality to decrease with total stand biomass (Figures 5.1, 5.2), there is no indication that significant increases in size inequality will occur in the foreseeable future.

The lack of a clear or significant relationship between density and size hierarchy development is consistent with other studies (Nilsson *et al.* 2002, Nilsson 1994, Newton 1990, Knox *et al.* 1989). The shape of the regressions between stand biomass and size inequality likely reflects the highly variable nature of microsites on poorer CH sites, with very low biomass associated with comparatively high size inequality. Wetter, bog-like pockets occurred on both CH and HA sites. Fluctuating water tables in these areas would have created highly variable conditions for plant growth (Asada *et al.* 2003, Lewis 1982). The 500-sph plantings have not yet have reached crown closure and may have allowed more competing non-crop vegetation to develop, especially in unfertilized stands, which would also have created more variable growing conditions for crop trees. A slight trend for size inequality to decrease as total stand biomass increased may also reflect the effect of symmetric competition on these sites. This effect may not develop further once crown closure has been achieved and stands begin to meet more of their nutritional needs through retranslocation from older or dying tissues (Miller 1995).

Development of a negative correlation between RGR and tree size has been observed in other studies and has been associated with developing symmetric competition on poor sites (Nilsson 1994). It may also indicate periods of low competitive pressure before the onset of asymmetric competition (Laroque and Marshall 1993). However, the following factors do not indicate emerging asymmetric competition in these stands: lack of difference in height development patterns between stand averages and leading-heights (Chapter 2); generally low but positive skewness values indicating weak differentiation potentials within stands (Newton 1990); a decrease in size skewness associated with fertilization indicating that fertilization increased the exploitation potential of smaller individuals and thus reducing the potential for asymmetric competition (Newton 1990); and the emerging negative trend between RGR and tree size. Rather, these factors suggest stands that have gone through a period of instability associated with the regeneration niche (Harper 1977), have closed, or are closing canopies, and entered a phase of growth where little differentiation is occurring. This growth phase is characterized by reduced average growth with increasing establishment density (competition), little apparent differentiation (some stands are becoming more uniform in size) and moderate to severe nutritional deficiencies for N and P (soil resources, Chapter 2). Thus, evidence for symmetric competition is present despite improved nutritional status associated with fertilization. Alternatively, the shade tolerant nature of the species used in the investigation may be delaying the onset of asymmetric competition and resulting stand differentiation. The apparent contradiction of fertilization promoting symmetric competition may be explained by noting that fertilization a) did not completely relieve the stress of nutrient supply limitations and b) benefited the most stressed individuals (the smaller trees in poorer microsites) more than those less affected. Whether this phase of, possibly, symmetric competition is the result of belowground competition or due to the shade-tolerance of these species is yet to be determined.

5.5 Conclusion

Fertilization reduced size hierarchies within juvenile stands of both western red redcedar and western hemlock by increasing the relative growth rates of smaller trees more so than larger trees. This effect was present on site types that varied in productivity. Density generally did not significantly influence the development of size hierarchies, although a weak trend of decreasing size inequality with increasing stand biomass was observed for all site-species combinations. Size hierarchy development patterns varied with species and site: the species with the greater growth developed the least diverse size structure on each site. Relative growth rates became negatively correlated with tree size over time. These results do not support theories suggesting that increased soil resource availability and density increase size inequality through the promotion of asymmetric competition.

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Chapter 6

Summary and Conclusions

Western red cedar and western hemlock have different growth rates on CH and HA sites. On CH sites, inherently low N and P supply and competition from salal limit growth of hemlock more so than growth of cedar. On HA sites, greater nutrient availability promotes greater growth of both species and growth of hemlock is greater than cedar. Fertilization and increased planting density have been proposed as cultural methods to increase forest productivity on CH sites by increasing nutrient supply and competitively displacing salal through shading. This thesis examined the effects of fertilization and three levels of planting density on the growth, structure and function of cedar and hemlock stands on CH and HA sites. Stands examined in these studies were 14 years of age with the last fertilizer applied 10 growing seasons previously.

Growth and Mass Accumulation

Fertilization resulted in larger trees and greater stand occupancy of sites 10 years after its last application and may have continued to increased growth rates up to the end of the experimental period. Total tree size, stand mass and basal area stocking were increased by fertilization for both species on both sites. Incremental growth during the interval between the 1997 and 2002 measurements was also increased by fertilization. However, it is possible that fertilization may not have increased growth rates by the end of the 1997 – 2002 period. Hemlock benefited more from fertilization on CH sites than did cedar; as a result fertilization reduced differences in species growth on CH sites. On HA sites, species response to fertilization was similar. Total growth and mass accumulation were greater on HA sites than on CH sites and greater in hemlock than in cedar stands on HA sites.

Increasing planting density affected tree size and growth more on CH than on HA sites. Both height and tree basal area size and growth rate in the 1997 – 2000 period were reduced by increasing establishment density on CH sites while only average basal area and basal area growth rate were reduced by increasing density on HA sites. Growth rates of hemlock stands on CH sites were most strongly affected by density than growth of redcedar stands. Total basal area and standing biomass within stands increased with increasing planting density. However, there were no differences in stand basal area and standing biomass between the 1500 and 2500 sph densities. Increasing planting density reduced stand foliage and wood mass on unfertilized CH sites, presumably by limiting tree size through competition for soil nutrients. While competition has lead to decreased average growth, particularly under more nutrient-limited conditions, it has not yet resulted in self-thinning.

It has been suggested that lack of acceptable microsites at higher planting densities may have resulted in lower average growth in 2500-sph treatments. However, if this were the case the poorer growth performance of trees planted in marginal microsites would have resulted in increased stratification of stands planted at higher densities and resulted in greater size hierarchy development. This was not the case, however: increased planting densities were not associated with increased size hierarchy development and may have reduced size hierarchy development, although this effect was weakly expressed (see below). Therefore, the increased use of marginal microsites at higher planting densities likely did not significantly affect tree and stand growth.

Salal Growth on CH Sites

Salal biomass was not affected by cedar planting density on CH sites. Fertilization significantly increased salal biomass on CH sites. The increase in salal growth in fertilized plots matched or exceeded the increase in tree growth on CH sites, in terms of proportional increase in mass associated with fertilization.

Salal has been show to reduce to growth of conifer trees and stands in the period before stands have begun to close. The influence of salal on conifer growth at the SCHIRP Installation as stands close and remains unclear. This study would have been more complete had the role of salal on conifer growth been investigated.

Foliar Nutrient Concentrations

Fertilization increased foliar P concentrations on both CH and HA sites and increased foliar N concentrations on HA sites ten years after treatment. Fertilization also increased the foliar concentrations of some nutrients that were not present in the fertilizer possibly because urea in the fertilizer product increased the solubility of nutrients in soil pools. Establishment density did not usually influence foliar nutrient concentrations. Cedar had consistently greater foliar concentrations of N, P, Ca, Mg, S and Zn than hemlock. Hemlock had consistently greater foliar concentrations of SO_4-S, Fe, Mn, Al and B than cedar. Growth of both species was significantly correlated with foliar P concentration on both sites and with foliar N concentration on HA sites. Growth of cedar on HA sites had a high correlation with foliar N concentration compared to hemlock.

Mass Component Proportions

Neither fertilization nor density has affected tree-level allometry of mass components in cedar. A similar lack of treatment influence on within-tree mass allocation was assumed for hemlock, given the result for cedar and the lower degree of variation in proportional size of mass components across treatment levels in hemlock compared to cedar.

Stand-level mass component proportions were likely influenced through treatment effects on tree size. As tree size increased, mass proportion of wood tended to increase while that of foliage tended to decrease. Therefore, fertilization tended to decrease foliage proportions in stands and increase proportion of wood. Hemlock showed greater allocation to bark than did cedar, while cedar had greater allocation to branches.

Regression relationships between establishment density and tree size or biomass proportion were strongest, in terms of r^2 values, on the least productive sites (unfertilized CH sites), and weakened as productivity increased (fertilized CH and unfertilized HA), becoming non-significant (for cedar) on fertilized HA sites. Relationships were significant for hemlock on fertilized CH, though with lower r^2 values than on unfertilized CH, and were not significant on HA sites. This pattern of relationships suggests that competition and its influence on stand structure was most important on sites with low growth potential associated with low nutrient availability. Hemlock was more strongly affected at the lowest site growth potential, while cedar was less affected at lower site productivities.

Foliar and Resource Use Efficiencies; Foliage Capacity

Fertilization reduced stand-level foliar efficiency of hemlock on CH sites but did not affect that of cedar. Increasing establishment density from 500 to 1500 or 2500 sph on CH sites reduced foliar efficiency of cedar stands. Hemlock tended to have greater foliar efficiency than cedar on CH sites, but there were no treatment or species effects on stand-level foliar efficiency on HA sites.

Foliar efficiency of individual trees tended to increase with tree size in cedar and decrease with tree size in hemlock. Increasing establishment density tended to reduce foliar efficiency of trees. Fertilization tended to reduce the relationship between tree size and growth efficiency in hemlock and promote it in cedar.

Light use efficiency was increased by both fertilization and increasing establishment density in cedar stands on CH sites. Light use efficiency decreased with increasing density and was not affected by fertilization. Average annual increment of total stand biomass and the masses of wood and foliage during the 1997 – 2002 period was exponentially related to PAR absorption in cedar stands on CH sites. This non-linear relationship between PAR absorption and mass components does not support the hypothesis that stem wood growth is exponentially related to PAR absorption while other components are lineally related (Balster and Marshall 2000).

Use efficiency of all nutrients examined (N, P, K, S, Ca, Mg, Zn and B) was increased by fertilization. On both sites, fertilization tended to increase nutrient use efficiencies of hemlock more than of cedar. The exception was use of P on HA, which was greater in cedar than in hemlock in fertilized stands. In general, use efficiencies tended to be greater in cedar on CH sites, with the exception of Ca, and greater in hemlock on HA sites. Establishment density tended not to influence nutrient use efficiencies, with the exception of N and Zn use, which increased with establishment density in cedar stands on CH sites.

Biomass increment of stands was strongly lineally correlated with stand foliage mass; suggesting that foliage carrying capacity has not yet been reached on the more productive sites i.e. those that were HA and/or fertilized.

The effect of fertilization on foliage longevity was not investigated in this study, largely due to the difficulties in determining age of cedar foliage. However, a more complete understanding of the influence of fertilization on foliage structure and function would have been attain had foliage longevity been examined.

Size Hierarchy Development

Fertilization reduced size inequality of both species on both sites. Within-stand size inequality tended to be least where stand growth was greatest and the relative size inequality of the two species changed with site and fertilization. On CH sites, hemlock size inequality declined more than cedar with fertilization, associated with stronger growth response. Hemlock on HA sites, which was the most productive site-species combination, showed a consistently stable or declining size hierarchy through stand development to date. All other species-site combinations showed an initial increase in size hierarchy development early in stand development, followed by a period of stability or, when fertilized, a decline in size hierarchies.

Establishment density did not affect size hierarchy development. However, there was a significant negative exponential trend between absolute biological stocking (standing biomass) and size inequality. Size inequality was greatest where stand mass development was least, which was associated with lower establishment density and no fertilization. Size inequality rapidly and asymptotically declined with increasing stand mass development.

Periods of decline in size inequality in fertilized treatments were associated with well-developed inverse relationships between tree size and relative growth rate (RGR). The tendency for RGR to be inversely proportional to tree size was common to all treatment-site-species combinations by the end of the investigation and tended to be stronger in unfertilized stands. Absolute growth rate was positively correlated with tree size to date and the relationship became stronger over time.

The study focused on variables that reflected total size of individuals. However, an examination of size hierarchy development in recent growth increments may have allowed a better understanding of current trends in the development of competition in treatments. Greater precision in determining current trends in size hierarchy development may have allowed more accurate predictions of future trends in stand development.

Applications to Management and Future Work

These results suggest that fertilization significantly enhanced stand growth and may continue to do so for the foreseeable future. The greatest absolute growth response to fertilization was in hemlock on HA sites. Growth response was greater on HA than on CH sites, in general. Thus, given a limited budget for fertilization, fertilization of hemlock stands should take priority from a volume growth perspective. However, when the greater value of cedar is factored in, the priority of fertilizing cedar on HA sites increases.

Establishment density showed the ability to limit stand productivity on unfertilized CH sites. Reduction in wood and foliage masses indicates increasing establishment density will both reduce the merchantable product of these stands (wood) and impair their ability to growth by reducing foliage mass of stands. Therefore, establishment densities under 1500 sph are recommended for operational use by these results on unfertilized CH sites.

Future work to better understand the influence of establishment density and fertilization on these sites would include: assessing the competitive influence of salal; quantifying both above and belowground competition by examining the growth of both above- and belowground tree biomass components and; investigating effects of fertilization on the chemistry of nutrients not applied in fertilizer and nutrient interactions. Ultimately, to understand the net effect of competition on stand growth and to better understand treatment effects, the influence of interspecific competition by salal needs to be examined concurrently with total intraspecific competition, including both aboveground and belowground components. Investigation of the effects of nutrients applied in fertilizer on availability of other nutrients of non-fertilizer origin and nutrient interactions will also give a more complete understanding of the effects of fertilization on stand nutrition and growth.

Synthesis

Fertilization likely continued to promote the growth of hemlock and cedar stands on both CH and HA sites. This continued enhancement of growth has been attributed to increased soil P availability of CH sites (Bennett *et al.* 2003) and may be due to increased soil N and P availability on HA sites. Increased availability of other soil nutrients associated with chemical activity of the fertilizer may also have occurred and promoted growth. However, nutrient use efficiency was greater in fertilized stands than in unfertilized stands. This increase in nutrient use efficiency may be the only significant structural or functional legacy of fertilization still promoting enhanced growth within these stands.

Competition is likely increasing in importance as a growth-influencing factor. Lack of increase in size hierarchy with density, N and P foliar nutrient deficiencies, despite fertilization and resulting elevated growth and more pronounced size-density relationships on less productive site-treatment combinations suggest that the dominant mode of competition is likely symmetric on these sites. That symmetric competition is a significant factor on these sites is also suggested by the tendency for inverse tree size-RGR relationships to develop.

Fertilization likely reduced size hierarchy development by establishing inverse size-RGR relationship earlier in the rotation than occurred in unfertilized stands. Cedar may have a tendency to develop more structurally diverse stands than hemlock, due to its stronger relation between tree size and foliar efficiency and because it tended to have greater size inequality on both sites. However, relative size inequality was not fixed between the two species, rather it was related to growth conditions: where growth was greatest, size inequality was least. This negative relationship between growth and size hierarchy and the lack of strong relationship between size hierarchy and density suggests that competition and its effect on community structure decreased under conditions of greater plant community productivity. This outcome supports the theories and findings that competition is unaffected under conditions that promote greater plant community productivity, including increased soil resource availability (Tilman 1988, Wilson and Tilman 1993), rather than those suggesting competition will increase under conditions of greater plant community productivity (Goldberg and Barton 1992, Grime 2001). Symmetric competition may have developed in these stands because the species examined where very shade-tolerant. Examination of shade-intolerant species under different conditions at a more advanced stage in stand development may have yielded different results.

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Appendix 1: Statistical Analysis for Chapter 2

Table A1.1. Analysis of average tree height for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (m)	SE
CH Sites:							
Sp:		1	33	40.80	<.0001		
	Cw					5.46b	1.04
	Hw					4.38a	1.04
ED:		2	33	29.57	<.0001		
	500					5.77c	1.04
	1500					4.86b	1.04
	2500					4.18a	1.04
Fz:		1	33	268.20	<.0001		
	F0					3.70a	1.04
	F1					6.48b	1.04
Sp x ED		2	33	1.57	0.2240		
Sp x Fz:		1	33	42.14	<.0001		
	CwF0					4.61b	1.05
	HwF0					2.97a	1.05
	CwF1					6.46c	1.05
	HwF1					6.49c	1.05
ED x Fz		2	33	1.31	0.2827		
Sp x ED x Fz		2	33	3.03	0.0619		
HA Sites:							
Sp:		1	33	28.80	<.0001		
	Cw					5.98a	1.07
	Hw					8.67b	1.07
ED		2	33	0.70	0.5055		
Fz:		1	33	41.08	<.0001		
	F0					5.75a	1.07
	F1					8.95b	1.07
Sp x ED		2	33	0.67	0.5189		
Sp x Fz		1	33	0.15	0.6978		
ED x Fz		2	33	2.27	0.1189		
Sp x ED x Fz		2	33	0.09	0.9164		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.2. Analysis of average annual height growth rate for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (m/yr)	SE
CH Sites:							
Sp:		1	33	24.24	<.0001		
	Cw					0.36b	0.11
	Hw					0.27a	0.11
ED:		2	33	18.02	<.0001		
	500					0.39b	0.11
	1500					0.30a	0.11
	2500					0.25a	0.11
Fz:		1	33	52.06	<.0001		
	F0					0.25a	0.11
	F1					0.39b	0.11
Sp x ED		2	33	0.53	0.5916		
Sp x Fz:		1	33	8.28	0.0070		
	CwF0					0.32b	0.11
	HwF0					0.20a	0.11
	CwF1					0.41c	0.11
	HwF1					0.36bc	0.11
ED x Fz		2	33	1.56	0.2245		
Sp x ED x Fz		2	33	1.44	0.2519		
HA Sites:							
Sp:		1	33	24.22	<.0001		
	Cw					0.40a	0.11
	Hw					0.56b	0.11
ED		2	33	0.27	0.7622		
Fz:		1	33	44.53	<.0001		
	F0					0.37a	0.11
	F1					0.59b	0.11
Sp x ED		2	33	1.18	0.3186		
Sp x Fz		1	33	2.78	0.1051		
ED x Fz		2	33	2.60	0.0892		
Sp x ED x Fz		2	33	0.32	0.7294		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.3. Analysis of height of leading height trees for CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (m)	SE
CH Sites:						
Sp:	1	33	21.90	<.0001		
Cw					7.03b	1.03
Hw					6.12a	1.03
ED:	2	33	31.50	<.0001		
500					7.66c	1.03
1500					6.40b	1.03
2500					5.76a	1.03
Fz:	1	33	194.65	<.0001		
F0					5.33a	1.03
F1					8.07b	1.03
Sp x ED:	2	33	3.47	0.0428		
Cw500					7.78d	1.04
Hw500					7.53d	1.04
Cw1500					6.95cd	1.04
Hw1500					5.90ab	1.04
Cw2500					6.42bc	1.04
Hw2500					5.16a	1.04
Sp x Fz:	1	33	40.32	<.0001		
CwF0					6.28b	1.04
HwF0					4.53a	1.04
CwF1					7.87c	1.04
HwF1					8.27c	1.04
ED x Fz	2	33	2.01	0.1504		
Sp x ED x Fz	2	33	1.39	0.2636		
HA Sites:						
Sp:	1	33	40.71	<.0001		
Cw					8.02a	0.41
Hw					10.66b	0.41
ED	2	33	0.06	0.9434		
Fz:	1	33	32.37	<.0001		
F0					8.16a	0.41
F1					10.52b	0.41
Sp x ED	2	33	0.86	0.4312		
Sp x Fz	1	33	2.48	0.1251		
ED x Fz	2	33	2.65	0.0860		
Sp x ED x Fz	2	33	0.34	0.7173		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.4. Analysis of average annual height growth rate for leading height trees for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (m/yr)	SE
CH Sites:							
Sp		1	33	2.33	0.1366		
ED:		2	33	10.71	0.0003		
	500					0.54b	0.02
	1500					0.43a	0.02
	2500					0.40a	0.02
Fz:		1	33	26.78	<.0001		
	F0					0.39a	0.02
	F1					0.52b	0.02
Sp x ED		2	33	0.27	0.7678		
Sp x Fz:		1	33	6.59	0.0150		
	CwF0					0.44b	0.03
	HwF0					0.33a	0.03
	CwF1					0.51b	0.03
	HwF1					0.54b	0.03
ED x Fz		2	33	0.63	0.5378		
Sp x ED x Fz		2	33	2.14	0.1335		
HA Sites:							
Sp:		1	33	27.86	<.0001		
	Cw					0.53a	0.04
	Hw					0.71b	0.04
ED		2	33	0.38	0.6885		
Fz:		1	33	33.91	<.0001		
	F0					0.52a	0.04
	F1					0.71b	0.04
Sp x ED		2	33	1.26	0.2983		
Sp x Fz		1	33	9.02	0.0051		
	CwF0					0.48a	0.05
	HwF0					0.56a	0.05
	CwF1					0.57a	0.05
	HwF1					0.85b	0.05
ED x Fz		2	33	2.52	0.0958		
Sp x ED x Fz		2	33	0.52	0.6004		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.5. Analysis of average tree BA for CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (cm^2)	SE
Sp:	1	33	77.49	<.0001		
Cw					48.04b	1.10
Hw					22.56a	1.10
ED:	2	33	56.15	<.0001		
500					58.50c	1.1
1500					31.69b	1.1
2500					19.24a	1.1
Fz:	1	33	327.99	<.0001		
F0					15.12a	1.10
F1					71.66b	1.10
Sp x ED	2	33	0.74	0.4850		
Sp x Fz:	1	33	45.02	<.0001		
CwF0					29.43b	1.12
HwF0					7.77a	1.12
CwF1					78.34c	1.12
HwF1					65.50c	1.12
ED x Fz	2	33	1.34	0.2759		
Sp x ED x Fz:	2	33	4.08	0.0260		
CwF0-500					51.06cde	1.18
HwF0-500					15.60bc	1.18
CwF0-1500					25.95c	1.18
HwF0-1500					9.04a	1.18
CwF0-2500					19.23c	1.18
HwF0-2500					3.33a	1.18
CwF1-500					124.46f	1.18
HwF1-500					118.16f	1.18
CwF1-1500					83.93e	1.18
HwF1-1500					51.16e	1.18
CwF1-2500					46.05cde	1.18
HwF1-2500					46.39cde	1.18

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.6. Analysis of average tree BA and BA/ha for HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean	SE
BA per Tree:						cm^2	
Sp:		1	33	12.80	0.0011		
	Cw					83.10a	1.16
	Hw					114.32b	1.16
ED:		2	33	4.75	0.0153		
	500					114.19b	1.18
	1500					90.02ab	1.18
	2500					64.88a	1.18
Fz:		1	33	56.26	<.0001		
	F0					52.46a	1.16
	F1					153.59b	1.16
Sp x ED:		2	33	0.04	0.9614		
Sp x Fz:		1	33	<0.00	0.9590		
ED x Fz		2	33	1.07	0.3553		
Sp x ED x Fz		2	33	0.17	0.8445		
BA per ha:						m^2	
Sp:		1	33	10.69	0.0025		
	Cw					7.89a	0.12
	Hw					12.85b	0.12
ED		2	33	20.86	<.0001		
						5.11a	0.12
						13.38b	0.12
						14.95b	
Fz:		1	33	54.82	<.0001		
	F0					5.79a	0.12
	F1					17.50b	0.12
Sp x ED		2	33	0.02	0.9793		
Sp x Fz		1	33	0.05	0.8239		
ED x Fz		2	33	1.51	0.2367		
Sp x ED x Fz		2	33	0.13	0.8771		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.7. Analysis of annual average BA growth rate per tree for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (cm^2/yr)	SE
CH Sites:							
Sp:		1	33	78.83	<.0001		
	Cw					6.35b	0.11
	Hw					3.09a	0.11
ED:		2	33	66.85	<.0001		
	500					8.04c	0.11
	1500					4.22b	0.11
	2500					2.55a	0.11
Fz:		1	33	293.88	<.0001		
	F0					2.21a	0.11
	F1					8.88b	0.11
Sp x ED		2	33	0.25	0.7802		
Sp x Fz:		1	33	42.85	<.0001		
	CwF0					4.13b	0.11
	HwF0					1.18a	0.11
	CwF1					9.76c	0.11
	HwF1					8.08c	0.11
ED x Fz		2	33	1.18	0.3189		
Sp x ED x Fz		2	33	2.67	0.0844		
HA Sites:							
Sp:		1	33	9.91	0.0035		
	Cw					8.30a	0.12
	Hw					12.94b	0.12
ED		2	33	6.37	0.0046		
	500					14.01b	0.12
	1500					10.49ab	0.12
	2500					7.57a	0.12
Fz:		1	33	56.12	<.0001		
	F0					6.12a	0.12
	F1					17.57b	0.12
Sp x ED		2	33	0.02	0.9833		
Sp x Fz		1	33	0.02	0.8958		
ED x Fz		2	33	1.05	0.3597		
Sp x ED x Fz		2	33	0.28	0.7552		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.8. Analysis of stand BA for CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (m^2)	SE
Sp:	1	33	88.69	<.0001		
Cw					5.91b	0.11
Hw					2.58a	0.11
ED:	2	33	17.05	<.0001		
500					2.72a	0.11
1500					4.83b	0.11
2500					4.53b	0.11
Fz:	1	33	322.54	<.0001		
F0					1.77a	0.11
F1					8.61b	0.11
Sp x ED	2	33	0.79	0.4603		
Sp x Fz:	1	33	49.18	<.0001		
CwF0					3.65b	0.11
HwF0					0.86a	0.11
CwF1					9.57c	0.11
HwF1					7.75c	0.11
ED x Fz	2	33	1.88	0.1690		
Sp x ED x Fz:	2	33	4.62	0.0170		
CwF0-500					2.50bc	0.12
HwF0-500					0.70a	0.12
CwF0-1500					4.12d	0.12
HwF0-1500					1.29ab	0.12
CwF0-2500					4.73cd	0.12
HwF0-2500					0.70a	0.12
CwF1-500					5.86d	0.12
HwF1-500					5.36cd	0.12
CwF1-1500					13.32e	0.12
HwF1-1500					7.66d	0.12
CwF1-2500					11.24e	0.12
HwF1-2500					11.33e	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.9. Analysis of annual stand BA growth rate for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (m^2/yr)	SE
CH Sites:							
Sp:		1	33	93.23	<.0001		
	Cw					0.93b	0.09
	Hw					0.59a	0.09
ED:		2	33	17.64	<.0001		
	500					0.50a	0.10
	1500					0.86b	0.10
	2500					0.92b	0.10
Fz:		1	33	288.31	<.0001		
	F0					0.35a	0.09
	F1					1.17b	0.09
Sp x ED		2	33	0.27	0.7659		
Sp x Fz:		1	33	46.74	<.0001		
	CwF0					0.55b	0.11
	HwF0					0.14a	0.11
	CwF1					1.30c	0.11
	HwF1					1.04c	0.11
ED x Fz		2	33	1.18	0.3189		
Sp x ED x Fz		2	33	2.67	0.0844		
HA Sites:							
Sp:		1	33	7.34	0.0106		
	Cw					1.38a	0.20
	Hw					2.37b	0.20
ED		2	33	24.17	<.0001		
	500					0.70a	0.21
	1500					1.94b	0.21
	2500					2.32b	0.21
Fz:		1	33	55.60	<.0001		
	F0					0.93a	0.20
	F1					2.37b	0.20
Sp x ED		2	33	0.01	0.9916		
Sp x Fz		1	33	0.09	0.7721		
ED x Fz		2	33	1.50	0.2388		
Sp x ED x Fz		2	33	0.18	0.8377		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.10. Analysis of mortality for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	17.60	0.0002		
	Cw					1.50a	0.67
	Hw					5.34b	0.67
ED:		2	33	3.20	0.0536		
Fz:		1	33	1.83	0.1859		
Sp x ED		2	33	1.89	0.1674		
Sp x Fz:		1	33	0.61	0.4413		
ED x Fz		2	33	0.67	0.5182		
Sp x ED x Fz		2	33	0.19	0.8300		
HA Sites:							
Sp:		1	33	10.54	0.0027		
	Cw					3.78a	1.27
	Hw					9.64b	1.27
ED		2	33	1.35	0.2737		
Fz:		1	33	4.72	0.0371		
	F0					4.75a	1.27
	F1					8.66b	1.27
Sp x ED		2	33	0.21	0.8081		
Sp x Fz		1	33	1.36	0.2525		
ED x Fz		2	33	0.68	0.5145		
Sp x ED x Fz		2	33	0.58	0.5675		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.11. Foliar N concentration for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	154.75	<.0001		
	Cw					1.0213b	0.0148
	Hw					0.7607a	0.0148
ED:		2	33	4.37	0.0207		
	500					0.9296b	0.0182
	1500					0.8538a	0.0182
	2500					0.8897ab	0.0182
Fz:		1	33	3.34	0.0767		
Sp x ED		2	33	0.47	0.6286		
Sp x Fz:		1	33	0.02	0.9001		
ED x Fz		2	33	0.52	0.5992		
Sp x ED x Fz		2	33	0.33	0.7191		
HA Sites:							
Sp:		1	33	31.47	<.0001		
	Cw					1.0738b	0.0307
	Hw					0.9277a	0.0307
ED		2	33	2.41	0.1056		
Fz:		1	33	11.57	0.0018		
	F0					0.9565a	0.0307
	F1					1.0450b	0.0307
Sp x ED		2	33	2.38	0.1085		
Sp x Fz		1	33	2.01	0.1652		
ED x Fz		2	33	4.64	0.0167		
Sp x ED x Fz		2	33	1.83	0.1761		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.12. Analysis of Foliar P Concentration for CH and HA Sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	5.14	0.0301		
	Cw					0.1571b	0.0067
	Hw					0.1446a	0.0067
ED:		2	33	0.10	0.9074		
Fz:		1	33	80.61	<.0001		
	F0					0.1259a	0.0067
	F1					0.1758b	0.0067
Sp x ED		2	33	0.59	0.5610		
Sp x Fz:		1	33	52.77	<.0001		
ED x Fz		2	33	1.27	0.2941		
Sp x ED x Fz		2	33	0.37	0.6968		
HA Sites:							
Sp:		1	33	29.95	<.0001		
	Cw					0.1732b	0.0086
	Hw					0.1417a	0.0086
ED		2	33	0.37	0.6925		
Fz:		1	33	80.60	<.0001		
	F0					0.1316a	0.0086
	F1					0.1834b	0.0086
Sp x ED		2	33	2.35	0.1108		
Sp x Fz:		1	33	23.06	<.0001		
	CwF0					0.1612b	0.0095
	HwF0					0.1019a	0.0095
	CwF1					0.1853c	0.0095
	HwF1					0.1814bc	0.0095
ED x Fz		2	33	0.03	0.9676		
Sp x ED x Fz		2	33	0.02	0.9793		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.13. Analysis of Foliar K Concentration for CH and HA Sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	39.03	<.0001		
	Cw					0.5078a	0.0139
	Hw					0.6305b	0.0139
ED:		2	33	1.78	0.1841		
Fz:		1	33	5.56	0.0245		
	F0					0.5923b	0.0139
	F1					0.5460a	0.0139
Sp x ED		2	33	2.02	0.1482		
Sp x Fz:		1	33	0.01	0.9388		
ED x Fz		2	33	0.43	0.6569		
Sp x ED x Fz		2	33	0.90	0.4151		
HA Sites:							
Sp:		1	33	6.06	0.0192		
	Cw					0.4919a	0.0178
	Hw					0.5426b	0.0178
ED		2	33	0.15	0.8645		
Fz:		1	33	7.14	0.0116		
	F0					0.5448a	0.0178
	F1					0.4897b	0.0178
Sp x ED		2	33	6.69	0.0036		
	Cw500					0.4441a	0.0272
	Hw500					0.6004b	0.0272
	Cw1500					0.5037ab	0.0272
	Hw1500					0.5152ab	0.0272
	Cw2500					0.5279ab	0.0272
	Hw2500					0.5123ab	0.0272
Sp x Fz:		1	33	0.97	0.3315		
ED x Fz		2	33	0.29	0.7472		
Sp x ED x Fz		2	33	0.51	0.6035		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.14. Analysis of Foliar S Concentration for CH and HA Sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:						
Sp:	1	33	15.90	0.0003		
Cw					0.0916b	0.0022
Hw					0.0827a	0.0022
ED:	2	33	1.94	0.1594		
Fz:	1	33	0.09	0.7708		
Sp x ED	2	33	3.99	0.0281		
Cw500					0.0983b	0.0032
Hw500					0.0807a	0.0032
Cw1500					0.0871ab	0.0032
Hw1500					0.0813a	0.0032
Cw2500					0.08894ab	0.0032
Hw2500					0.0862a	0.0032
Sp x Fz:	1	33	0.50	0.4835		
ED x Fz	2	33	0.02	0.9836		
Sp x ED x Fz	2	33	0.50	0.6092		
HA Sites:						
Sp:	1	33	1.08	0.3055		
ED	2	33	01.08	0.3526		
Fz:	1	33	0.02	0.8987		
Sp x ED	2	33	3.04	0.0612		
Sp x Fz:	1	33	0.16	0.6961		
ED x Fz	2	33	2.73	0.0803		
Sp x ED x Fz	2	33	1.34	0.2766		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.15. Analysis of foliar SO_4-S concentration for CH and HA sites.

Source	NDF	DDF	F	p	LS Mean (ppm)	SE
CH Sites:						
Sp:	1	33	132.90	<.0001		
Cw					131.00a	8.20
Hw					264.64b	8.20
ED:	2	33	0.49	0.6178		
Fz:	1	33	0.15	0.7022		
Sp x ED	2	33	1.97	0.1560		
Sp x Fz:	1	33	2.70	0.1098		
ED x Fz	2	33	0.36	0.6998		
Sp x ED x Fz	2	33	1.29	0.2899		
HA Sites:						
Sp:	1	33	83.61	<.0001		
Cw					126.65a	10.38
Hw					242.38b	10.38
ED	2	33	0.86	0.4315		
Fz:	1	33	11.12	0.0021		
F0					205.62b	10.38
F1					163.42a	10.38
Sp x ED	2	33	2.12	0.1363		
Sp x Fz:	1	33	1.06	0.3110		
ED x Fz	2	33	1.22	0.3092		
Sp x ED x Fz	2	33	3.34	0.0478		
CwF0-500					145.95a	22.55
HwF0-500					261.76b	22.55
CwF0-1500					129.68a	22.55
HwF0-1500					290.36b	22.55
CwF0-2500					148.11a	22.55
HwF0-2500					257.87b	22.55
CwF1-500					125.67a	22.55
HwF1-500					171.11ab	22.55
CwF1-1500					109.92a	22.55
HwF1-1500					196.41ab	22.55
CwF1-2500					100.59a	22.55
HwF1-2500					276.79b	22.55

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.16. Analysis of foliar Ca concentration for CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:						
Sp:	1	33	841.23	<.0001		
Cw					0.7700b	0.0131
Hw					0.2400a	0.0131
ED:	2	33	0.34	0.7160		
Fz:	1	33	15.67	0.0004		
F0					0.4688a	0.0131
F1					0.5412b	0.0131
Sp x ED	2	33	0.12	0.8856		
Sp x Fz:	1	33	7.27	0.0109		
CwF0					0.7092b	0.0184
HwF0					0.2285a	0.0184
CwF1					0.8308c	0.0184
HwF1					0.2515a	0.0184
ED x Fz	2	33	0.97	0.3888		
Sp x ED x Fz	2	33	0.45	0.6404		
HA Sites:						
Sp:	1	33	749.16	<.0001		
Cw					0.9233b	0.0228
Hw					0.3027a	0.0228
ED	2	33	2.72	0.0809		
Fz:	1	33	38.50	<.0001		
F0					0.5426a	0.0228
F1					0.6833b	0.0228
Sp x ED:	2	33	4.39	0.0203		
Cw500					0.9388c	0.0322
Hw500					0.2240a	0.0322
Cw1500					0.9041c	0.0322
Hw1500					0.3188ab	0.0322
Cw2500					0.9270c	0.0322
Hw2500					0.3651b	0.0322
Sp x Fz:	1	33	0.89	0.3520		
ED x Fz	2	33	0.59	0.5609		
Sp x ED x Fz	2	33	3.22	0.0529		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.17. Analysis of foliar Mg concentration for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	89.11	<.0001		
	Cw					0.1249b	0.0030
	Hw					0.0943a	0.0030
ED:		2	33	0.12	0.8876		
Fz:		1	33	7.26	0.0110		
	F0					0.1052a	0.0030
	F1					0.1139b	0.0030
Sp x ED		2	33	0.72	0.4933		
Sp x Fz:		1	33	22.34	<.0001		
	CwF0					0.1281c	0.0038
	HwF0					0.0823a	0.0038
	CwF1					0.1216c	0.0038
	HwF1					0.1063b	0.0038
ED x Fz		2	33	0.97	0.3913		
Sp x ED x Fz		2	33	3.28	0.0503		
HA Sites:							
Sp:		1	33	8.56	0.0062		
	Cw					0.1173b	0.0047
	Hw					0.1024a	0.0047
ED		2	33	0.53	0.5907		
Fz:		1	33	5.78	0.0220		
	F0					0.1037a	0.0047
	F1					0.1160b	0.0047
Sp x ED		2	33	0.64	0.5330		
Sp x Fz:		1	33	9.89	0.0035		
	CwF0					0.1192b	0.0059
	HwF0					0.0883a	0.0059
	CwF1					0.1154b	0.0059
	HwF1					0.1165b	0.0059
ED x Fz		2	33	0.42	0.6581		
Sp x ED x Fz		2	33	0.50	0.6106		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.18. Analysis of foliar Fe concentration for CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (ppm)	SE
CH Sites:							
Sp:		1	33	5.58	0.0242		
	Cw					36.83a	3.28
	Hw					41.51b	3.28
ED:		2	33	9.81	0.0005		
	500					45.30b	3.43
	1500					36.96a	3.43
	2500					35.25a	3.43
Fz:		1	33	0.07	0.8002		
Sp x ED		2	33	0.52	0.5997		
Sp x Fz:		1	33	0.08	0.7752		
ED x Fz		2	33	1.75	0.1896		
Sp x ED x Fz		2	33	0.12	0.8864		
HA Sites:							
Sp:		1	33	0.62	0.4377		
ED		2	33	0.07	0.9366		
Fz:		1	33	0.45	0.5068		
Sp x ED		2	33	1.33	0.2781		
Sp x Fz		1	33	<0.00	0.9548		
ED x Fz		2	33	0.06	0.9455		
Sp x ED x Fz		2	33	0.08	0.9210		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.19. Analysis of Foliar Cu Concentration for CH and HA Sites.

Source	NDF	DDF	*F*	*p*
CH Sites:				
Sp:	1	33	2.82	0.1025
ED:	2	33	2.22	0.1242
Fz:	1	33	0.35	0.5598
Sp x ED	2	33	2.25	0.1218
Sp x Fz:	1	33	0.29	0.5916
ED x Fz	2	33	0.41	0.6665
Sp x ED x Fz	2	33	0.44	0.6478
HA Sites:				
Sp:	1	33	3.44	0.0724
ED	2	33	1.20	0.3136
Fz:	1	33	0.30	0.5902
Sp x ED	2	33	0.83	0.4430
Sp x Fz	1	33	1.41	0.2439
ED x Fz	2	33	1.96	0.1572
Sp x ED x Fz	2	33	0.37	0.6964

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.20. Analysis of Foliar Zn Concentration for CH and HA Sites.

Source		NDF	DDF	*F*	*p*	LS Mean (ppm)	SE
CH Sites:							
Sp:		1	33	22.38	<.0001		
	Cw					12.34b	0.75
	Hw					7.87a	0.75
ED:		2	33	2.58	0.0912		
Fz:		1	33	0.81	0.3737		
Sp x ED		2	33	1.32	0.2812		
Sp x Fz:		1	33	<0.00	0.9797		
ED x Fz		2	33	0.55	0.5843		
Sp x ED x Fz		2	33	0.27	0.7683		
HA Sites:							
Sp:		1	33	152.42	<.0001		
	Cw					13.30b	0.51
	Hw					7.64a	0.51
ED:		2	33	5.75	0.0072		
	500					9.37a	0.56
	1500					11.04b	0.56
	2500					11.00b	0.56
Fz:		1	33	6.91	0.0129		
	F0					9.87a	0.51
	F1					11.08b	0.51
Sp x ED		2	33	0.58	0.5651		
Sp x Fz		1	33	0.71	0.4055		
ED x Fz		2	33	1.94	0.1600		
Sp x ED x Fz		2	33	0.22	0.8030		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.21. Analysis of Foliar Mn Concentration for CH and HA Sites.

Source		NDF	DDF	*F*	*p*	LS Mean (ppm)	SE
CH Sites:							
Sp:		1	33	277.68	<.0001		
	Cw					343.50a	79.12
	Hw					2077.23b	79.12
ED:		2	33	0.70	0.5023		
Fz:		1	33	5.79	0.0219		
	F0					1335.55b	79.12
	F1					1085.17a	79.12
Sp x ED		2	33	0.59	0.5583		
Sp x Fz:		1	33	4.21	0.0483		
	CwF0					362.01a	108.04
	HwF0					2309.10c	108.04
	CwF1					324.99a	108.04
	HwF1					1845.35b	108.04
ED x Fz		2	33	0.77	0.4723		
Sp x ED x Fz		2	33	0.12	0.8876		
HA Sites:							
Sp:		1	33	218.59	<.0001		
	Cw					349.62a	74.26
	Hw					1821.68b	74.26
ED:		2	33	0.87	0.4299		
Fz:		1	33	1.21	0.2799		
Sp x ED		2	33	1.64	0.2090		
Sp x Fz		1	33	2.13	0.1540		
ED x Fz		2	33	1.23	0.3052		
Sp x ED x Fz		2	33	2.92	0.0680		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.22. Analysis of Foliar Al Concentration for CH and HA Sites.

Source		NDF	DDF	*F*	*p*	LS Mean (ppm)	SE
CH Sites:							
Sp:		1	33	238.89	<.0001		
	Cw					39.39a	10.77
	Hw					274.71b	10.77
ED:		2	33	2.48	0.0996		
Fz:		1	33	3.56	0.0680		
Sp x ED		2	33	2.42	0.1050		
Sp x Fz:		1	33	3.78	0.0603		
ED x Fz		2	33	0.65	0.5289		
Sp x ED x Fz		2	33	1.25	0.2987		
HA Sites:							
Sp:		1	33	381.64	<.0001		
	Cw					36.40a	11.84
	Hw					363.62b	11.84
ED		2	33	0.77	0.4697		
Fz:		1	33	9.08			
	F0				0.0036	173.79	11.84
	F1					226.22	11.84
Sp x ED		2	33	0.55	0.5814		
Sp x Fz:		1	33	9.24	0.0046		
	CwF0					35.64a	16.75
	HwF0					311.95b	16.75
	CwF1					37.15a	16.75
	HwF1					415.29c	16.75
ED x Fz		2	33	1.72	0.1943		
Sp x ED x Fz		2	33	1.62	0.2134		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.23. Analysis of Foliar B Concentration for CH and HA Sites.

Source	NDF	DDF	*F*	*p*	LS Mean (ppm)	SE
CH Sites:						
Sp:	1	33	101.23	<.0001		
Cw					11.35a	0.70
Hw					19.27b	0.70
ED:	2	33	1.53	0.2313		
Fz:	1	33	0.35	0.5603		
Sp x ED	2	33	1.27	0.2949		
Sp x Fz:	1	33	11.66	0.0017		
CwF0					10.24a	0.89
HwF0					20.85c	0.89
CwF1					12.46a	0.89
HwF1					17.70b	0.89
ED x Fz	2	33	0.08	0.9265		
Sp x ED x Fz	2	33	1.29	0.2898		
HA Sites:						
Sp:	1	33	692.13	<.0001		
Cw					9.89a	0.44
Hw					23.87b	0.44
ED	2	33	0.32	0.7281		
Fz	1	33	1.12	0.2969		
Sp x ED	2	33	<0.00	0.9973		
Sp x Fz	1	33	3.74	0.0617		
ED x Fz	2	33	0.10	0.9036		
Sp x ED x Fz	2	33	0.21	0.8105		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A1.24. Pearson Correlation Analysis of height increment with foliar nutrient concentration.

Nutrient		Cw CH	Hw CH	Cw HA	Hw HA	Cw Combined	Hw Combined
N	R^2	0.288	0.205	0.716	0.552	0.594	0.678
	p	0.1093*	0.2601	<.0001*	0.0011*	<.0001*	<.0001*
P	R^2	0.618	0.623	0.309	0.591	0.512	0.438
	p	0.0002*	0.0001*	0.0850	0.0004*	<.0001*	0.0003*
K	R^2	0.235	-0.140	-0.080	-0.484	0.110	-0.465
	p	0.1927	0.4450	0.6635	0.0050*	0.3864	0.0001*
S	R^2	0.475	0.189	0.534	0.356	0.549*	0.498
	p	0.0060*	0.2994	0.0017*	0.0456*	<.0001	<.0001*
Ca	R^2	0.251	0.0719	0.516	0.693	0.453	0.566
	p	0.1661	0.6960	0.0025*	<.0001*	0.0002*	<.0001*
Mg	R^2	0.240	0.172	-0.139	0.576	-0.013	0.403
	p	0.1852	0.3476	0.4472	0.0006*	0.9175	0.0010*
Zn	R^2	0.511	0.293	0.400	0.555	0.481	0.250
	p	0.0028*	0.1042	0.0232*	0.0010*	<.0001*	0.0461*
Cu	R^2	-0.037	0.320	0.483	-0.046	0.367	0.032
	p	0.840	0.0740	0.0051*	0.8011	0.0029*	0.7992
Fe	R^2	0.060	0.035	-0.251	0.114	-0.061	0.038
	p	0.7431	0.8495	0.1652	0.536	0.6315	0.7645
Mn	R^2	-0.173	-0.231	-0.026	-0.152	-0.081	-0.279
	p	0.3433	0.2041	0.8870	0.4075	0.5266	0.0257*
Al	R^2	-0.095	0.464	0.077	0.365	-0.132	0.534
	p	0.605	0.0075*	0.6739	0.040*	0.2975	<.0001
B	R^2	0.381	-0.581	0.515	-0.700	0.509	-0.786
	p	0.0317*	0.0005*	0.0026*	<.0001*	<.0001*	<.0001*
SO_4-S	R^2	0.355	0.082	-0.449	-0.080	0.177	-0.148
	p	0.0465*	0.6556	0.0099*	0.6639	0.1619	0.2419

CH = CH Sites, HA = HA Sites; Cw = Cedar, Hw = Hemlock; significance level of $p < 0.05$ was used for *F* tests

Table A1.25. Analysis of Salal Mass.

Source		NDF	DDF	*F*	*p*	LS Mean (g/plot)	SE
Fz:		1	15	42.27	<.0001		
	F0					340.43a	59.69
	F1					837.06b	59.69
ED		2	15	0.26	0.7712		
ED x Fz		2	15	0.11	0.8998		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Appendix 2: Statistical Analysis for Chapter 3

Table A2.1. Model statistics for covariate Ln (d^2h) as predictor variable for cedar on CH sites.

Dependent Variable	NDF	DDF	F	p	r^2
Ln(Total Dry Matter)	13	58	125.15	<.0001	0.966
Ln(Foliage Mass)	13	58	34.83	<.0001	0.886
Ln(Bark Mass)	13	58	149.57	<.0001	0.971
Ln(Branch Mass)	13	58	45.41	<.0001	0.911
Ln(Wood Mass)	13	58	280.08	<.0001	0.984

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; significance level of $p < 0.05$ was used for F tests

Table A2.2. Covariate analysis of cedar mass and mass components on CH sites.

Mass Component	Source of Variation	DF	*F*	*p*
Total Tree Mass	NR	2	0.64	0.5295
	ED	2	0.88	0.4183
	LnDSH	2	254.24	<.0001
	LnDSH x NR	2	0.59	0.5551
	LnDSH x ED	2	0.73	0.4870
	NR x ED	4	1.07	0.3775
Wood Mass	NR	2	0.68	0.5110
	ED	2	0.29	0.7493
	LnDSH	2	505.26	<.0001
	LnDSH x NR	2	0.52	0.5977
	LnDSH x ED	2	0.30	0.7470
	NR x ED	4	0.61	0.6565
Bark Mass	NR	2	0.18	0.8330
	ED	2	0.42	0.6604
	LnDSH	2	309.52	<.0001
	LnDSH x NR	2	0.18	0.8340
	LnDSH x ED	2	0.44	0.6430
	NR x ED	4	2.50	0.0525
Foliage Mass	NR	2	2.02	0.1425
	ED	2	1.75	0.1831
	LnDSH	2	88.31	<.0001
	LnDSH x NR	2	1.96	0.1508
	LnDSH x ED	2	1.48	0.2358
	NR x ED	4	0.96	0.4383
Twig Mass	NR	2	2.53	0.0887
	ED	2	1.19	0.3105
	LnDSH	2	94.05	<.0001
	LnDSH x NR	2	2.25	0.1141
	LnDSH x ED	2	1.01	0.3714
	NR x ED	4	1.28	0.2897

DF = Degrees of Freedom; NR = Nutrient Regime; ED = Establishment Density; LnDSH = Ln(d^2h); significance level of $p < 0.05$ was used for F tests

Table A2.3. Analysis of average tree mass on CH sites.

Source		NDF	DDF	*F*	*p*	LS Mean (kg)	SE
Sp:		1	33	37.92	<.0001		
	Cw					9.35b	0.11
	Hw					5.53a	0.11
ED:		2	33	49.57	<.0001		
	500					12.30c	0.11
	1500					6.93b	0.11
	2500					4.36a	0.11
Fz:		1	33	312.53	<.0001		
	F0					3.38a	0.11
	F1					15.27b	0.11
Sp x ED		2	33	1.02	0.3716		
Sp x Fz:		1	33	44.81	<.0001		
	CwF0					5.85b	0.11
	HwF0					1.96a	0.11
	CwF1					14.92c	0.11
	HwF1					15.62c	0.11
ED x Fz		2	33	1.32	0.2819		
Sp x ED x Fz		2	33	3.94	0.0293		
	CwF0-500					9.70cd	0.12
	HwF0-500					3.79b	0.12
	CwF0-1500					5.23bc	0.12
	HwF0-1500					2.25b	0.12
	CwF0-2500					3.95b	0.12
	HwF0-2500					0.88a	0.12
	CwF1-500					22.36ef	0.12
	HwF1-500					27.80f	0.12
	CwF1-1500					16.08ef	0.12
	HwF1-1500					12.16de	0.12
	CwF1-2500					9.24cd	0.12
	HwF1-2500					11.28de	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.4. Analysis of average tree mass on HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (kg)	SE
Sp:		1	33	27.86	<.0001		
	Cw					12.85a	0.12
	Hw					28.84b	0.12
ED:		2	33	3.07	0.0599		
Fz:		1	33	51.78	<.0001		
	F0					11.10a	0.12
	F1					33.40b	0.12
Sp x ED		2	33	0.10	0.9063		
Sp x Fz:		1	33	0.07	0.7860		
ED x Fz		2	33	1.38	0.2650		
Sp x ED x Fz		2	33	0.07	0.9328		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.5. Analysis of total stand mass for CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Site:	1	69	117.75	<.0001		
CH					8.53a	1.12
HA					22.18b	1.12
Sp:	1	69	0.82	0.3673		
ED:	2	69	41.73	<.0001		
500					7.80a	1.13
1500					17.71b	1.13
2500					18.86b	1.13
Fz:	1	69	219.91	<.0001		
F0					7.16a	1.12
F1					26.43b	1.12
Site x Sp:	1	69	59.29	<.0001		
CH-Cw					11.50b	1.14
CH-Hw					6.32a	1.14
HA-Cw					15.18b	1.14
HA-Hw					32.41c	1.14
Site x Fert	1	69	6.64	0.0121		
CH-F0					3.96a	1.14
CH-F1					18.36c	1.14
HA-F0					12.93b	1.14
HA-F1					38.06d	1.14
Site x ED	2	69	3.97	0.0234		
CH-500					5.72a	1.16
CH-1500					10.56b	1.16
CH-2500					10.28b	1.16
HA-500					10.63b	1.16
HA-1500					29.69c	1.16
HA-2500					34.59c	1.16
Sp x ED	2	69	0.06	0.9442		
Sp x Fz:	1	69	12.09	0.0009		
Cw-F0					8.02a	1.14
Cw-F1					21.79b	1.14
Hw-F0					6.39a	1.14
Hw-F1					32.07c	1.14
ED x Fz	2	69	3.07	0.0530		

Table A2.5. (continued)

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Site x Sp x Fz	1	69	12.04	0.0009		
CH-Cw-F0					7.26b	1.17
CH-Cw-F1					18.23c	1.17
CH-Hw-F0					2.16a	1.17
CH-Hw-F1					18.49c	1.17
HA-Cw-F0					8.85b	1.17
HA-Cw-F1					26.04c	1.17
HA-Hw-F0					18.89c	1.17
HA-Hw-F1					55.62d	1.17
Site x Fz x ED	2	69	0.64	0.5288		
Sp x ED x Fz	2	69	0.74	0.4825		
Sp x Site x ED	2	69	0.63	0.5358		
Site x Sp x Fz x ED	2	69	1.43	0.2473		

Sp=Species, Cw=Western Red Cedar, Hw=Western Hemlock; ED=Establishment Density; Fz=Fertilization, F0=Unfertilized, F1=Fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A2.6. Analysis of wood mass on HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Sp:	1	33	33.95	<.0001		
Cw					5.68a	0.12
Hw					15.17b	0.12
ED:	2	33	3.17	0.0550		
Fz:	1	33	52.33	<.0001		
F0					5.04a	0.12
F1					17.09b	0.12
Sp x ED	2	33	0.12	0.8875		
Sp x Fz:	1	33	0.03	0.8654		
ED x Fz	2	33	1.41	0.2575		
Sp x ED x Fz	2	33	0.07	0.9299		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.7. Analysis of stand wood mass on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Sp:	1	33	22.32	<.0001		
Cw					3.91a	0.11
Hw					2.50b	0.11
ED:	2	33	49.96	<.0001		
500					5.71c	0.11
1500					2.99b	0.11
2500					1.79a	0.11
Fz:	1	33	305.88	<.0001		
F0					1.36a	0.11
F1					7.17b	0.11
Sp x ED	2	33	0.79	0.4616		
Sp x Fz:	1	33	39.94	<.0001		
CwF0					2.30b	0.11
HwF0					0.81a	0.11
CwF1					6.65c	0.11
HwF1					7.74c	0.11
ED x Fz	2	33	1.27	0.2939		
Sp x ED x Fz	2	33	3.56	0.0398		
CwF0-500					4.13cd	0.12
HwF0-500					1.68b	0.12
CwF0-1500					2.01bc	0.12
HwF0-1500					0.93b	0.12
CwF0-2500					1.47b	0.12
HwF0-2500					0.33a	0.12
CwF1-500					10.53ef	0.12
HwF1-500					14.55f	0.12
CwF1-1500					7.22def	0.12
HwF1-1500					5.89de	0.12
CwF1-2500					3.87cd	0.12
HwF1-2500					5.40de	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.8. Analysis of stand bark mass on CH sites.

Source	NDF	DDF	F	p	LS Mean (t/ha)	SE
Sp:	1	33	70.07	<.0001		
Cw					0.83b	0.11
Hw					0.42a	0.11
ED:	2	33	29.69	<.0001		
500					0.38a	0.11
1500					0.73b	0.11
2500					0.73b	0.11
Fz:	1	33	319.52	<.0001		
F0					0.28a	0.11
F1					1.22b	0.11
Sp x ED	2	33	1.91	0.1646		
Sp x Fz:	1	33	61.86	<.0001		
CwF0					0.55b	0.11
HwF0					0.15a	0.11
CwF1					1.24c	0.11
HwF1					1.19c	0.11
ED x Fz	2	33	2.08	0.1414		
Sp x ED x Fz	2	33	4.51	0.0186		
CwF0-500					0.34bc	0.12
HwF0-500					0.11a	0.12
CwF0-1500					0.64cd	0.12
HwF0-1500					0.22ab	0.12
CwF0-2500					0.77d	0.12
HwF0-2500					0.13a	0.12
CwF1-500					0.69d	0.12
HwF1-500					0.80d	0.12
CwF1-1500					1.73e	0.12
HwF1-1500					1.18de	0.12
CwF1-2500					1.62e	0.12
HwF1-2500					1.79e	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.9. Analysis of stand bark and branch masses on HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Bark Mass:							
Sp:		1	33	22.19	<.0001		
	Cw					1.04a	0.12
	Hw					2.06b	0.12
ED:		2	33	27.79	<.0001		
	500					0.69a	0.12
	1500					1.96b	0.12
	2500					2.33b	0.12
Fz:		1	33	49.05	<.0001		
	F0					0.89a	0.12
	F1					2.43b	0.12
Sp x ED		2	33	0.06	0.9448		
Sp x Fz:		1	33	0.09	0.7665		
ED x Fz		2	33	1.83	0.1757		
Sp x ED x Fz		2	33	0.04	0.9587		
Branch Mass:							
Sp:		1	33	15.71	0.0004		
	Cw					4.09a	1.16
	Hw					7.36b	1.16
ED:		2	33	25.32	<.0001		
	500					2.62a	1.18
	1500					7.33b	1.18
	2500					8.60b	1.18
Fz:		1	33	50.36	<.0001		
	F0					3.24a	1.16
	F1					9.28b	1.16
Sp x ED		2	33	0.12	0.8858		
Sp x Fz:		1	33	0.01	0.9137		
ED x Fz		2	33	1.90	0.1657		
Sp x ED x Fz		2	33	0.06	0.9408		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.10. Analysis of stand branch mass on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Sp:	1	33	69.87	<.0001		
Cw					3.11b	0.11
Hw					1.53a	0.11
ED:	2	33	24.01	<.0001		
500					1.44a	0.11
1500					2.70b	0.11
2500					2.66b	0.11
Fz:	1	33	308.00	<.0001		
F0					1.04a	0.11
F1					4.59b	0.11
Sp x ED	2	33	0.88	0.4248		
Sp x Fz:	1	33	46.42	<.0001		
CwF0					1.97b	0.11
HwF0					0.54a	0.11
CwF1					4.90c	0.11
HwF1					4.30c	0.11
ED x Fz	2	33	1.82	0.1774		
Sp x ED x Fz	2	33	4.26	0.0226		
CwF0-500					1.28bc	0.12
HwF0-500					0.41a	0.12
CwF0-1500					2.26cd	0.12
HwF0-1500					0.81ab	0.12
CwF0-2500					2.64cd	0.12
HwF0-2500					0.48a	0.12
CwF1-500					2.82d	0.12
HwF1-500					2.87d	0.12
CwF1-1500					6.86e	0.12
HwF1-1500					4.28de	0.12
CwF1-2500					6.10e	0.12
HwF1-2500					6.50e	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.11. Analysis of stand foliage mass on CH sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Sp:		1	33	53.75	<.0001		
	Cw					2.16b	0.11
	Hw					1.28a	0.11
ED:		2	33	49.28	<.0001		
	500					2.60c	0.11
	1500					1.62b	0.11
	2500					1.09a	0.11
Fz:		1	33	329.51	<.0001		
	F0					0.87a	0.11
	F1					3.17b	0.11
Sp x ED		2	33	2.07	0.1426		
Sp x Fz:		1	33	61.37	<.0001		
	CwF0					1.49b	0.11
	HwF0					0.51a	0.11
	CwF1					3.12c	0.11
	HwF1					3.23c	0.11
ED x Fz		2	33	1.55	0.2283		
Sp x ED x Fz		2	33	4.07	0.0263		
	CwF0-500					2.19de	0.12
	HwF0-500					0.90bc	0.12
	CwF0-1500					1.38cd	0.12
	HwF0-1500					0.58b	0.12
	CwF0-2500					1.10c	0.12
	HwF0-2500					0.25a	0.12
	CwF1-500					4.28fg	0.12
	HwF1-500					5.38g	0.12
	CwF1-1500					3.31efg	0.12
	HwF1-1500					2.58ef	0.12
	CwF1-2500					2.14de	0.12
	HwF1-2500					2.43ef	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.12. Analysis of stand foliage mass on HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Sp:		1	33	28.97	<.0001		
	Cw					2.73a	0.11
	Hw					5.55b	0.11
ED:		2	33	2.84	0.0725		
Fz:		1	33	50.08	<.0001		
	F0					2.45a	0.11
	F1					6.20b	0.11
Sp x ED		2	33	0.05	0.9516		
Sp x Fz:		1	33	0.42	0.5216		
ED x Fz		2	33	1.29	0.2885		
Sp x ED x Fz		2	33	0.05	0.9503		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.13. Analysis of ZBark on CH sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
Sp:		1	33	125.46	<.0001		
	Cw					7.21b	0.05
	Hw					6.62a	0.05
ED:		2	33	28.16	<.0001		
	500					6.67a	0.05
	1500					6.94b	0.05
	2500					7.15c	0.05
Fz:		1	33	103.95	<.0001		
	F0					7.19b	0.05
	F1					6.64a	0.05
Sp x ED		2	33	9.35	0.0006		
	Cw500					6.81b	0.07
	Hw500					6.51a	0.07
	Cw1500					7.25c	0.07
	Hw1500					6.63ab	0.07
	Cw2500					7.58d	0.07
	Hw2500					6.71ab	0.07
Sp x Fz:		1	33	17.46	0.0002		
	CwF0					7.60c	0.06
	HwF0					6.78b	0.06
	CwF1					6.83b	0.06
	HwF1					6.46a	0.06
ED x Fz		2	33	0.93	0.4037		
Sp x ED x Fz		2	33	1.13	0.3353		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.14. Analysis of ZBark on HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
Sp:	1	33	51.53	<.0001		
Cw					6.90b	0.07
Hw					6.36a	0.07
ED:	2	33	3.61	0.0383		
500					6.51a	0.08
1500					6.63ab	0.08
2500					6.76b	0.08
Fz:	1	33	40.10	<.0001		
F0					6.87b	0.07
F1					6.39a	0.07
Sp x ED	2	33	1.95	0.1582		
Sp x Fz:	1	33	16.08	0.0003		
CwF0					7.30c	0.09
HwF0					6.45ab	0.09
CwF1					6.51b	0.09
HwF1					6.27ab	0.09
ED x Fz	2	33	1.64	0.2090		
Sp x ED x Fz	2	33	0.91	0.4132		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.15. Analysis of ZBrch on HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
Sp:	1	33	1463.41	<.0001		
Cw					26.92b	0.10
Hw					22.71a	0.10
ED:	2	33	2.02	0.1486		
Fz:	1	33	33.73	<.0001		
F0					25.14b	0.10
F1					24.49a	0.10
Sp x ED	2	33	0.46	0.6326		
Sp x Fz:	1	33	10.77	0.0024		
CwF0					27.06c	0.13
HwF0					23.21b	0.13
CwF1					26.78c	0.13
HwF1					22.21a	0.13
ED x Fz	2	33	0.83	0.4449		
Sp x ED x Fz	2	33	0.16	0.8545		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.16. Analysis of ZWood on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:							
Sp:		1	33	62.09	<.0001		
	Cw					42.03a	0.45
	Hw					45.44b	0.45
ED:		2	33	50.25	<.0001		
	500					46.59c	0.50
	1500					43.32b	0.50
	2500					41.29a	0.50
Fz:		1	33	241.92	<.0001		
	F0					40.35a	0.45
	F1					47.12b	0.45
Sp x ED		2	33	0.09	0.9140		
Sp x Fz:		1	33	13.73	0.0008		
	CwF0					39.42a	0.55
	HwF0					41.27b	0.55
	CwF1					44.64c	0.55
	HwF1					49.60d	0.55
ED x Fz		2	33	0.29	0.7506		
Sp x ED x Fz		2	33	2.03	0.1477		
HA Sites:							
Sp:		1	33	134.09	<.0001		
	Cw					44.37a	0.75
	Hw					52.77b	0.75
ED:		2	33	3.88	0.0307		
	500					49.78b	0.83
	1500					48.65ab	0.83
	2500					47.27a	0.83
Fz:		1	33	59.17	<.0001		
	F0					45.76a	0.75
	F1					51.37b	0.75
Sp x ED		2	33	0.26	0.7739		
Sp x Fz:		1	33	<0.00	0.9725		
ED x Fz		2	33	1.43	0.2531		
Sp x ED x Fz		2	33	0.06	0.9502		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.17. Analysis of ZBrch on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
Sp:	1	33	2029.56	<.0001		
Cw					27.03b	0.06
Hw					24.21a	0.06
ED:	2	33	45.72	<.0001		
500					25.23a	0.07
1500					25.66b	0.07
2500					25.96c	0.07
Fz:	1	33	285.14	<.0001		
F0					26.15b	0.06
F1					25.09a	0.06
Sp x ED	2	33	18.63	<.0001		
Cw500					26.89d	0.09
Hw500					23.57a	0.09
Cw1500					27.04d	0.09
Hw1500					24.29b	0.09
Cw2500					27.16d	0.09
Hw2500					24.77c	0.09
Sp x Fz:	1	33	161.21	<.0001		
CwF0					27.16d	0.07
HwF0					25.14b	0.07
CwF1					26.90c	0.07
HwF1					23.28a	0.07
ED x Fz	2	33	3.47	0.0429		
F0-500					25.69c	0.09
F1-500					24.77a	0.09
F0-1500					26.15d	0.09
F1-1500					25.18b	0.09
F0-2500					26.61e	0.09
F1-2500					25.31b	0.09
Sp x ED x Fz	2	33	3.94	0.0293		
CwF0-500					27.00f	0.12
HwF0-500					24.39c	0.12
CwF0-1500					27.21f	0.12
HwF0-1500					25.09d	0.12
CwF0-2500					27.28f	0.12
HwF0-2500					25.93e	0.12
CwF1-500					26.79f	0.12
HwF1-500					22.75a	0.12
CwF1-1500					26.88f	0.12
HwF1-1500					23.48b	0.12
CwF1-2500					27.03f	0.12
HwF1-2500					23.60b	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.18. Analysis of ZFol on CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (%)	SE
CH Sites:						
Sp:	1	33	<0.00	0.9672		
ED:	2	33	43.58	<.0001		
500					21.23a	0.39
1500					23.52b	0.39
2500					25.29c	0.39
Fz:	1	33	195.00	<.0001		
F0					25.84b	0.35
F1					20.86a	0.35
Sp x ED	2	33	1.06	0.3581		
Sp x Fz:	1	33	0.67	0.4182		
ED x Fz	2	33	2.37	0.1088		
Sp x ED x Fz	2	33	1.97	0.1559		
HA Sites:						
Sp:	1	33	18.10	0.0002		
Cw					21.52b	0.50
Hw					19.32a	0.50
ED:	2	33	4.18	0.0240		
500					19.53a	0.56
1500					20.36ab	0.56
2500					21.36b	0.56
Fz:	1	33	48.98	<.0001		
F0					22.23b	0.50
F1					18.60a	0.50
Sp x ED	2	33	0.88	0.4239		
Sp x Fz:	1	33	4.40	0.0438		
CwF0					23.87c	0.62
HwF0					20.59b	0.62
CwF1					19.16ab	0.62
HwF1					18.04a	0.62
ED x Fz	2	33	2.04	0.1464		
Sp x ED x Fz	2	33	0.45	0.6437		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A2.19. Regression slopes and significance for linear relationships between tree mass and mass proportions versus stand density (stems per ha).

Site	Species	Fertilization	Component	b_1	p	r^2
CH	Cw	F0	Tree Mass	-0.00045	0.0016	0.613
			ZBark	0.00042	0.0014	0.624
			ZWood	-0.00271	0.0016	0.613
			ZFol	0.00265	0.0013	0.627
			ZBrch	0.00014	0.0014	0.620
CH	Cw	F1	Tree Mass	-0.00044	0.0044	0.530
			ZBark	0.00035	0.0034	0.552
			ZWood	-0.00258	0.0019	0.597
			ZFol	0.00205	0.0045	0.528
			ZBran	0.00012	0.0027	0.573
HA	Cw	F0	Tree Mass	-0.00045	0.0485	0.269
			ZBark	0.00036	0.0357	0.308
			ZWood	-0.00235	0.0357	0.308
			ZFol	0.00223	0.0361	0.306
			ZBrch	0.00012	0.0355	0.308
HA	Cw	F1	Tree Mass	-0.00008	0.5412	n.s.
			ZBark	0.00008	0.4746	n.s.
			ZWood	-0.00069	0.4410	n.s.
			ZFol	0.00041	0.4886	n.s.
			ZBrch	0.00002	0.4605	n.s.
CH	Hw	F0	Tree Mass	-0.00073	<0.0001	0.864
			ZBark	0.00013	<0.0001	0.872
			ZWood	-0.0031	<0.0001	0.867
			ZFol	0.00232	<0.0001	0.873
			ZBrch	0.00077	<0.0001	0.872
CH	Hw	F1	Tree Mass	-0.00045	0.0136	0.419
			ZBark	0.00007	0.0093	0.459
			ZWood	-0.00223	0.0084	0.469
			ZFol	0.00035	0.0101	0.450
			ZBran	0.00043	0.0094	0.457
HA	Hw	F0	Tree Mass	-0.00031	0.3208	n.s.
			ZBark	0.00005	0.2583	n.s.
			ZWood	-0.00152	0.2662	n.s.
			ZFol	0.00083	0.2552	n.s.
			ZBrch	0.00031	0.2574	n.s.
HA	Hw	F1	Tree Mass	-0.00008	0.2952	n.s.
			ZBark	0.00001	0.2607	n.s.
			ZWood	-0.00046	0.2586	n.s.
			ZFol	0.00018	0.2726	n.s.
			ZBrch	0.00008	0.2610	n.s.

CH = CH Sites, HA = HA Sites; Cw = Cedar, Hw = Hemlock; F0 = Non-fertilized; F1 = Fertilized; significance level of $p < 0.05$ was used for F tests of regression significance, n.s. = Non-significant regression

Appendix 3: Statistical Analysis for Chapter 4

Table A3.1. Analysis of stand-level average annual dry mass growth rate (1997 – 2002) on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/yr)	SE
CH Sites:							
Sp:		1	33	45.92	<.0001		
	Cw					1.53a	0.11
	Hw					8.62b	0.11
ED:		2	33	20.29	<.0001		
	500					0.78a	0.11
	1500					1.39b	0.11
	2500					1.38b	0.11
Fz:		1	33	259.38	<.0001		
	F0					0.58a	0.11
	F1					2.27b	0.11
Sp x ED		2	33	0.47	0.6307		
Sp x Fz:		1	33	43.19	<.0001		
	CwF0					1.02b	0.11
	HwF0					0.33a	0.11
	CwF1					2.29c	0.11
	HwF1					2.25c	0.11
ED x Fz		2	33	1.38	0.2657		
Sp x ED x Fz		2	33	2.70	0.0823		
HA Sites:							
Sp:		1	33	22.89	<.0001		
	Cw					1.93a	0.12
	Hw					3.79b	0.12
ED:		2	33	27.43	<.0001		
	500					1.30a	0.12
	1500					3.57b	0.12
	2500					4.25b	0.12
Fz:		1	33	52.03	<.0001		
	F0					1.63a	0.12
	F1					4.49b	0.12
Sp x ED		2	33	0.12	0.8908		
Sp x Fz:		1	33	0.02	0.8843		
ED x Fz		2	33	1.96	0.1563		
Sp x ED x Fz		2	33	0.07	0.9330		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.2 Analysis of stand-level foliage efficiency (E) on CH sites.

Source	NDF	DDF	F	p	LS Mean (kg/kg/yr)	SE
Sp:	1	33	8.44	0.0065		
Cw					0.87a	0.03
Hw					0.98b	0.03
ED:	2	33	6.17	0.0053		
500					1.02b	0.04
1500					0.89a	0.04
2500					0.88a	0.04
Fz:	1	33	8.24	0.0071		
F0					0.98b	0.03
F1					0.87a	0.03
Sp x ED	2	33	4.40	0.0203		
Cw-500					1.05c	0.05
Hw-500					1.00bc	0.05
Cw-1500					0.80ab	0.05
Hw-1500					0.97bc	0.05
Cw-2500					0.76a	0.05
Hw-2500					0.99bc	0.05
Sp x Fz:	1	33	7.73	0.0089		
CwF0					0.87a	0.04
HwF0					1.09b	0.04
CwF1					0.87a	0.04
HwF1					0.88a	0.04
ED x Fz	2	33	1.45	0.2495		
Sp x ED x Fz	2	33	3.91	0.0300		
CwF0-500					1.06abc	0.07
HwF0-500					1.01ab	0.07
CwF0-1500					0.83ab	0.07
HwF0-1500					1.07bc	0.07
CwF0-2500					0.73a	0.07
HwF0-2500					1.20c	0.07
CwF1-500					1.03abc	0.07
HwF1-500					0.99abc	0.07
CwF1-1500					0.78a	0.07
HwF1-1500					0.87ab	0.07
CwF1-2500					0.80ab	0.07
HwF1-2500					0.77a	0.07

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.3. Analysis of stand-level foliage efficiency (E) on HA sites.

Source	NDF	DDF	F	p
Sp:	1	33	0.08	0.7844
ED:	2	33	1.70	0.1974
Fz:	1	33	3.02	0.918
Sp x ED	2	33	0.46	0.6333
Sp x Fz:	1	33	0.05	0.8213
ED x Fz	2	33	0.72	0.4938
Sp x ED x Fz	2	33	0.10	0.9027

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species; ED = Establishment Density; Fz = Fertilization; significance level of $p < 0.05$ was used for F tests and mean separation test

Table A3.4. Analysis of tree-level foliar efficiency (E) of Cw on CH sites.

Source	Df	*F*	*p*	LS Mean (kg/kg/yr)
Sz:	4	6.24	<.0001	
1				0.75ab
2				0.78abc
3				0.78abc
4				0.82bcd
5				0.86d
ED:	2	136.19	<.0001	
500				0.98c
1500				0.76b
2500				0.67a
Fz:	1	0.76	0.3821	
ED x Fz	2	16.33	<.0001	
F0-500				0.99e
F1-500				0.98e
F0-1500				0.79cd
F1-1500				0.72bc
F0-2500				0.63a
F1-2500				0.73bcd
ED x Sz	8	0.28	0.972	
Fz x Sz	4	0.90	0.4610	
Sz x ED x Fz	8	3.85	0.0002	

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sz = Size Class; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.4. (cont.)

Source	Df	*F*	*p*	LS Mean (kg/kg/yr)
Sz x ED x Fz	8	3.85	0.0002	
1-500-F0				0.94fghij
2-500-F0				0.89efghij
3-500-F0				1.00gij
4-500-F0				1.04ij
5-500-F0				1.10j
1-500-F1				0.93fghij
2-500-F1				1.00ghij
3-500-F1				0.94fghij
4-500-F1				0.99ghij
5-500-F1				1.02hij
1-1500-F0				0.89efghij
2-1500-F0				0.80defghi
3-1500-F0				0.73bcdef
4-1500-F0				0.75cdef
5-1500-F0				0.81defghi
1-1500-F1				0.57a
2-1500-F1				0.71abcde
3-1500-F1				0.75cdef
4-1500-F1				0.77defg
5-1500-F1				0.79defgh
1-2500-F0				0.54a
2-2500-F0				0.61abc
3-2500-F0				0.63abcd
4-2500-F0				0.66abcd
5-2500-F0				0.70abcde
1-2500-F1				0.72abcdef
2-2500-F1				0.70abcde
3-2500-F1				0.71abcde
4-2500-F1				0.76bcdefg
5-2500-F1				0.79cdefgh

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sz = Size Class; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.5. Analysis of tree-level foliar efficiency (E) of Hw on CH sites.

Source		Df	*F*	*p*	LS Mean (kg/kg/yr)
Sz:		4	21.23	<.0001	
	1				1.09de
	2				1.02cde
	3				0.96bcd
	4				0.93bc
	5				0.82a
ED:		2	7.62	0.0005	
	500				1.01b
	1500				0.93a
	2500				0.93a
Fz:		1	135.82	<.0001	
	F0				1.08b
	F1				0.85a
ED x Fz		2	38.95	<.0001	
	F0-500				1.03c
	F1-500				1.00c
	F0-1500				1.03c
	F1-1500				0.84b
	F0-2500				1.18d
	F1-2500				0.74a
ED x Sz		8	1.03	0.4135	
Fz x Sz		4	19.39	<.0001	
	F0-1				1.39e
	F0-2				1.25e
	F0-3				1.03cd
	F0-4				1.00bcd
	F0-5				0.82ab
	F1-1				0.85ab
	F1-2				0.84ab
	F1-3				0.89abc
	F1-4				0.86ab
	F1-5				0.82ab
Sz x ED x Fz		8	1.65	0.1054	

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sz = Size Class; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.6. Analysis of tree-level foliar efficiency (E) of Cw on HA sites.

Source	Df	F	p	LS Mean (kg/kg/yr)
Sz:	4	11.61	<.0001	
1				0.83bc
2				0.74ab
3				0.78abc
4				0.82bc
5				0.90d
ED:	2	17.04	<.0001	
500				0.87b
1500				0.78a
2500				0.78a
Fz:	1	6.19	0.0129	
F0				0.79a
F1				0.83b
ED x Fz	2	2.68	0.0692	
ED x Sz	8	3.66	0.0003	
500-1				0.93cde
500-2				0.81abcde
500-3				0.85bcde
500-4				0.86bcde
500-5				0.92cde
1500-1				0.71abc
1500-2				0.70abc
1500-3				0.77abcd
1500-4				0.85bcde
1500-5				0.91cde
2500-1				0.86bcde
2500-2				0.72abc
2500-3				0.73abcd
2500-4				0.74abcd
2500-5				0.86bcde
Fz x Sz	4	20.23	<.0001	
F0-1				0.95defg
F0-2				0.71ab
F0-3				0.73ab
F0-4				0.77abcde
F0-5				0.83bcde
F1-1				0.72ab
F1-2				0.78abcde
F1-3				0.84bcdef
F1-4				0.87bcdefg
F1-5				0.96efg
Sp x ED x Fz	8	1.29	0.2451	

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Size Class; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.7. Analysis of tree-level foliar efficiency (E) of Hw on HA sites.

Source		Df	*F*	*p*	LS Mean (kg/kg/yr)
Sz:		4	18.74	<.0001	
	1				1.01b
	2				0.89a
	3				0.86a
	4				0.86a
	5				0.87a
ED:		2	7.73	0.0005	
	500				0.93b
	1500				0.86a
	2500				0.88a
Fz:		1	0.14	0.7105	
ED x Fz		2	5.49	0.0042	
	F0-500				0.94bc
	F1-500				0.93bc
	F0-1500				0.85ab
	F1-1500				0.91abc
	F0-2500				0.90abc
	F1-2500				0.86ab
ED x Sz		8	1.35	0.2153	
Fz x Sz		4	10.74	<.0001	
	F0-1				1.09f
	F0-2				0.91bcde
	F0-3				0.81abc
	F0-4				0.83abcd
	F0-5				0.85abcd
	F1-1				0.94cde
	F1-2				0.87abcde
	F1-3				0.90abcde
	F1-4				0.89abcde
	F1-5				0.89abcde
Sp x ED x Fz		8	0.31	0.9618	

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sz = Size Class; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.8. Analysis of nitrogen use efficiency on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
Sp:	1	33	17.00	0.0002		
Cw					1.48b	0.11
Hw					1.10a	0.11
ED:	2	33	32.67	<.0001		
500					0.85a	0.11
1500					1.55b	0.11
2500					1.59b	0.11
Fz:	1	33	331.69	<.0001		
F0					0.66a	0.11
F1					2.47b	0.11
Sp x ED	2	33	1.61	0.2142		
Sp x Fz:	1	33	72.94	<.0001		
CwF0					1.05b	0.11
HwF0					0.42a	0.11
CwF1					2.11c	0.11
HwF1					2.90d	0.11
ED x Fz	2	33	2.34	0.1125		
Sp x ED x Fz	2	33	4.53	0.0182		
CwF0-500					0.66bc	0.12
HwF0-500					0.31a	0.12
CwF0-1500					1.21cd	0.12
HwF0-1500					0.62ab	0.12
CwF0-2500					1.44d	0.12
HwF0-2500					0.38ab	0.12
CwF1-500					1.25d	0.12
HwF1-500					2.10de	0.12
CwF1-1500					2.72ef	0.12
HwF1-1500					2.84ef	0.12
CwF1-2500					2.75ef	0.12
HwF1-2500					4.25f	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.9. Analysis of nitrogen use efficiency on HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
Sp:		1	33	43.94	<.0001		
	Cw					1.89a	0.11
	Hw					4.19b	0.11
ED:		2	33	34.74	<.0001		
	500					1.39a	0.12
	1500					3.72b	0.12
	2500					4.30b	0.12
Fz:		1	33	49.81	<.0001		
	F0					1.84a	0.11
	F1					4.30b	0.11
Sp x ED		2	33	0.04	0.2142		
Sp x Fz:		1	33	0.01	<.0001		
ED x Fz		2	33	1.28	0.1125		
Sp x ED x Fz		2	33	0.26	0.0182		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.10. Analysis of zinc use efficiency on HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/ppm/yr)	SE
Sp:		1	33	47.40	<.0001		
	Cw					1.28a	0.12
	Hw					3.36b	0.12
ED:		2	33	25.95	<.0001		
	500					1.03a	0.12
	1500					2.66b	0.12
	2500					3.26b	0.12
Fz:		1	33	42.71	<.0001		
	F0					1.31a	0.12
	F1					3.27b	0.12
Sp x ED		2	33	0.07	0.9332		
Sp x Fz:		1	33	0.07	0.7865		
ED x Fz		2	33	1.03	0.3685		
Sp x ED x Fz		2	33	0.06	0.9410		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.11. Analysis of phosphorus use efficiency on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
CH Sites:							
Sp:		1	33	28.53	<.0001		
	Cw					0.80b	0.11
	Hw					0.48a	0.11
ED:		2	33	19.95	<.0001		
	500					0.41a	0.11
	1500					0.75b	0.11
	2500					0.78b	0.11
Fz:		1	33	75.30	<.0001		
	F0					0.41a	0.11
	F1					0.93b	0.11
Sp x ED		2	33	1.25	0.2989		
Sp x Fz:		1	33	11.72	0.0017		
	CwF0					0.62b	0.11
	HwF0					0.28a	0.11
	CwF1					1.02c	0.11
	HwF1					0.85bc	0.11
ED x Fz		2	33	1.95	0.1586		
Sp x ED x Fz		2	33	2.49	0.0983		
HA Sites:							
Sp:		1	33	24.41	<.0001		
	Cw					1.08a	0.12
	Hw					2.28b	0.12
ED:		2	33	26.30	<.0001		
	500					0.73a	0.12
	1500					2.12b	0.12
	2500					2.51b	0.12
Fz:		1	33	7.57	0.0095		
	F0					1.28a	0.12
	F1					1.93b	0.12
Sp x ED		2	33	0.41	0.6647		
Sp x Fz:		1	33	4.60	0.0395		
	CwF0					0.75a	0.12
	HwF0					2.18b	0.12
	CwF1					1.57b	0.12
	HwF1					2.39b	0.12
ED x Fz		2	33	0.85	0.4357		
Sp x ED x Fz		2	33	0.17	0.8409		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.12. Analysis of potassium use efficiency on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
CH Sites:							
Sp:		1	33	91.69	<.0001		
	Cw					0.28b	0.01
	Hw					0.12a	0.01
ED:		2	33	22.51	<.0001		
	500					0.12a	0.01
	1500					0.20b	0.01
	2500					0.23b	0.01
Fz:		1	33	263.65	<.0001		
	F0					0.09a	0.01
	F1					0.37b	0.01
Sp x ED		2	33	1.82	0.1777		
Sp x Fz:		1	33	32.34	<.0001		
	CwF0					0.18b	0.01
	HwF0					0.05a	0.01
	CwF1					0.44d	0.01
	HwF1					0.31c	0.01
ED x Fz		2	33	1.22	0.3086		
Sp x ED x Fz		2	33	2.41	0.1053		
HA Sites:							
Sp:		1	33	4.90	0.0338		
	Cw					0.38a	0.01
	Hw					0.53b	0.01
ED:		2	33	23.65	<.0001		
	500					0.21a	0.01
	1500					0.60b	0.01
	2500					0.70b	0.01
Fz:		1	33	48.23	<.0001		
	F0					0.26a	0.01
	F1					0.76b	0.01
Sp x ED		2	33	0.25	0.7739		
Sp x Fz:		1	33	0.10	0.9725		
ED x Fz		2	33	1.01	0.2531		
Sp x ED x Fz		2	33	0.06	0.9465		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.13. Analysis of sulphur use efficiency on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
CH Sites:							
Sp:		1	33	32.98	<.0001		
	Cw					16.77a	1.11
	Hw					10.46b	1.11
ED:		2	33	24.46	<.0001		
	500					8.83a	1.12
	1500					16.64b	1.12
	2500					15.81b	1.12
Fz:		1	33	277.03	<.0001		
	F0					6.68a	1.11
	F1					26.26b	1.11
Sp x ED		2	33	1.63	0.2106		
Sp x Fz:		1	33	48.49	<.0001		
	CwF0					11.26b	1.13
	HwF0					3.96a	1.13
	CwF1					24.98c	1.13
	HwF1					27.61c	1.13
ED x Fz		2	33	1.37	0.2679		
Sp x ED x Fz		2	33	2.99	0.0643		
HA Sites:							
Sp:		1	33	28.90	<.0001		
	Cw					20.94a	1.12
	Hw					40.08b	1.12
ED:		2	33	34.37	<.0001		
	500					14.36a	1.14
	1500					37.79b	1.14
	2500					44.79b	1.14
Fz:		1	33	69.75	<.0001		
	F0					17.49a	1.12
	F1					47.98b	1.12
Sp x ED		2	33	<0.00	0.9980		
Sp x Fz:		1	33	0.06	0.8103		
ED x Fz		2	33	1.50	0.2376		
Sp x ED x Fz		2	33	0.28	0.7544		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.14. Analysis of calcium use efficiency on CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
CH Sites:						
Sp:	1	33	34.79	<.0001		
Cw					2.57a	1.14
Hw					4.41b	1.14
ED:	2	33	17.88	<.0001		
500					2.29a	1.15
1500					4.24b	1.15
2500					3.93b	1.15
Fz:	1	33	228.74	<.0001		
F0					1.69a	1.14
F1					6.73b	1.14
Sp x ED	2	33	0.43	0.6557		
Sp x Fz:	1	33	66.28	<.0001		
CwF0					1.87a	1.16
HwF0					1.52a	1.16
CwF1					3.54b	1.16
HwF1					12.81c	1.16
ED x Fz	2	33	0.52	0.5981		
Sp x ED x Fz	2	33	3.16	0.0555		
HA Sites:						
Sp:	1	33	185.55	<.0001		
Cw					2.88a	1.18
Hw					19.89b	1.18
ED:	2	33	23.08	<.0001		
500					3.86a	1.20
1500					9.61b	1.20
2500					11.67b	1.20
Fz:	1	33	51.07	<.0001		
F0					4.56a	1.18
F1					12.56b	1.18
Sp x ED	2	33	0.14	0.8703		
Sp x Fz:	1	33	0.94	0.3402		
ED x Fz	2	33	1.16	0.3259		
Sp x ED x Fz	2	33	0.18	0.8353		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.15. Analysis of magnesium use efficiency on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha/%/yr)	SE
CH Sites:							
Sp:		1	33	17.38	0.0002		
	Cw					9.71b	1.11
	Hw					6.72a	1.11
ED:		2	33	16.96	<.0001		
	500					5.62a	1.12
	1500					9.92b	1.12
	2500					9.45b	1.12
Fz:		1	33	198.42	<.0001		
	F0					4.33a	1.11
	F1					15.05b	1.11
Sp x ED		2	33	0.54	0.5904		
Sp x Fz:		1	33	24.73	<.0001		
	CwF0					6.49b	1.13
	HwF0					2.89a	1.13
	CwF1					14.52c	1.13
	HwF1					15.59c	1.13
ED x Fz		2	33	0.84	0.4401		
Sp x ED x Fz		2	33	2.21	0.1262		
HA Sites:							
Sp:		1	33	24.04	<.0001		
	Cw					13.78a	1.17
	Hw					29.20b	1.17
ED:		2	33	20.44	<.0001		
	500					10.06a	1.19
	1500					26.83b	1.19
	2500					29.90b	1.19
Fz:		1	33	42.02	<.0001		
	F0					12.21a	1.17
	F1					32.96b	1.17
Sp x ED		2	33	0.05	0.9477		
Sp x Fz:		1	33	0.13	0.7243		
ED x Fz		2	33	1.57	0.2231		
Sp x ED x Fz		2	33	0.18	0.8328		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for *F* tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.16. Analysis of zinc use efficiency on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha/ppm/yr)	SE
Sp:	1	33	13.52	0.0008		
Cw					1.13b	0.11
Hw					0.84a	0.11
ED:	2	33	32.78	<.0001		
500					0.62a	0.11
1500					1.31b	0.11
2500					1.14b	0.11
Fz:	1	33	244.70	<.0001		
F0					0.52a	0.11
F1					1.82b	0.11
Sp x ED	2	33	2.42	0.1042		
Sp x Fz:	1	33	52.98	<.0001		
CwF0					0.81b	0.12
HwF0					0.34a	0.12
CwF1					1.57c	0.12
HwF1					2.10c	0.12
ED x Fz	2	33	2.23	0.1231		
Sp x ED x Fz	2	33	4.47	0.0192		
CwF0-500					0.53bc	0.12
HwF0-500					0.24a	0.12
CwF0-1500					0.96cd	0.12
HwF0-1500					0.58c	0.12
CwF0-2500					1.04cd	0.12
HwF0-2500					0.28ab	0.12
CwF1-500					0.81cd	0.12
HwF1-500					1.49de	0.12
CwF1-1500					2.30e	0.12
HwF1-1500					2.28e	0.12
CwF1-2500					2.11e	0.12
HwF1-2500					2.71e	0.12

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.17. Analysis of boron use efficiency on CH and HA sites.

Source	NDF	DDF	*F*	*p*	LS Mean (t/ha/ppm/yr)	SE
CH Sites:						
Sp:	1	33	269.39	<.0001		
Cw					0.16b	0.01
Hw					0.04a	0.01
ED:	2	33	19.14	<.0001		
500					0.05a	0.01
1500					0.09b	0.01
2500					0.09b	0.01
Fz:	1	33	240.74	<.0001		
F0					0.04a	0.01
F1					0.15b	0.01
Sp x ED	2	33	0.53	0.5946		
Sp x Fz:	1	33	48.02	<.0001		
CwF0					0.11b	0.01
HwF0					0.01a	0.01
CwF1					0.23c	0.01
HwF1					0.10b	0.01
ED x Fz	2	33	1.17	0.3242		
Sp x ED x Fz	2	33	2.92	0.0679		
HA Sites:						
Sp:	1	33	0.89	0.3525		
ED:	2	33	25.48	<.0001		
500					0.09a	0.01
1500					0.24b	0.01
2500					0.31b	0.01
Fz:	1	33	41.66	<.0001		
F0					0.11a	0.01
F1					0.31b	0.01
Sp x ED	2	33	0.32	0.7288		
Sp x Fz:	1	33	1.58	0.2170		
ED x Fz	2	33	1.60	0.2169		
Sp x ED x Fz	2	33	0.10	0.9044		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; Sp = Species, Cw = Cedar, Hw = Hemlock; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Table A3.18. Analysis of IPAR and light use efficiency on CH sites.

Source	NDF	DDF	*F*	*p*	LS Mean	SE
IPAR :					*% PAR*	
ED:	2	33	9.70	0.0020		
500					24.84a	0.17
1500					41.30b	0.17
2500					48.30b	0.17
Fz:	1	33	42.18	<.0001		
F0					23.82a	0.11
F1					53.02b	0.11
ED x Fz	2	33	0.92	0.4216		
Light Use Efficiency:					*t/ha/% IPAR*	
ED:	2	33	111.75	<.0001		
500					9.19c	1.09
1500					3.24b	1.09
2500					1.70a	1.09
Fz:	1	33	0.06	0.8072		
ED x Fz	2	33	1.36	0.2855		

NDF = Numerator Degrees of Freedom; DDF = Denominator Degrees of Freedom; ED = Establishment Density; Fz = Fertilization, F0 = Non-fertilized, F1 = Fertilized, LS Mean = Least Square Mean; SE = Standard Error of Estimate; significance level of $p < 0.05$ was used for F tests and mean separation tests; LS Means followed by the same letter do not significantly differ

Appendix 4: Statistical Analysis for Chapter 5

Table A4.1. Analysis of height inequality within stands on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (*G*)	SE
CH Sites:							
Sp:		1	33	24.34	<.0001		
	Cw					0.13a	0.01
	Hw					0.17b	0.01
ED:		2	33	1.17	0.3239		
Fz:		1	33	70.85	<.0001		
	F0					0.18b	0.01
	F1					0.12a	0.01
Sp x ED		2	33	0.42	0.6600		
Sp x Fz:		1	33	0.67	0.4203		
ED x Fz		2	33	2.38	0.1086		
Sp x ED x Fz		2	33	0.85	0.4368		
HA Sites:							
Sp:		1	33	13.89	0.0007		
	Cw					0.14b	0.01
	Hw					0.10a	0.01
ED:		2	33	1.03	0.3699		
Fz:		1	33	54.99	<.0001		
	F0					0.16b	0.01
	F1					0.09a	0.01
Sp x ED		2	33	1.41	0.2580		
Sp x Fz:		1	33	0.07	0.7941		
ED x Fz		2	33	0.78	0.4663		
Sp x ED x Fz		2	33	0.30	0.7397		

Sp=Species, Cw=western red cedar, Hw=western hemlock; ED=Establishment Density; Fz=Fertilization, F0=unfertilized, F1=fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A4.2. Analysis of tree biomass inequality within stands on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (*G*)	SE
CH Sites:							
Sp:		1	33	16.41	0.0003		
	Cw					0.35a	0.01
	Hw					0.41b	0.01
ED:		2	33	3.23	0.0522		
Fz:		1	33	108.35	<.0001		
	F0					0.45b	0.01
	F1					0.30a	0.01
Sp x ED		2	33	0.25	0.7811		
Sp x Fz:		1	33	13.05	0.0010		
	CwF0					0.40b	0.02
	HwF0					0.51c	0.02
	CwF1					0.30a	0.02
	HwF1					0.31a	0.02
ED x Fz		2	33	4.14	0.0250		
Sp x ED x Fz		2	33	3.46	0.0433		
HA Sites:							
Sp:		1	33	28.41	<.0001		
	Cw					0.36b	0.11
	Hw					0.26a	0.11
ED:		2	33	0.44	0.6477		
Fz:		1	33	32.66	<.0001		
	F0					0.37b	0.11
	F1					0.25a	0.11
Sp x ED		2	33	0.31	0.7335		
Sp x Fz:		1	33	0.09	0.7689		
ED x Fz		2	33	0.17	0.8481		
Sp x ED x Fz		2	33	0.72	0.4919		

Sp=Species, Cw=western red cedar, Hw=western hemlock; ED=Establishment Density; Fz=Fertilization, F0=unfertilized, F1=fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A4.3. Analysis of tree volume index inequality within stands on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (*G*)	SE
CH Sites:							
Sp:		1	33	8.94	0.0052		
	Cw					0.44a	0.10
	Hw					0.49b	0.10
ED:		2	33	2.96	0.0657		
Fz:		1	33	96.65	<.0001		
	F0					0.55b	0.10
	F1					0.38a	0.10
Sp x ED		2	33	0.95	0.3975		
Sp x Fz:		1	33	5.91	0.0206		
ED x Fz		2	33	3.54	0.0403		
Sp x ED x Fz		2	33	2.76	0.0780		
HA Sites:							
Sp:		1	33	30.14	<.0001		
	Cw					0.46b	0.11
	Hw					0.33a	0.11
ED:		2	33	0.52	0.6016		
Fz:		1	33	31.96	<.0001		
	F0					0.46b	0.11
	F1					0.33a	0.11
Sp x ED		2	33	0.24	0.7895		
Sp x Fz:		1	33	025	0.6180		
ED x Fz		2	33	0.24	0.7897		
Sp x ED x Fz		2	33	0.70	0.5033		

Sp=Species, Cw=western red cedar, Hw=western hemlock; ED=Establishment Density; Fz=Fertilization, F0=unfertilized, F1=fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A4.4. Analysis of tree mass skewness within stands on CH and HA sites.

Source		NDF	DDF	*F*	*p*	LS Mean (g_1)	SE
CH Sites:							
Sp:		1	33	1.25	0.2713		
ED:		2	33	2.17	0.1305		
Fz:		1	33	24.13	<.0001		
	F0					1.39b	0.11
	F1					0.75a	0.11
Sp x ED		2	33	6.56	0.0040		
Sp x Fz:		1	33	1.81	0.1876		
ED x Fz		2	33	1.59	0.2199		
Sp x ED x Fz		2	33	0.13	0.8786		
HA Sites:							
Sp:		1	33	9.07	0.0049		
	Cw					0.95b	0.14
	Hw					0.50a	0.14
ED:		2	33	1.43	0.2542		
Fz:		1	33	13.77	0.0008		
	F0					1.01b	0.14
	F1					0.44a	0.14
Sp x ED		2	33	0.08	0.9224		
Sp x Fz:		1	33	0.08	0.7739		
ED x Fz		2	33	0.23	0.7968		
Sp x ED x Fz		2	33	0.74	0.4834		

Sp=Species, Cw=western red cedar, Hw=western hemlock; ED=Establishment Density; Fz=Fertilization, F0=unfertilized, F1=fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A4.5. Analysis of total stand mass.

Source		NDF	DDF	*F*	*p*	LS Mean (t/ha)	SE
Site:		1	69	117.75	<.0001		
	CH					8.53a	1.12
	HA					22.18b	1.12
Sp:		1	69	0.82	0.3673		
ED:		2	69	41.73	<.0001		
	500					7.80a	1.13
	1500					17.71b	1.13
	2500					18.86b	1.13
Fz:		1	69	219.91	<.0001		
	F0					7.16a	1.12
	F1					26.43b	1.12
Site x Sp:		1	69	59.29	<.0001		
	CH-Cw					11.50b	1.14
	CH-Hw					6.32a	1.14
	HA-Cw					15.18b	1.14
	HA-Hw					32.41c	1.14
Site x Fert		1	69	6.64	0.0121		
Site x ED		2	69	3.97	0.0234		
Sp x ED		2	69	0.06	0.9442		
Sp x Fz:		1	69	12.09	0.0009		
	Cw-F0					8.02a	1.14
	Cw-F1					21.79b	1.14
	Hw-F0					6.39a	1.14
	Hw-F1					32.07c	1.14
ED x Fz		2	69	3.07	0.0530		
Site x Sp x Fz		1	69	12.04	0.0009		
	CH-Cw-F0					7.26b	1.17
	CH-Cw-F1					18.23c	1.17
	CH-Hw-F0					2.16a	1.17
	CH-Hw-F1					18.49c	1.17
	HA-Cw-F0					8.85b	1.17
	HA-Cw-F1					26.04c	1.17
	HA-Hw-F0					18.89c	1.17
	HA-Hw-F1					55.62d	1.17
Site x Fz x ED		2	69	0.64	0.5288		
Sp x ED x Fz		2	69	0.74	0.4825		
Sp x Site x ED		2	69	0.63	0.5358		
Site x Sp x Fz x ED		2	69	1.43	0.2473		

Sp=Species, Cw=Western Red Cedar, Hw=Western Hemlock; ED=Establishment Density; Fz=Fertilization, F0=Unfertilized, F1=Fertilized; NDF=Numerator Degrees of Freedom; DDF=Denominator Degrees of Freedom; LS Mean=Least Square Mean; SE=Standard Error of Estimate; Significance level of $p<0.01$ for main effects and interaction tests, $p<0.05$ for mean separation tests.

Table A4.6. Regression parameters and statistics for relationships between *G* (tree mass) and absolute biological stocking (t/ha).

Site-Species	*a*	SE (*a*)	*b*	SE (*b*)	*F*	*p*
CH – Western Red Cedar	0.5474	0.0745	-0.1874	0.0573	382.33	<.0001
CH – Western Hemlock	0.5909	0.0252	-0.2208	0.0257	716.47	<.0001
HA – Western Red Cedar	0.6684	0.0736	-0.2224	0.0434	373.40	<.0001
HA – Western Hemlock	0.6764	0.0961	-0.2743	0.0456	270.75	<.0001

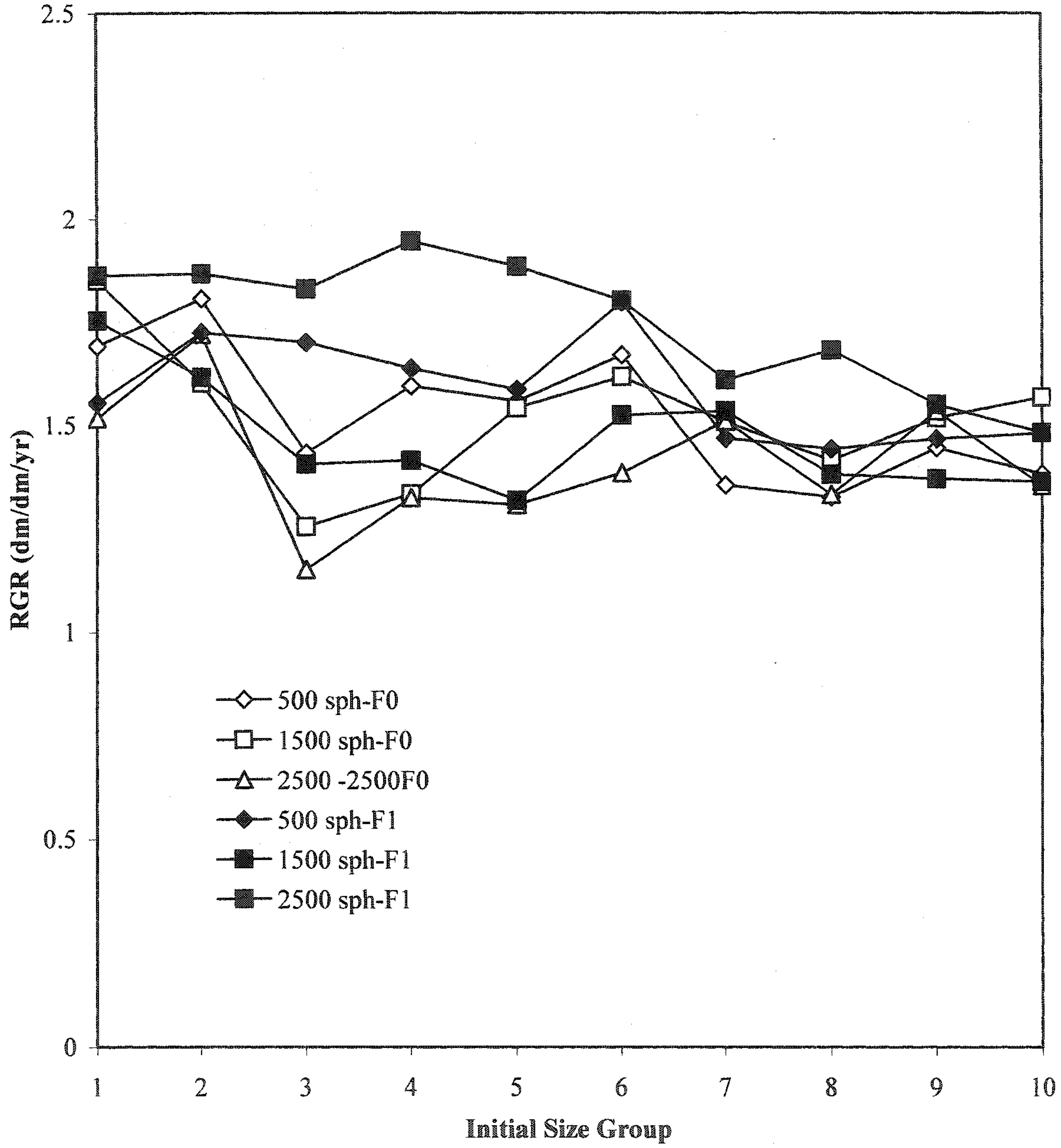

Figure A4.1. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1988 – 1989.

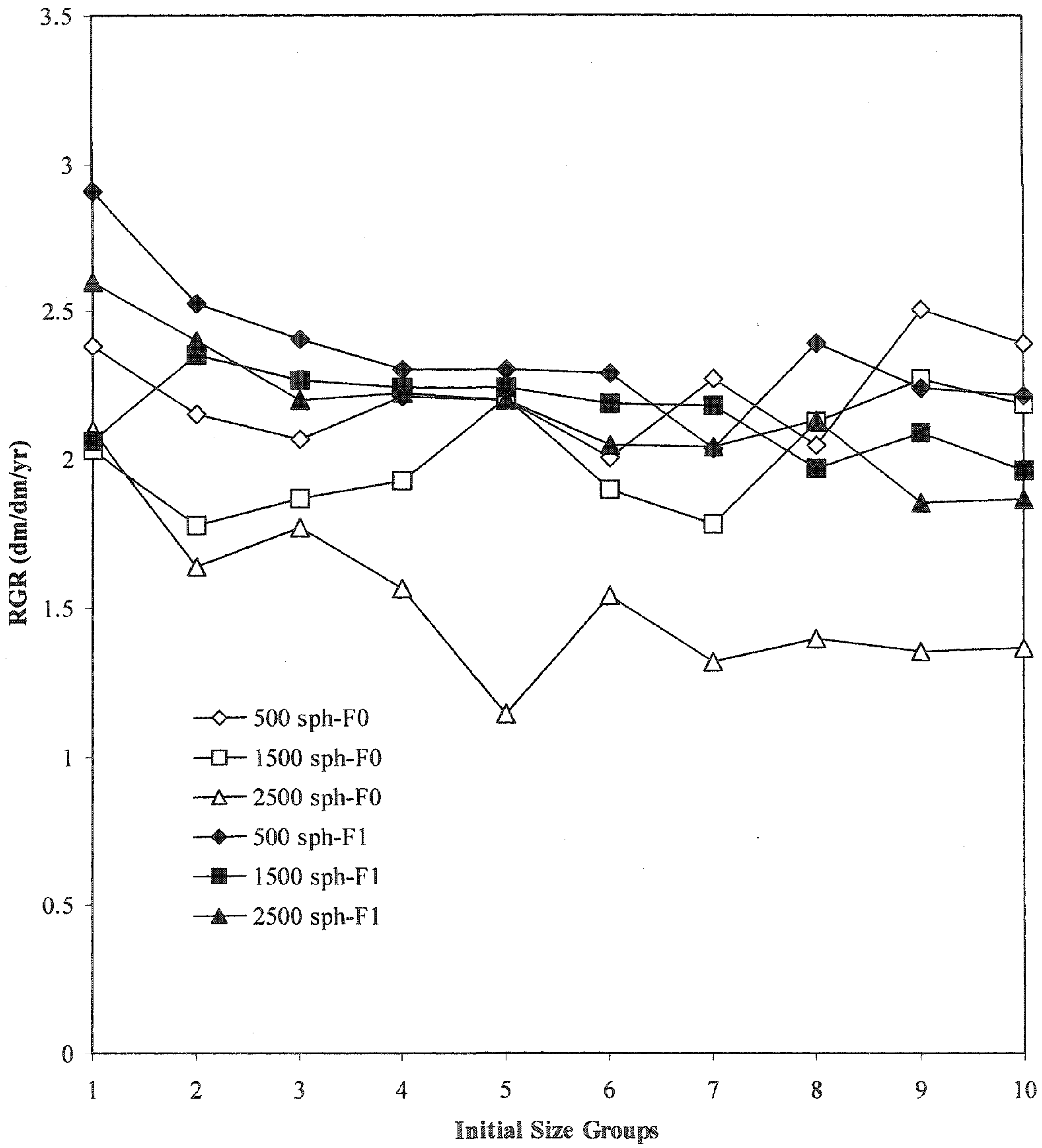

Figure A4.2. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1988 – 1989.

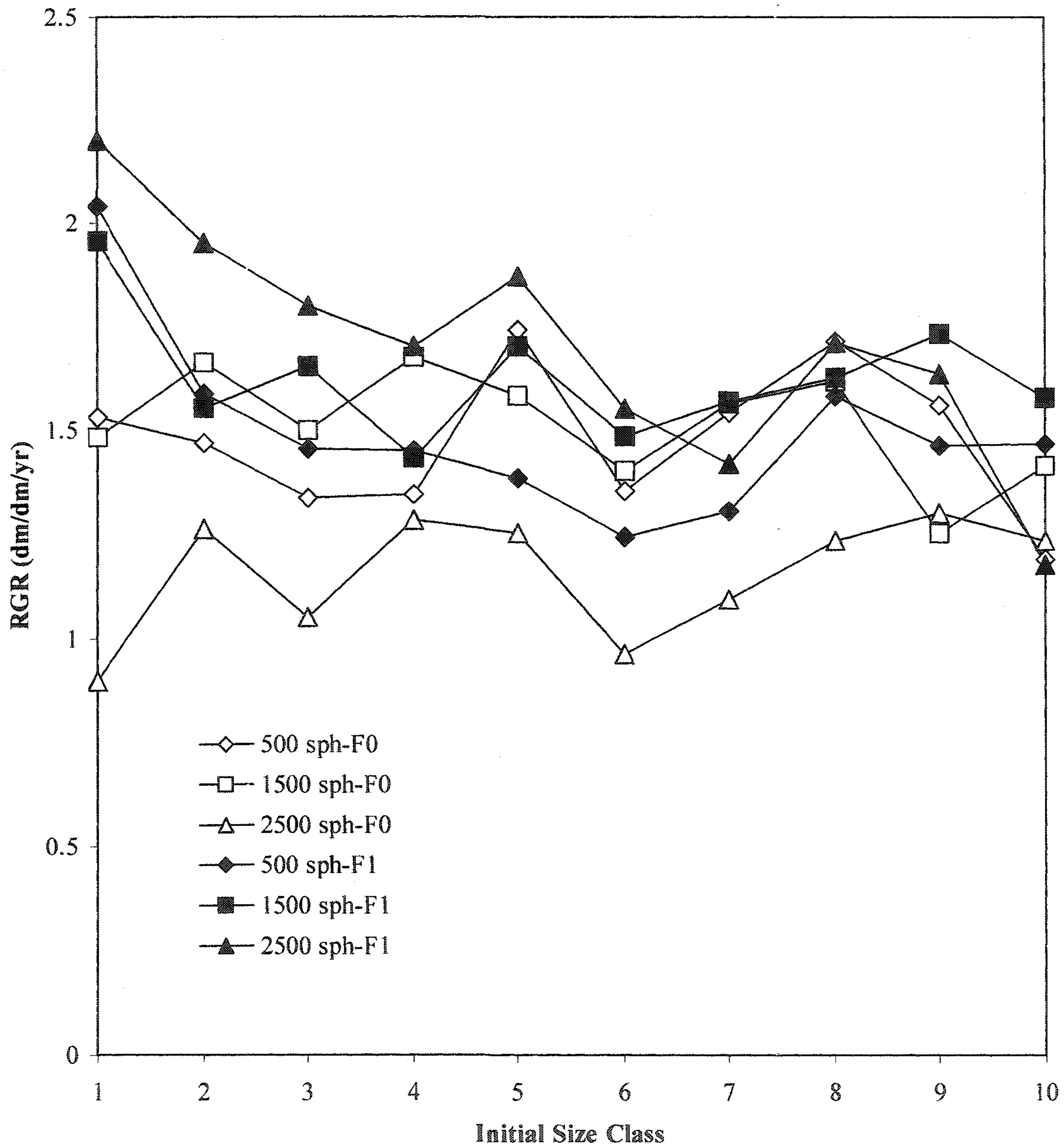

Figure A4.3. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1988 – 1989.

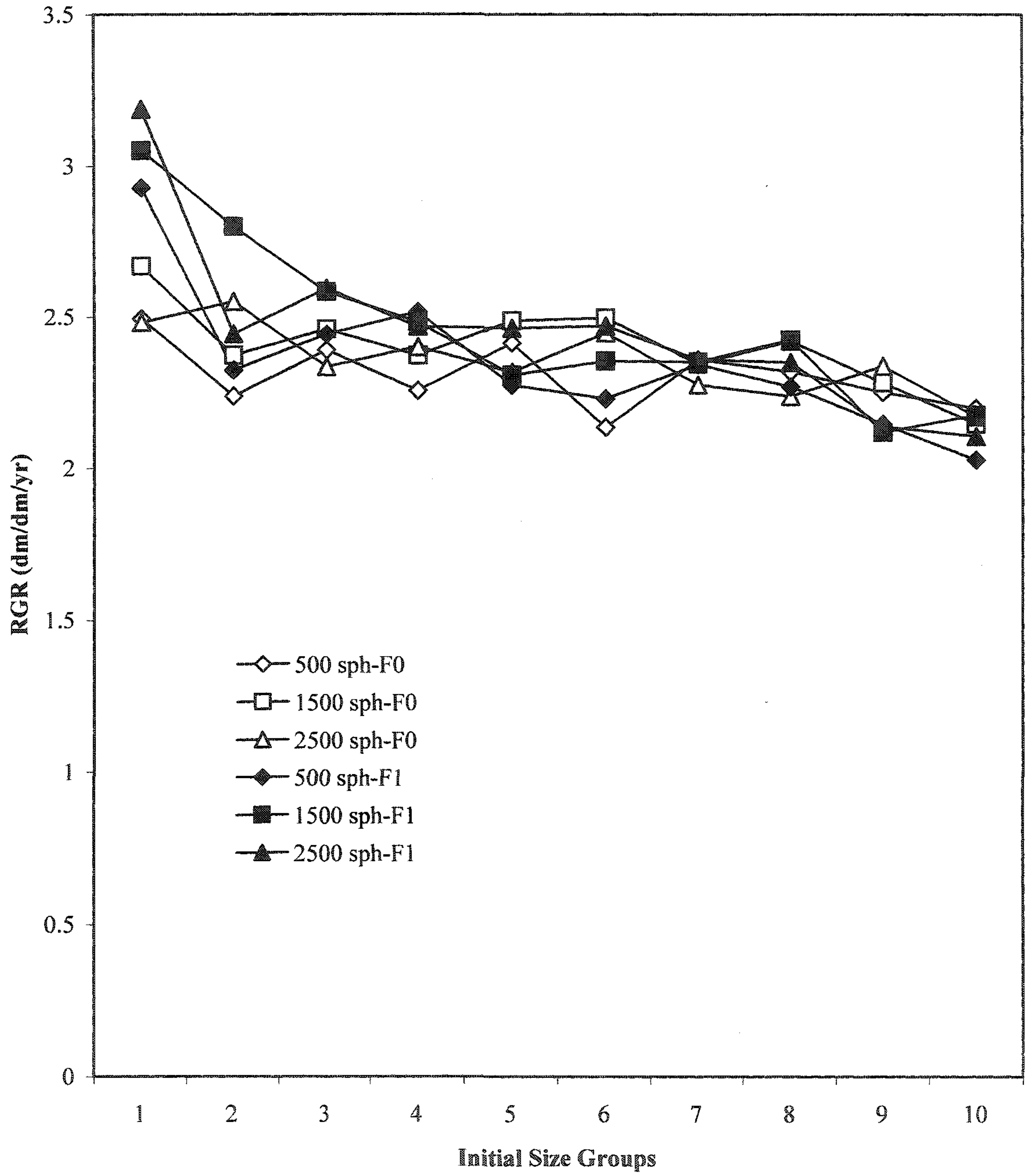

Figure A4.4. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1988 – 1989.

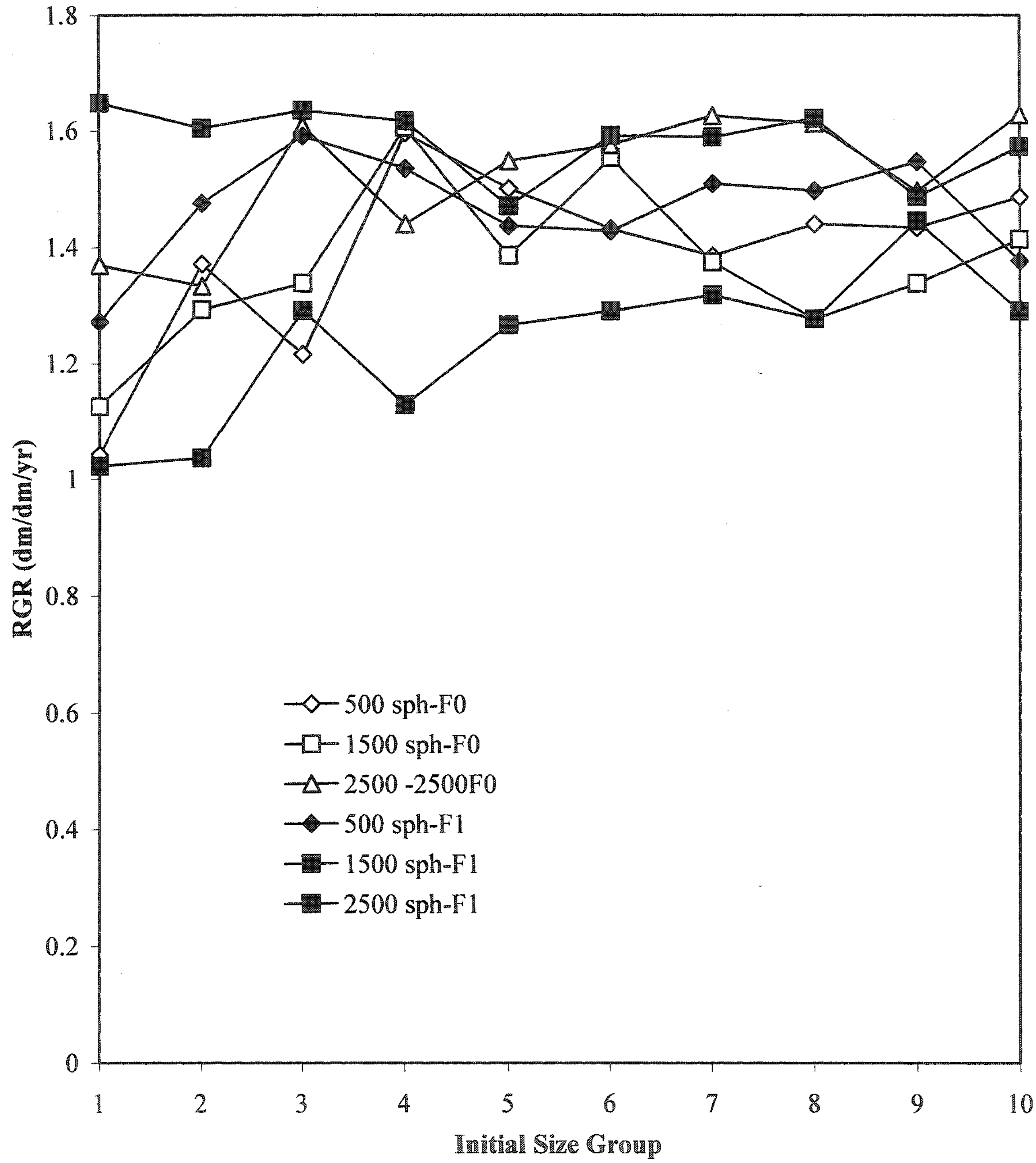

Figure A4.5. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1989 – 1990.

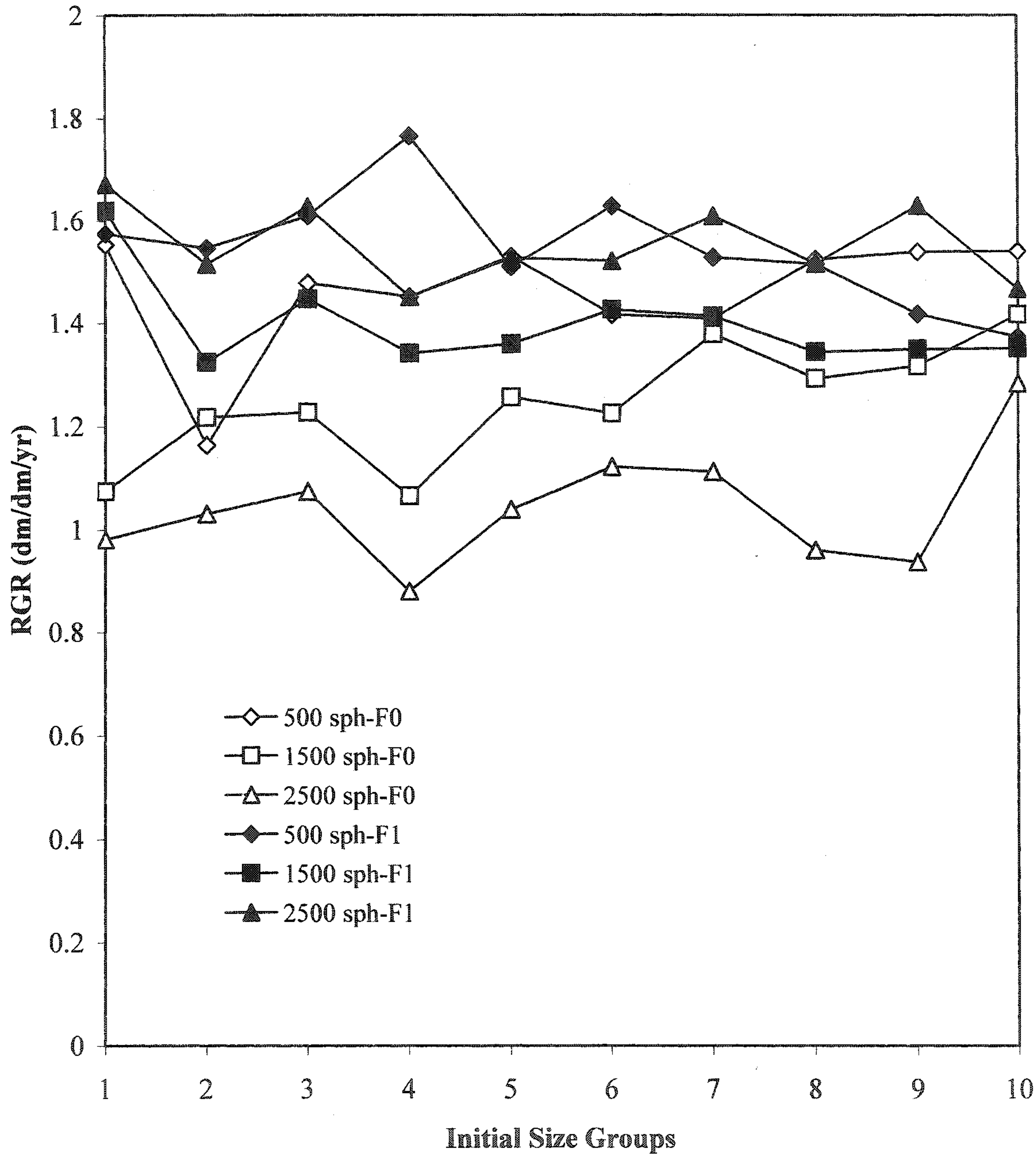

Figure A4.6. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1989 – 1990.

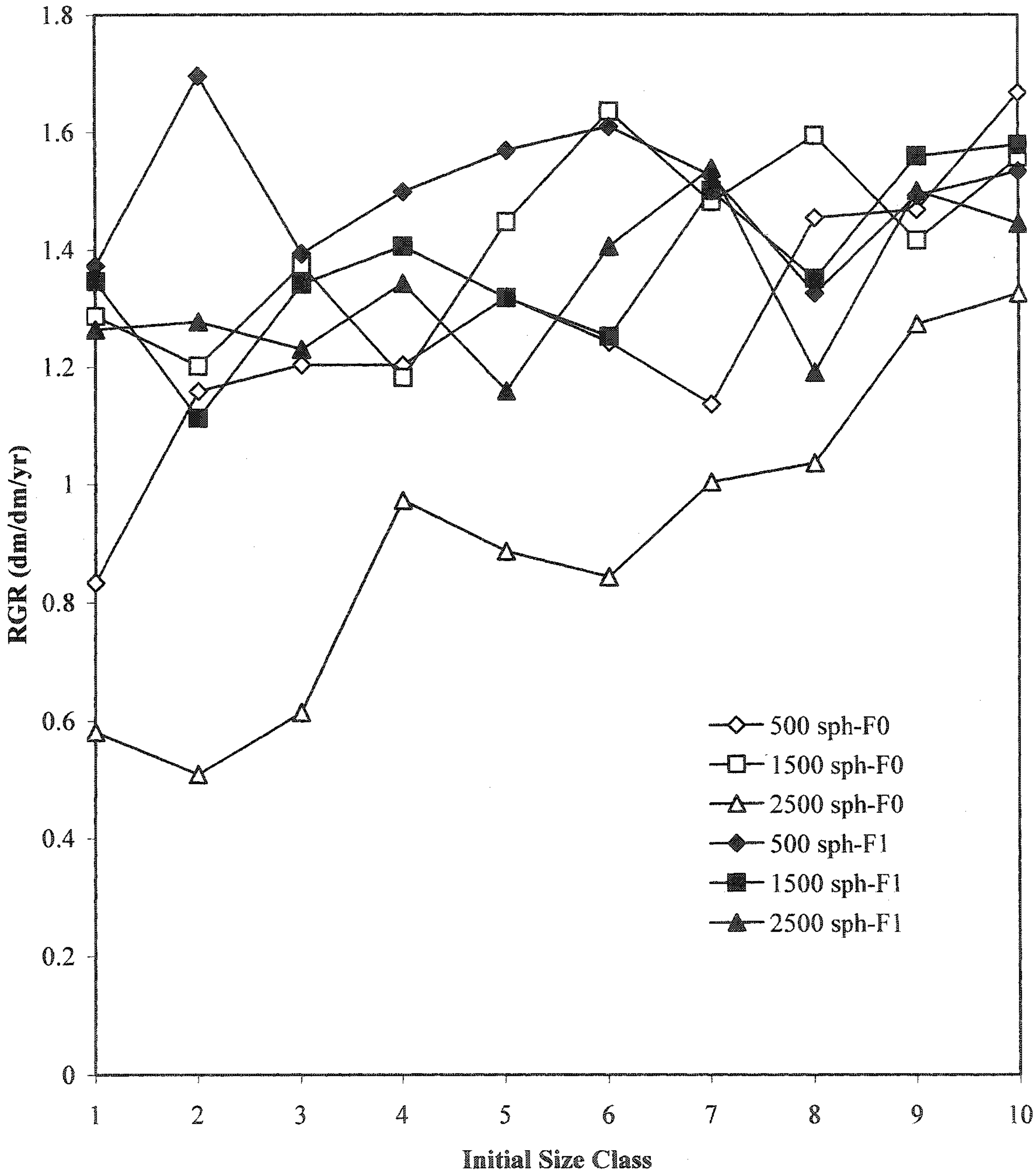

Figure A4.7. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1989 – 1990.

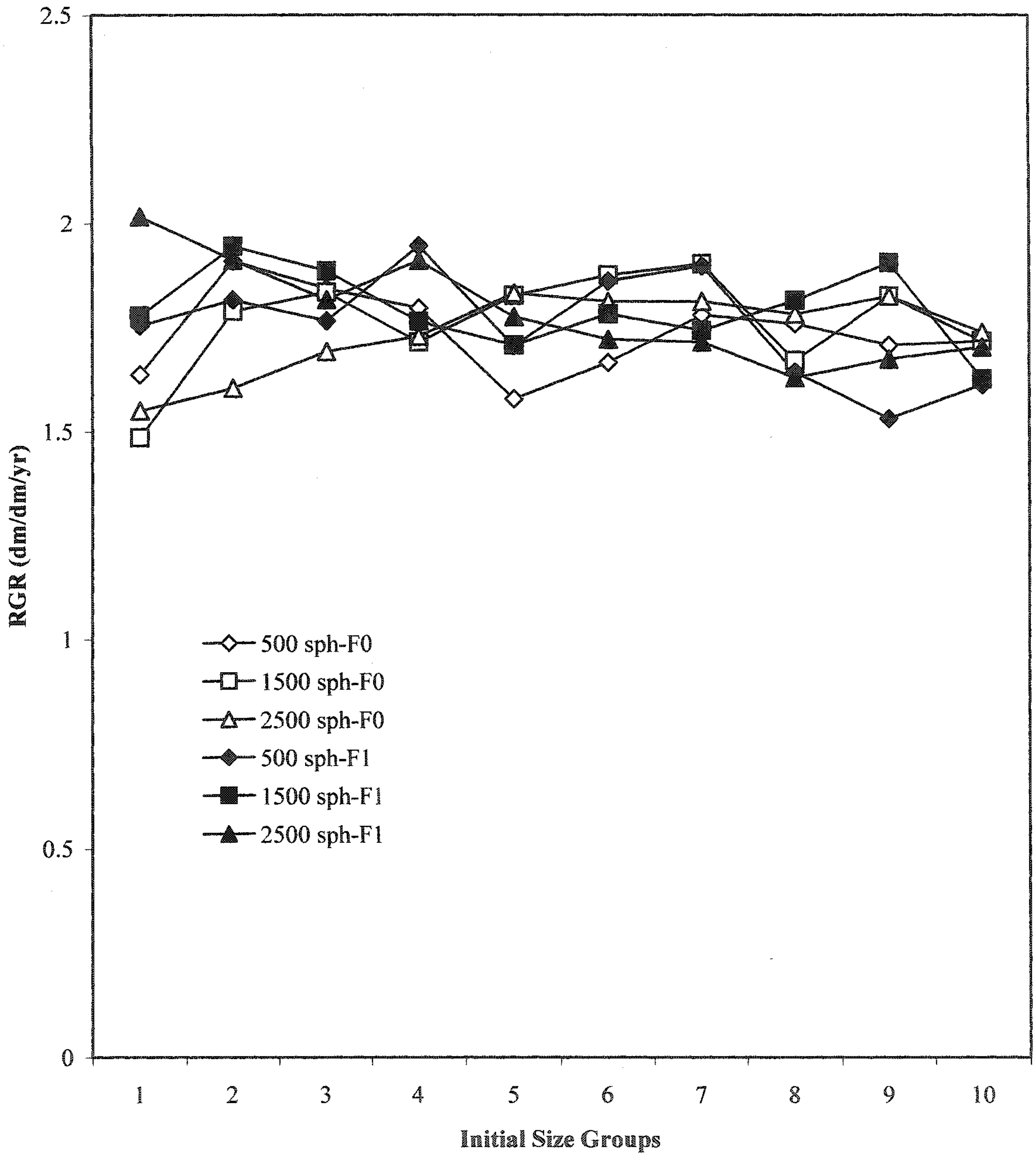

Figure A4.8. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1989 – 1990.

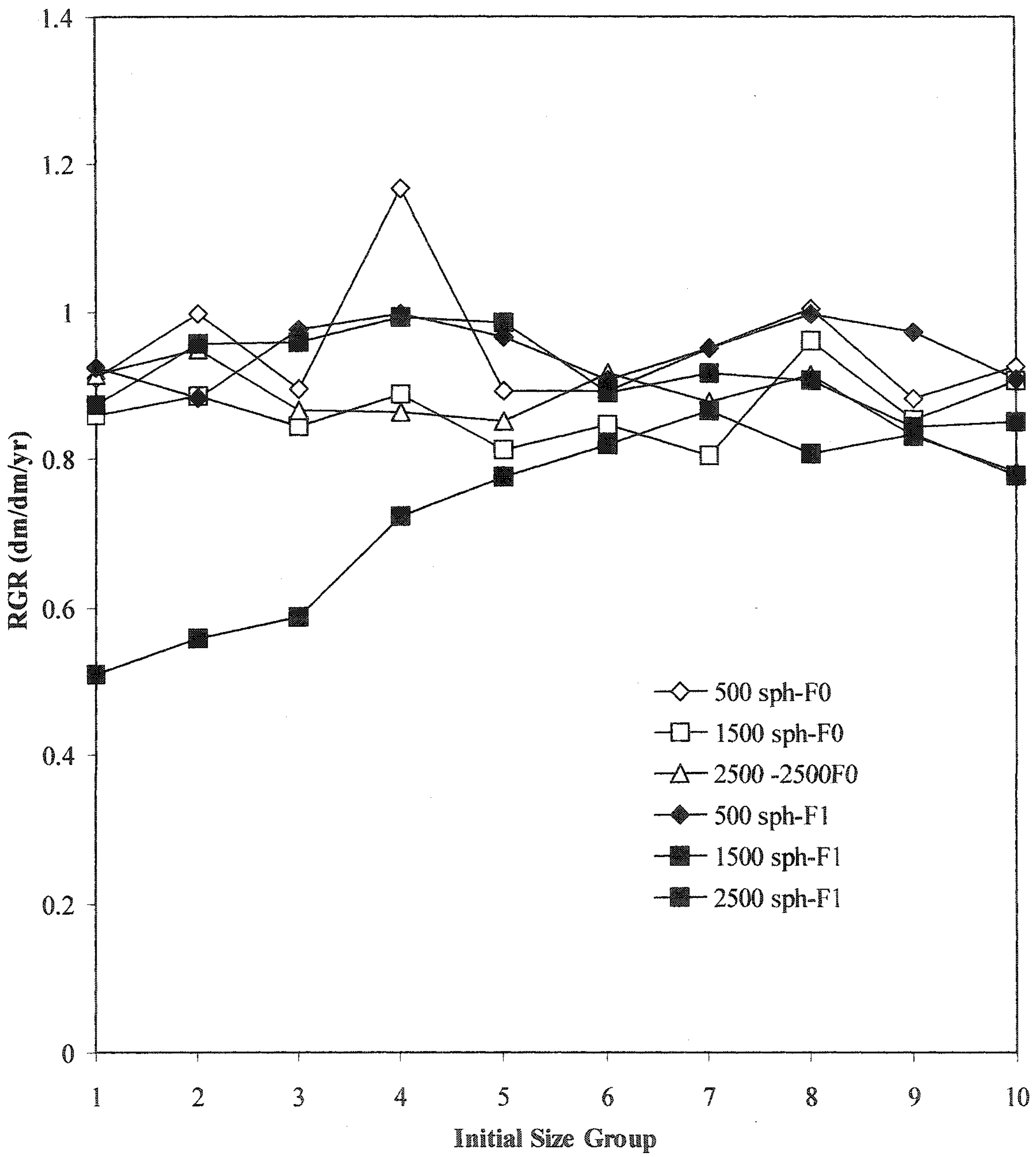

Figure A4.9. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1990 – 1992.

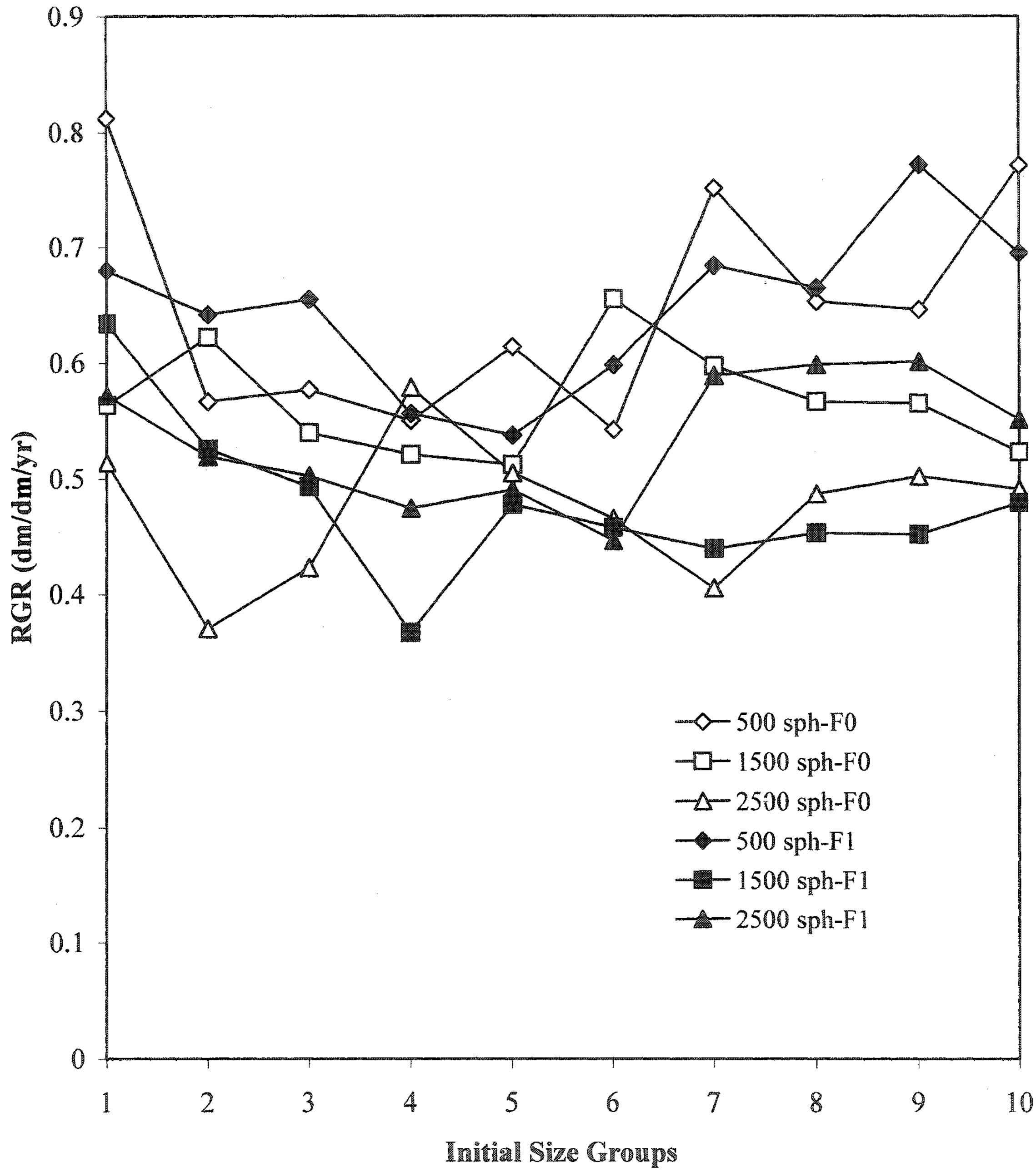

Figure A4.10. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1990 – 1992.

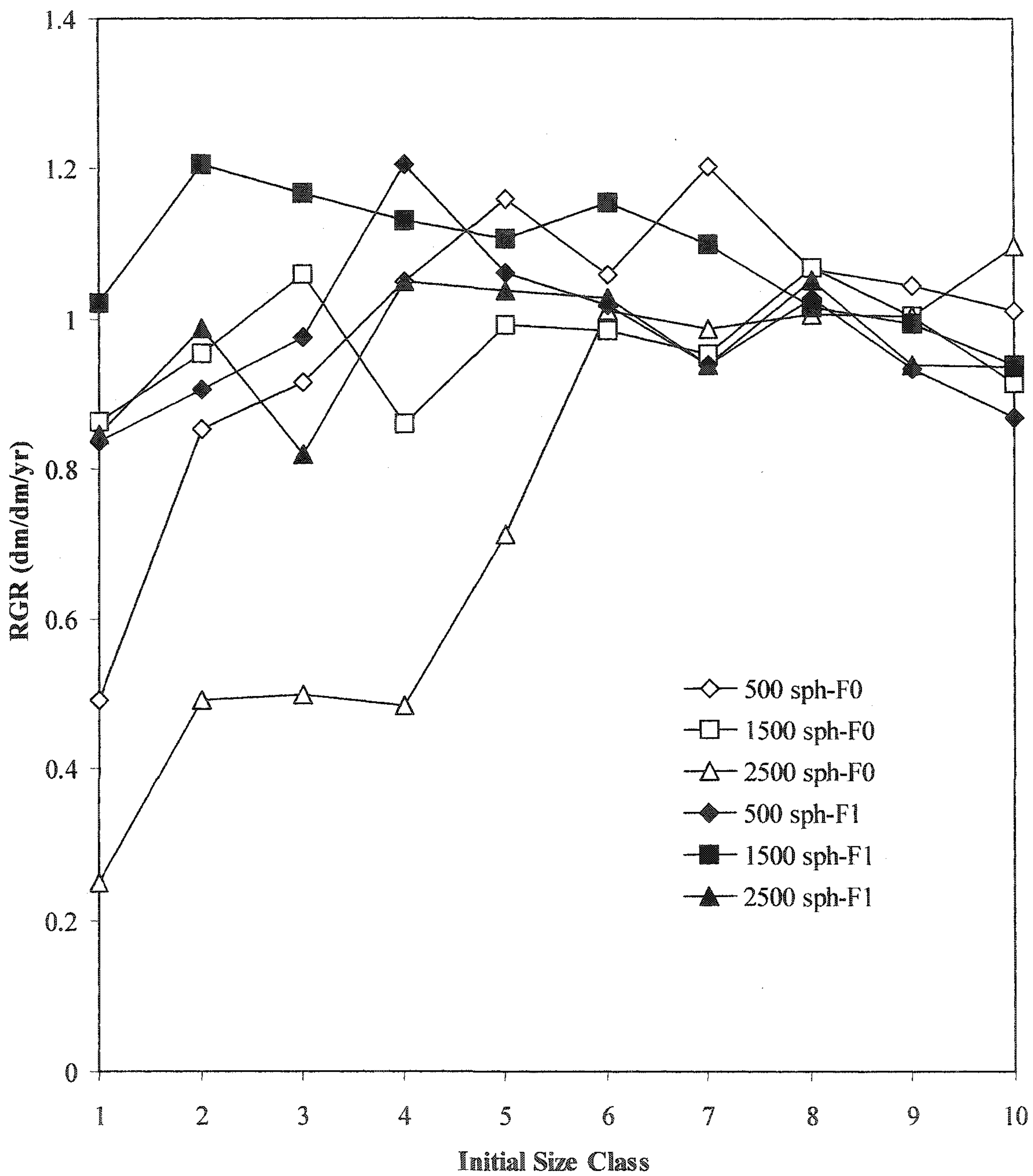

Figure A4.11. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1990 – 1992.

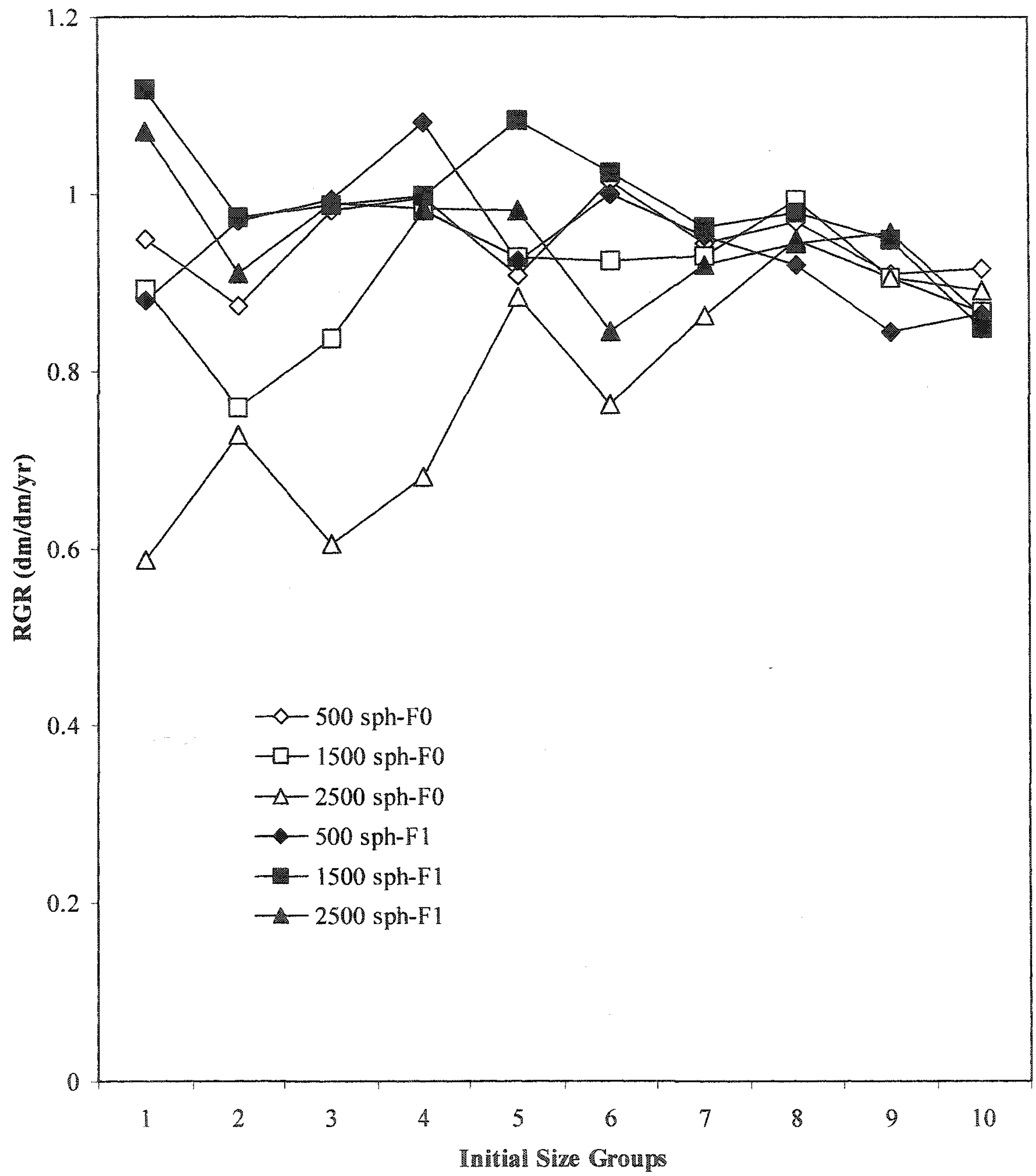

Figure A4.12. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1990 – 1992.

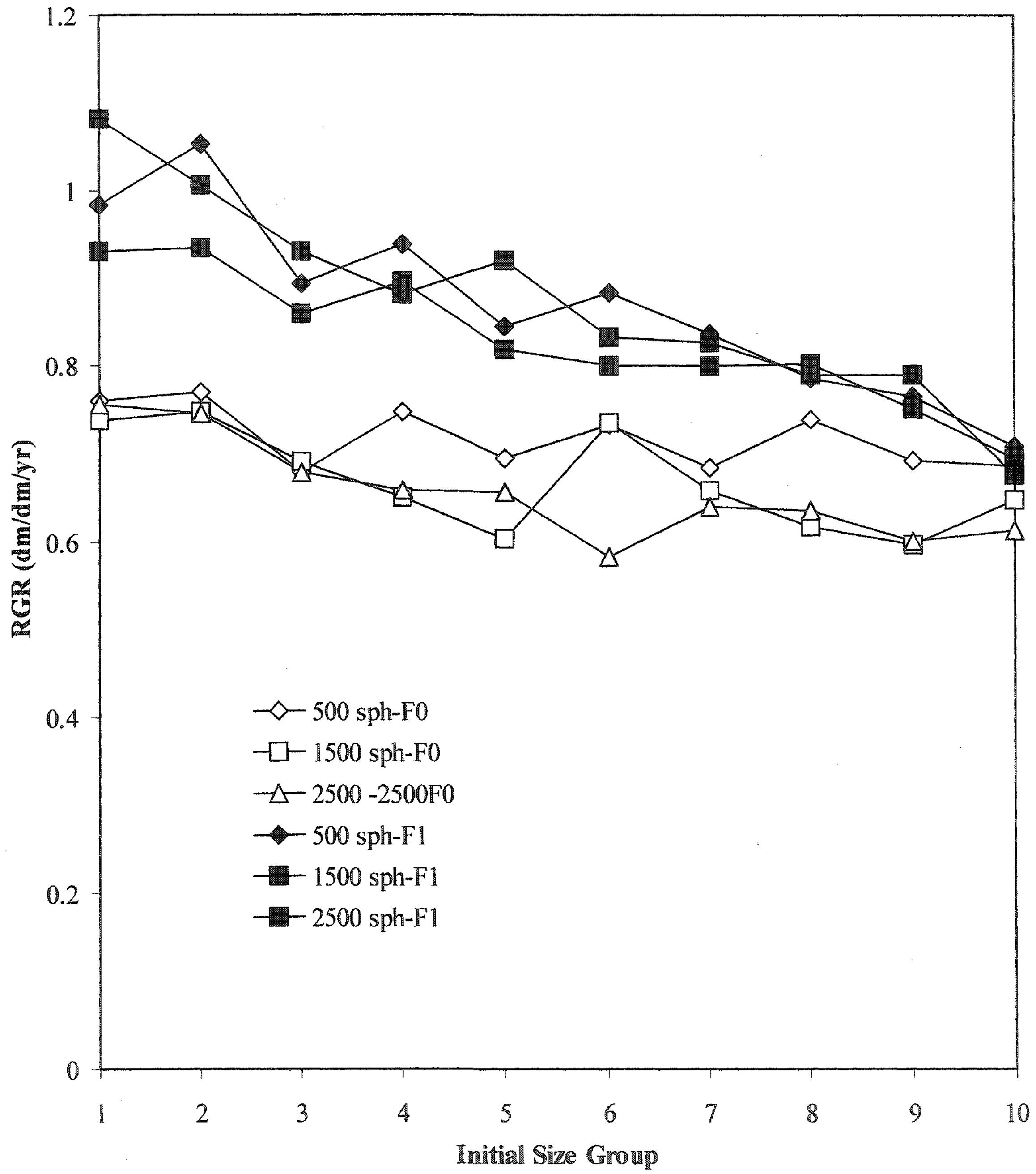

Figure A4.13. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1992 – 1994.

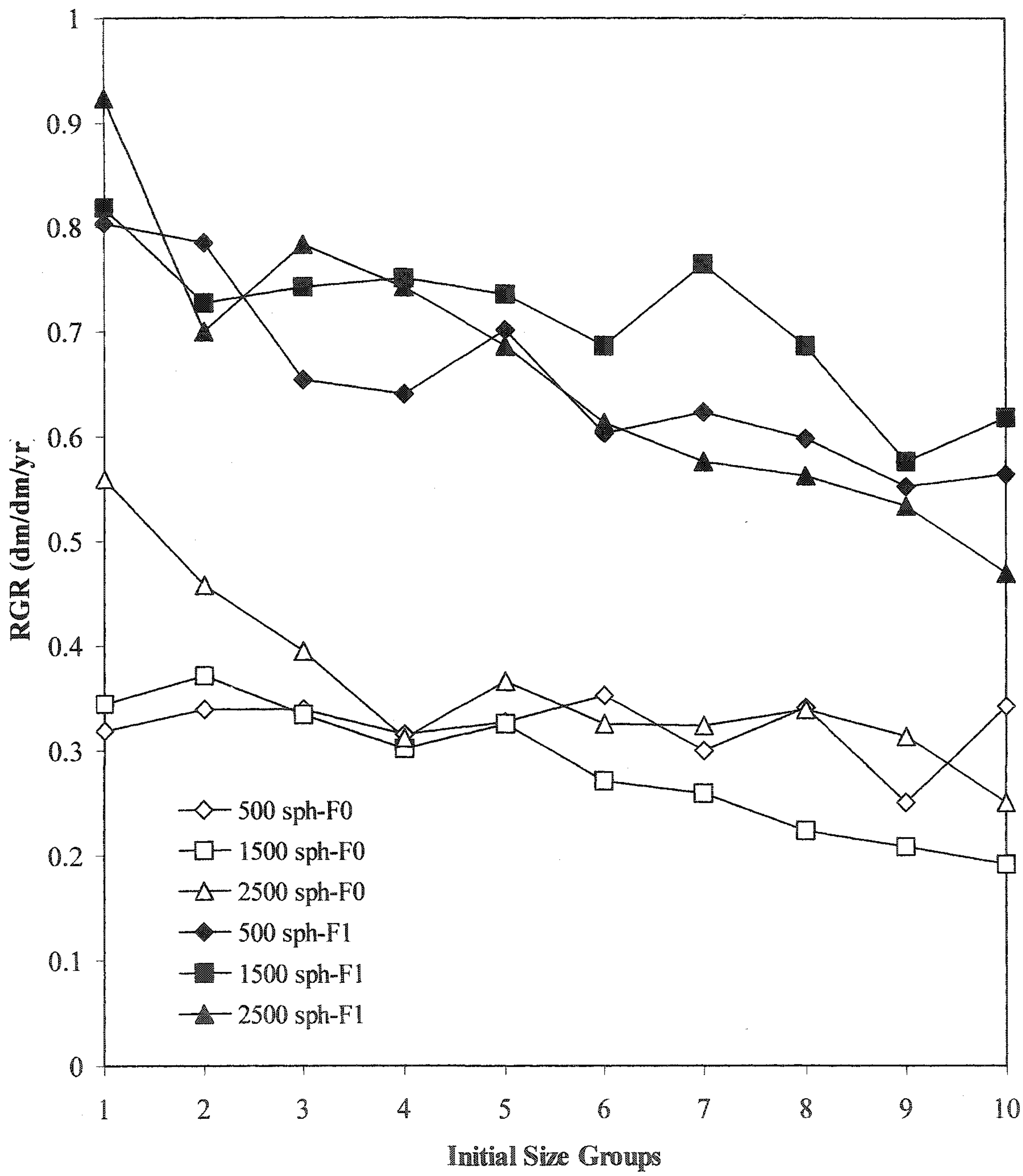

Figure A4.14. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1992 – 1994.

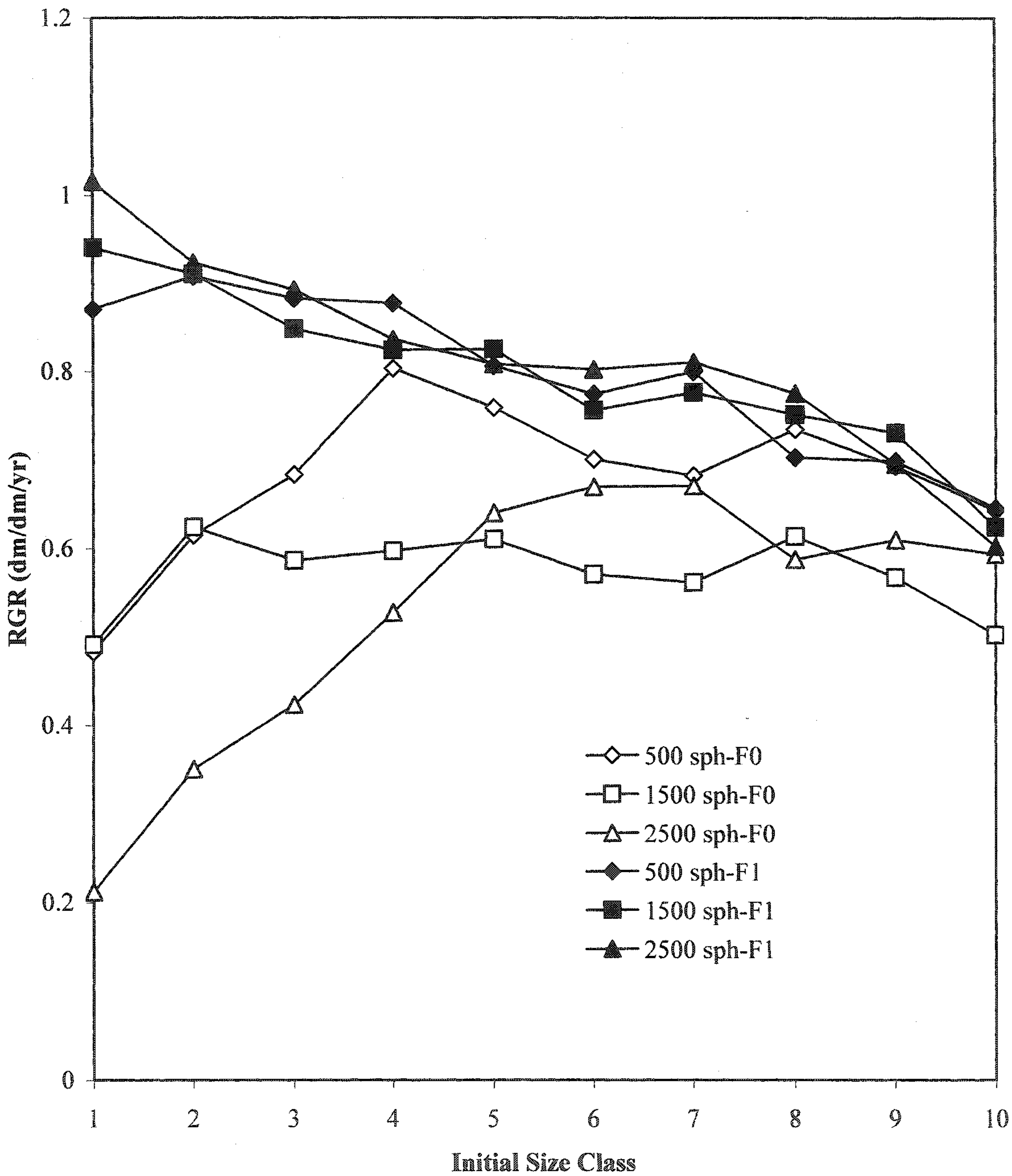

Figure A4.15. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1992 – 1994.

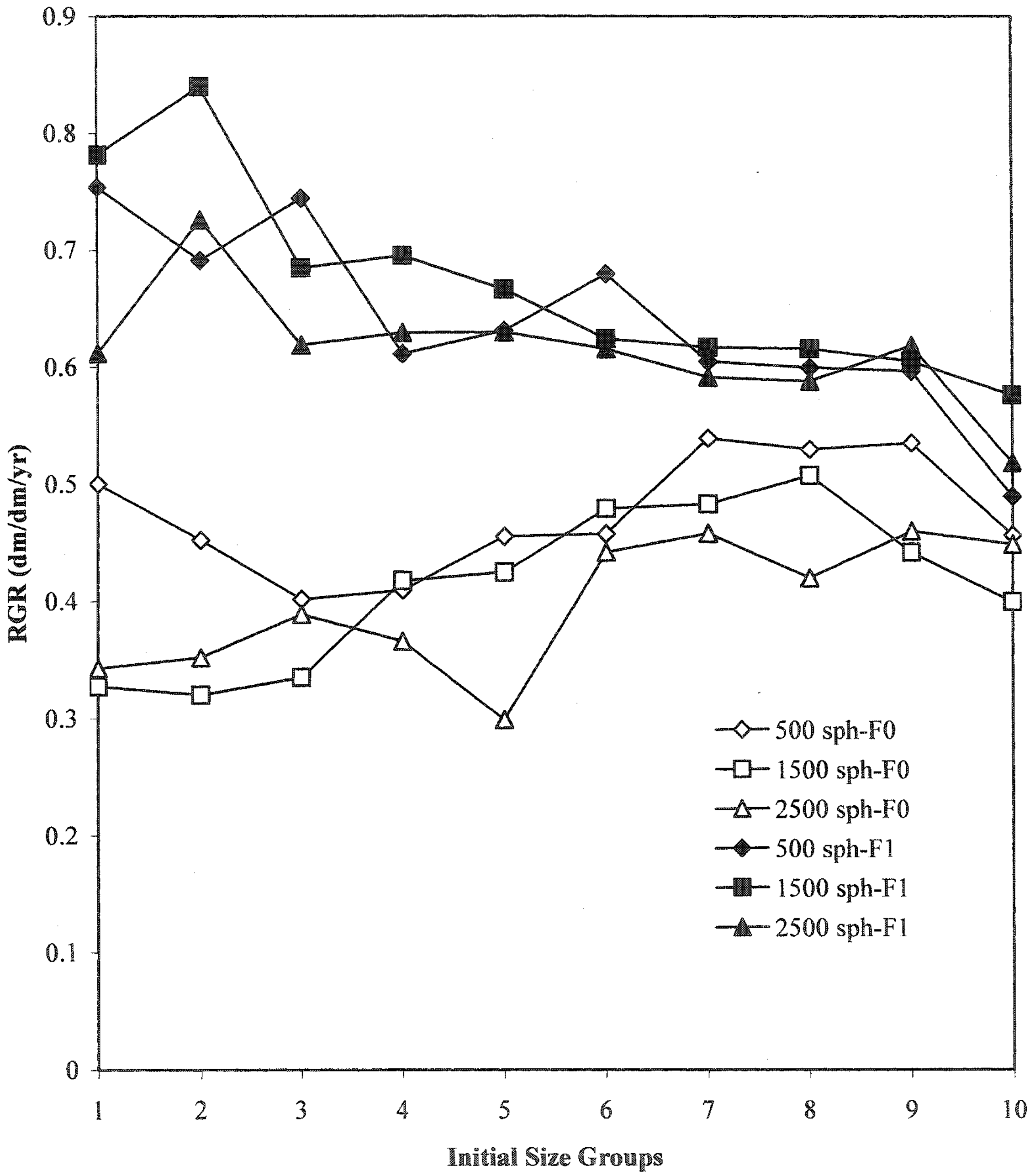

Figure A4.16. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1992 – 1994.

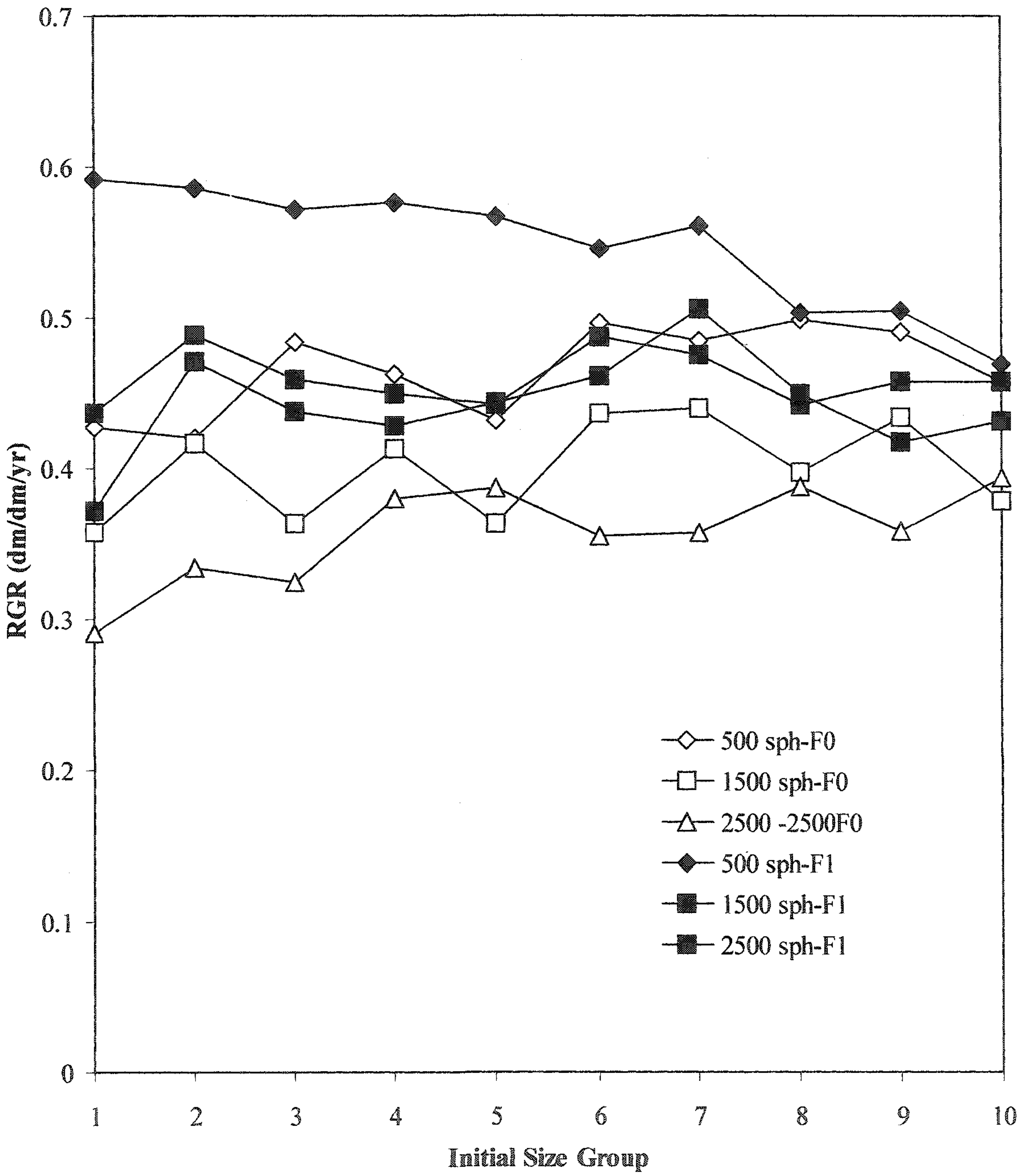

Figure A4.17. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1994 – 1997.

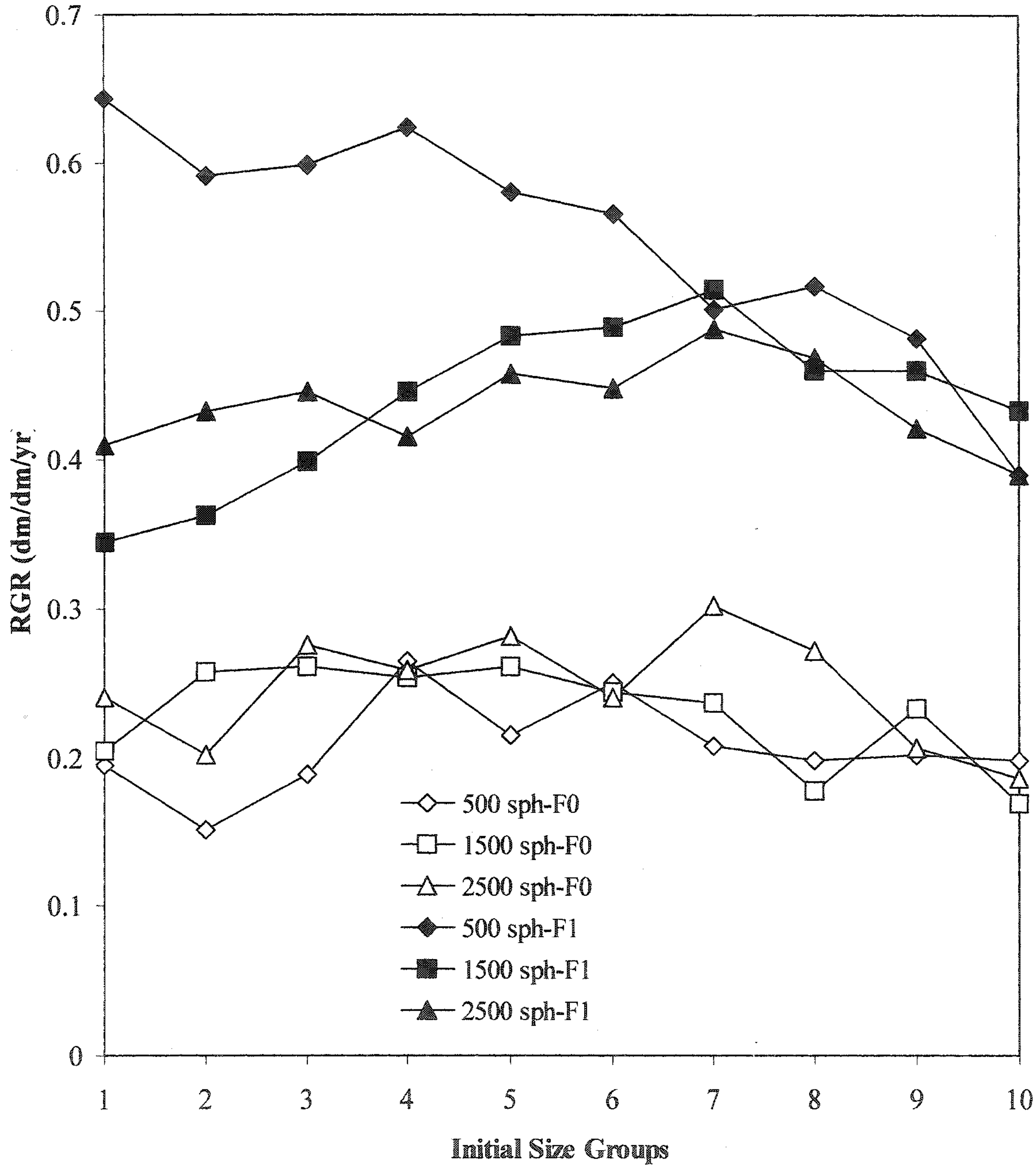

Figure A4.18. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1994 – 1997.

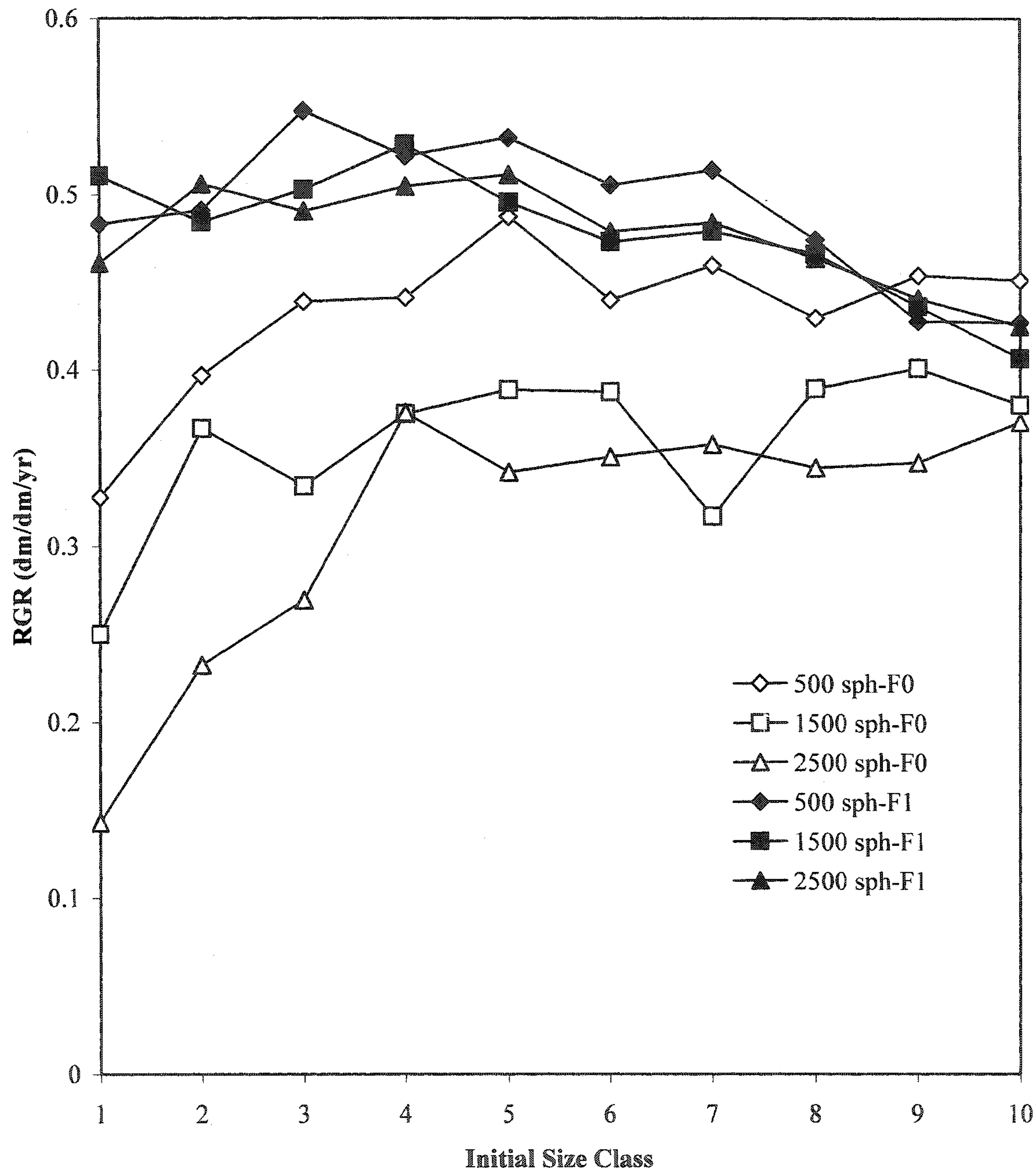

Figure A4.19. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1994 – 1997.

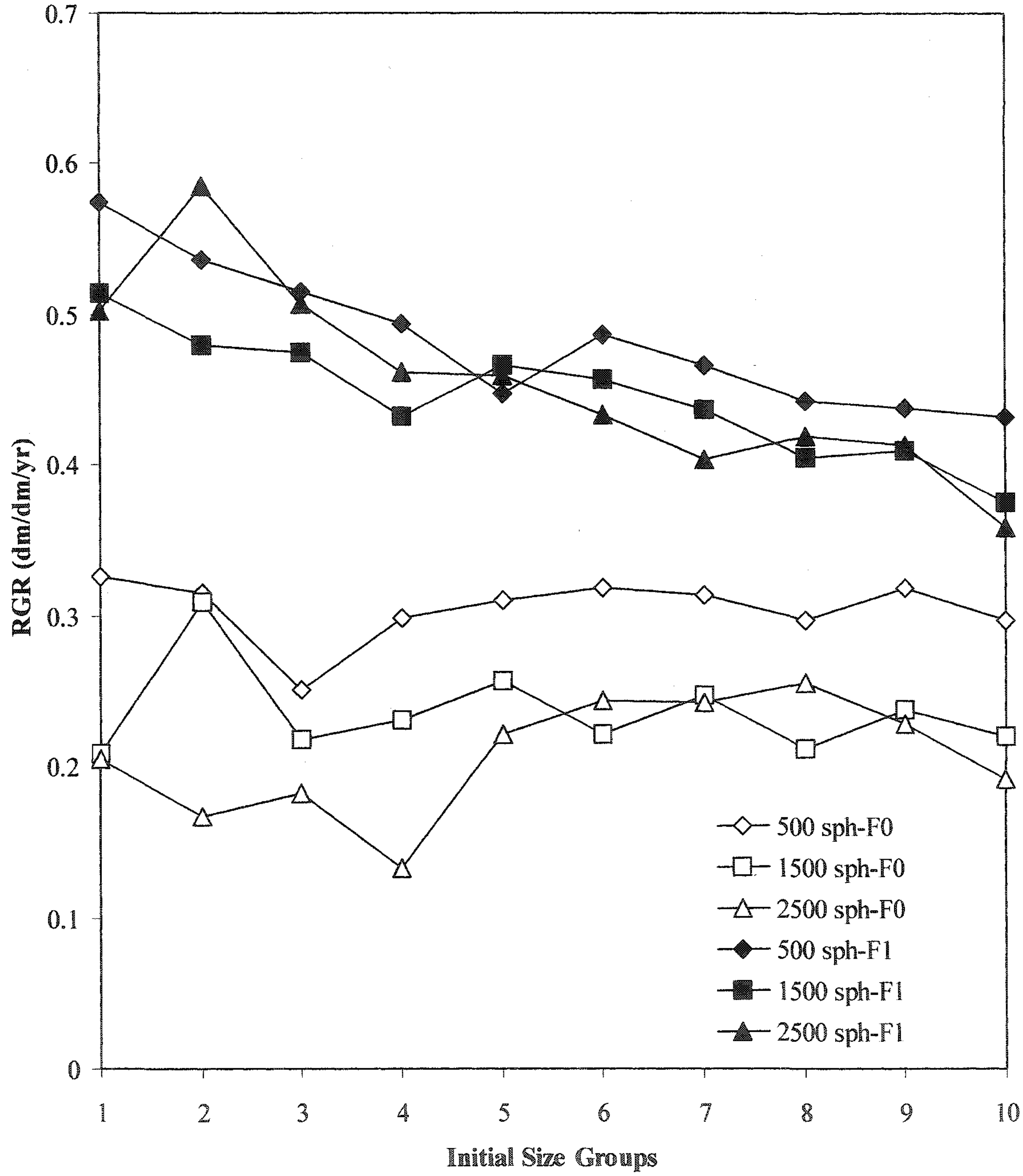

Figure A4.20. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1994 – 1997.

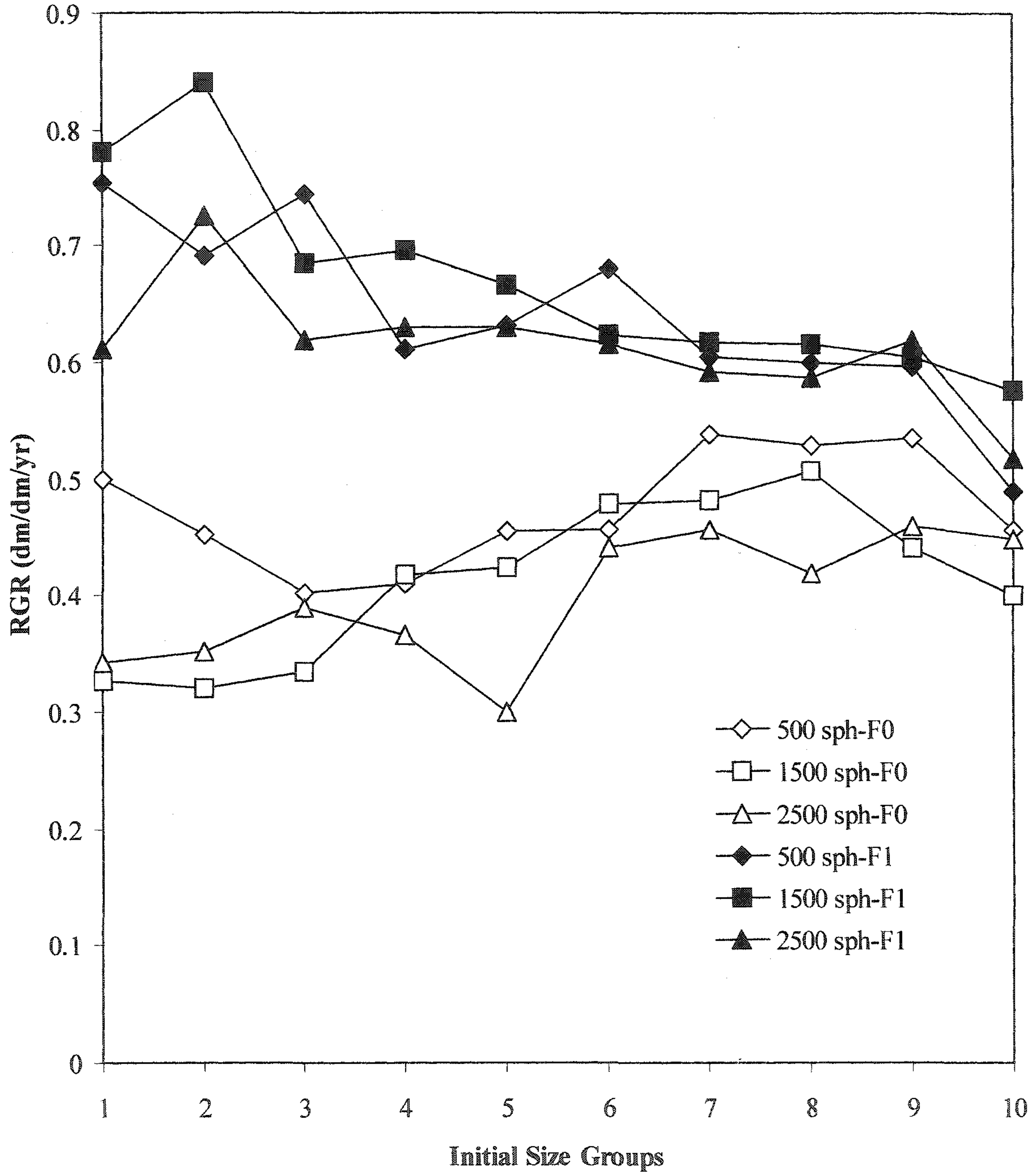

Figure A4.21. Relative volume index growth rate (RGR) by size group for cedar stands on CH sites, 1997 – 2002.

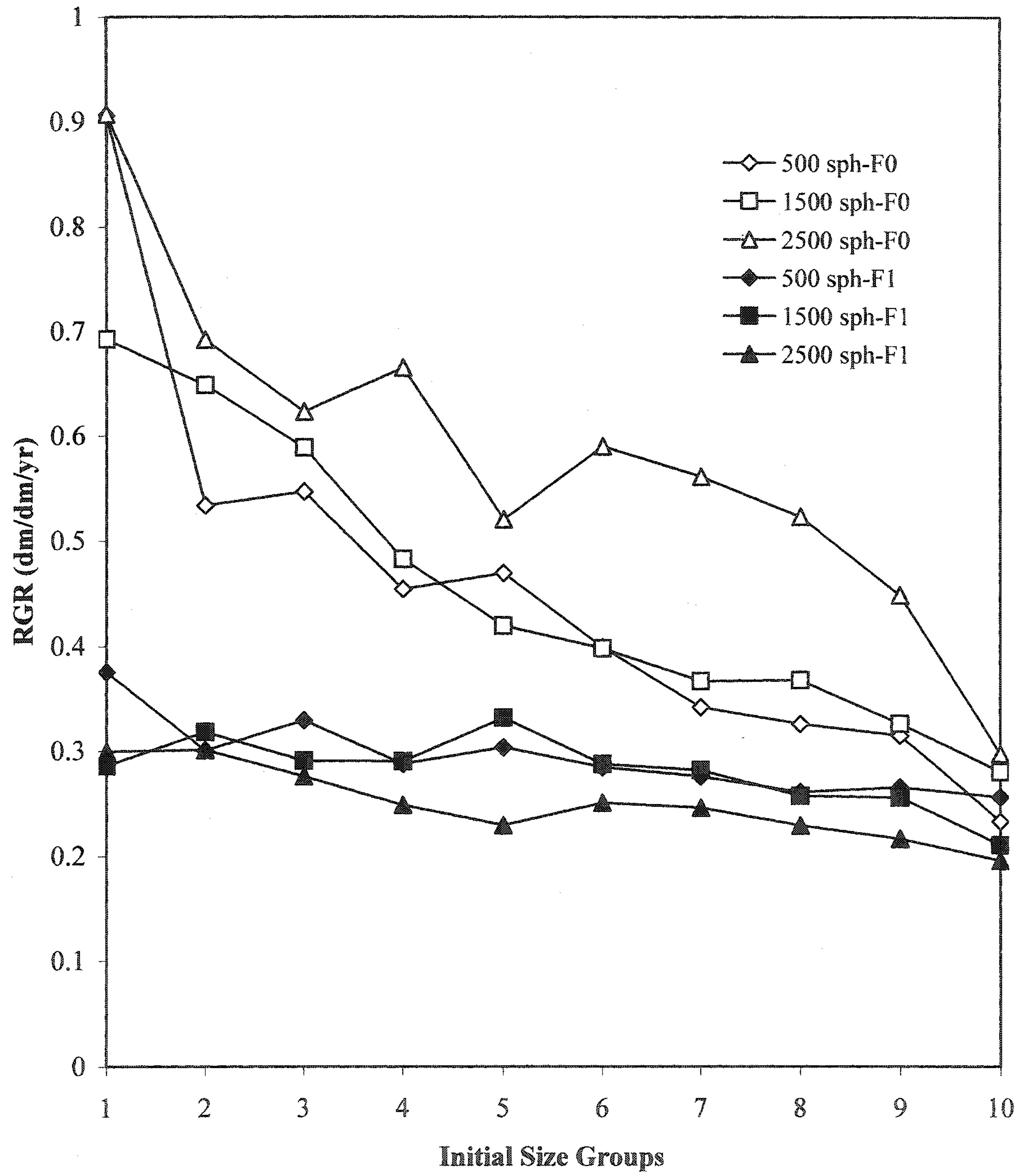

Figure A4.22. Relative volume index growth rate (RGR) by size group for hemlock stands on CH sites, 1997 – 2002.

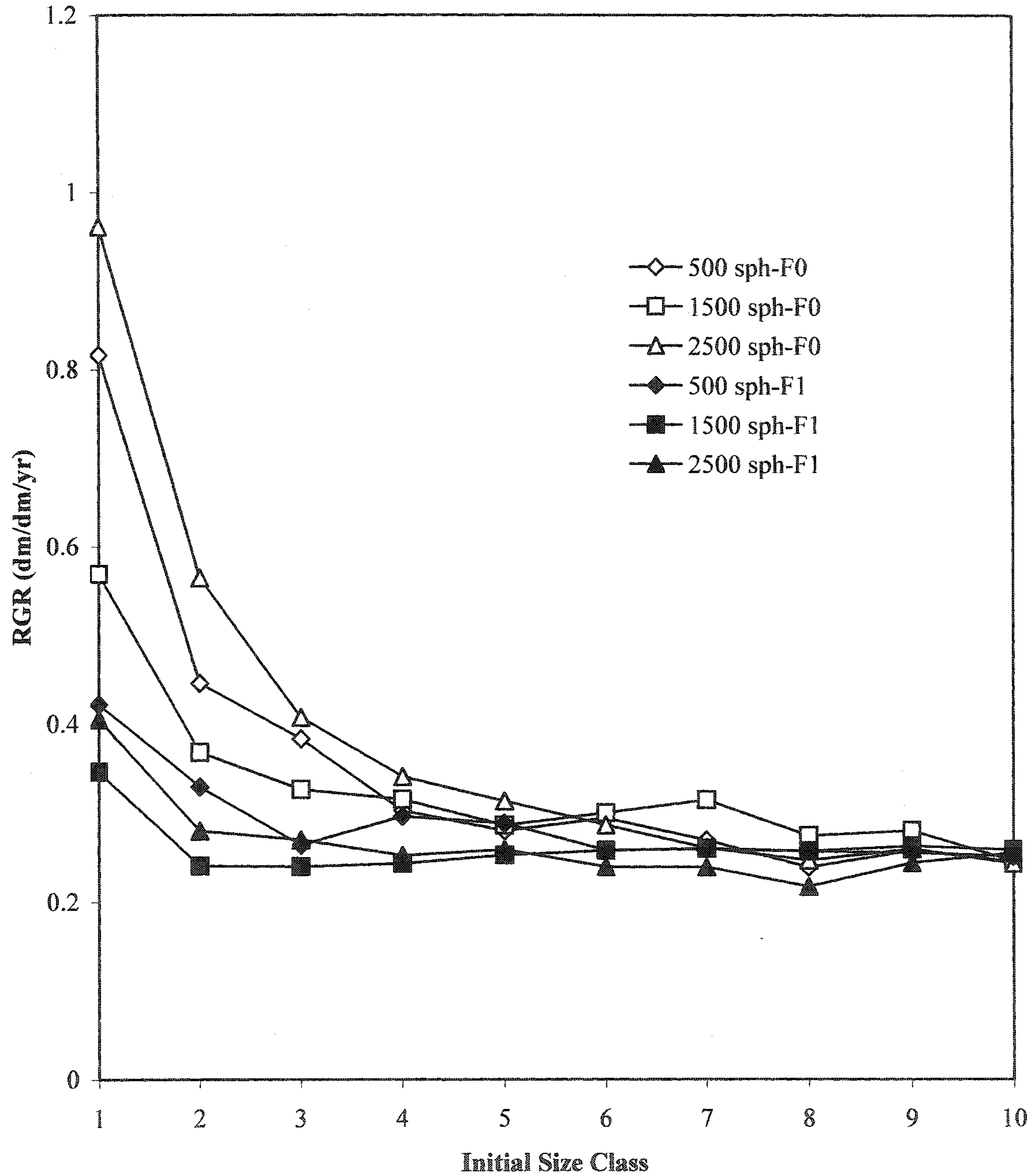

Figure A4.23. Relative volume index growth rate (RGR) by size group for cedar stands on HA sites, 1997 – 2002.

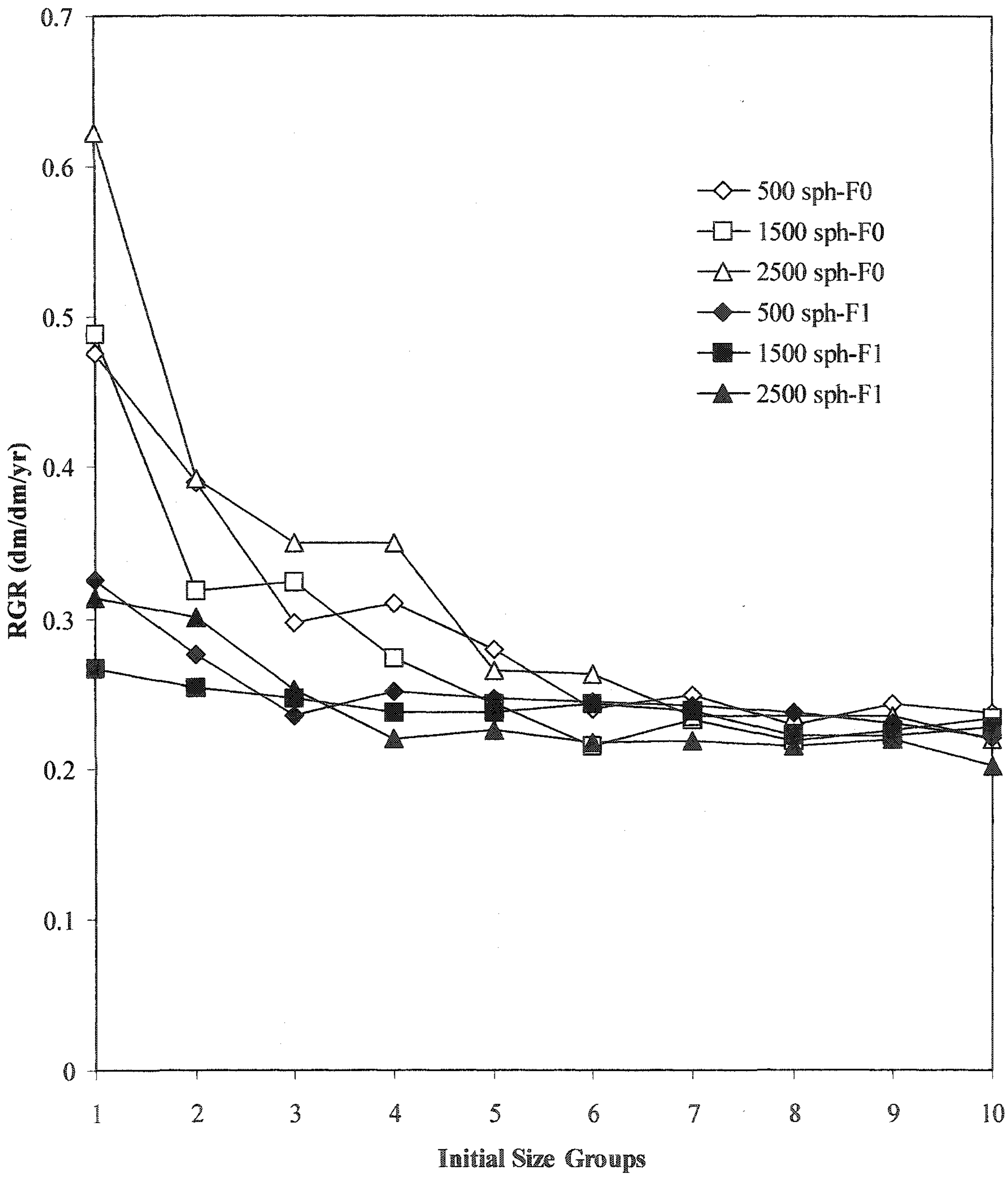

Figure A4.24. Relative volume index growth rate (RGR) by size group for hemlock stands on HA sites, 1997 – 2002.