Effects of stand density on the growth of young Douglas-fir trees

David R. Woodruff, Barbara J. Bond, Gary A. Ritchie, and William Scott

Abstract: The objectives of this study were (*i*) to provide further evidence of a positive correlation of stand density with early growth of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*); (*ii*) to determine when after planting the positive growth response occurs and how long it lasts; and (*iii*) to use stable isotopes of carbon to test whether the mechanism(s) responsible for the positive growth response to density are related to variables affecting photosynthesis, such as nutrient or moisture availability. We measured annual height (h) and diameter (d) growth (retrospectively) of 8- and 12-year-old trees in initial planting densities of 300, 1360, and 2960 trees/ha. Both height and diameter growth increased with density through the fifth year after planting and decreased with density by year 7. Diameter squared × height (d^2h) was used as a volume index to assess increase in tree volume. Second-year increase in d^2h for the high-density treatments was 300% of that in the low-density treatments. The δ^{13}C values of wood cellulose from annual rings of the second and third years after planting were not significantly different among densities, suggesting either (*i*) no significant differences in the effects of water availability, nutrient availability, or source air on photosynthesis in the three density treatments or (*ii*) differences that produced no net effect on δ^{13}C.

Résumé : Cette recherche avait comme objectifs (*i*) de fournir de nouvelles preuves qu'il existe une corrélation positive entre la densité du peuplement et la croissance juvénile du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) dans la région côtière; (*ii*) de déterminer à quel moment après la plantation survient la réponse positive en croissance et combien de temps elle dure et (*iii*) d'utiliser les isotopes stables du carbone pour vérifier si les mécanismes responsables de la réponse positive en croissance à la densité sont reliés aux variables qui affectent la photosynthèse, telles que la disponibilité des nutriments et de l'eau. Nous avons mesuré la croissance annuelle (rétrospectivement) en hauteur (h) et en diamètre (d) d'arbres âgés de 8 et 12 ans dans des plantations avec une densité initiale de 300, 1360 et 2960 tiges/ha. La croissance en hauteur et en diamètre ont augmenté avec la densité jusqu'à la cinquième année après la plantation et diminué avec la densité à compter de la septième année. L'augmentation du volume des arbres a été évaluée à l'aide d'un indice constitué du diamètre au carré × la hauteur (d^2h). L'augmentation de la valeur de d^2h la deuxième année dans les traitements avec la densité élevée représentait 300% de l'augmentation dans les traitements avec la faible densité. Les valeurs de δ^{13}C de la cellulose du bois dans les cernes annuels de la deuxième et de la troisième années après la plantation ne différaient pas significativement selon la densité indiquant soit (*i*) qu'il n'y avait pas de différences significatives entre les trois niveaux de densité dans les effets de la disponibilité de l'eau, de la disponibilité des nutriments ou de l'air original sur la photosynthèse; ou (*ii*) que les différences n'ont pas eu d'effet net sur la valeur de δ^{13}C.

[Traduit par la Rédaction]

Introduction

Silvicultural prescriptions involving stand density are often based on the assumption that individual tree productivity is inversely related to stand density at higher stocking levels (Evert 1971; Clark et al. 1994; Smith et al. 1997). Many sources indicate that height growth is insensitive to density and that radial growth increases with increased spacing (Hiley 1959; Sjolte-Jorgensen 1967; Dahms 1973; Schmidt et al. 1976; Seidel 1984; Lanner 1985). However, a few detailed studies show that in very young forest plantations, seedlings planted at high densities show more rapid growth than those planted at lower densities. For example, annual height growth has been shown to be positively correlated with stocking density at a young age for several species of broad-leaved and coniferous trees (Helmers 1948; DeBell and Giordano 1994; Gilbert et al. 1995; Knowe and Hibbs 1996; Ritchie 1997). In addition, there are reports of greater annual diameter growth occurring at higher density at an early age (Cameron et al. 1989; Scott et al. 1998).

All of these studies indicate that over time, annual growth in the higher stocking densities decreases to a level below that of the lower densities. This shift is presumably caused by increasing intraspecific competition, which suppresses growth in the higher density stands. Some studies have shown greater annual tree growth for seedlings in intermediate densities than in high and low densities (Belanger and Pepper 1978; Bormann and Gordon 1984; Cole and Newton 1987; Giordano and Hibbs 1993; Pienaar and Shiver 1993).

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These studies reported initial measurements taken several years after planting (initial measurements: 3–6 years after planting) and, therefore, may have missed an early phase in which annual growth was greatest in the highest density.

A possible explanation for the apparent contradiction in the literature is that studies that indicate only a negative growth response to density may have missed the early stage of the growth when a positive growth response to density may occur. This highlights the importance of investigating the early dynamics in the responses of growth to stand density. Because the positive growth response to density is somewhat counterintuitive, it is possible that it has been noted in even more studies but not reported.

Where it has been noted, positive growth response to density is a short-lived phenomenon. Knowledge of the timing involved could allow foresters to develop thinning and silvicultural prescriptions to maintain ideal stocking densities for maximum tree growth. In addition, increased knowledge of this phenomenon could lead to new ways of thinking about the biology and physiology of plant interaction and competition.

Using stable carbon isotopes

Analysis of stable carbon isotopes (^{12}C and ^{13}C) can provide a means to investigate a variety of issues in plant physiology (O'Leary 1981, 1988). During photosynthesis, C3 plants discriminate against the heavier stable isotope of carbon, ^{13}C (Farquhar et al. 1982). Differences in moisture availability (in soil or atmosphere) and nutrient availability can affect the degree of discrimination. Greater moisture availability tends to increase stomatal conductance (Tyree and Sperry 1988; Jones and Sutherland 1991), leading to increased discrimination against ^{13}C, and greater nutrient availability tends to decrease discrimination (Sparks and Ehleringer 1997; Livingston et al. 1998, 1999). Also, if respired CO_2 is "trapped" in the canopy atmosphere because of low mixing with the bulk atmosphere, the relative abundance of ^{13}C in the CO_2 used in photosynthesis is decreased. As the isotopic signal for any given year of tree growth is contained within the annual growth rings of stems, stable isotope analysis of wood cellulose can be used to test for variations in water availability, nutrient availability, or CO_2 concentration of source air between years or between treatments or sites within years. However, the interpretations must be made cautiously because many environmental variations may effect similar changes in C isotope discrimination, and it is also possible that changes in more than one of these factors can cancel each other out.

Objectives

The first objective of this study was to provide further evidence of high initial stocking density resulting in a short-lived increase in height and diameter growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) seedlings. The second objective was to determine the timing and duration of the positive response to density. These objectives are accomplished by retrospectively analyzing annual height and diameter growth beginning with the second year of growth following planting and continuing through the eighth year of growth of Douglas-fir planted in densities of 300, 1360, and 2960 trees/ha. The third objective was to attempt to differentiate among potential causes of the increased growth in the observed positive growth response to density. This objective was accomplished by analyzing carbon isotope ratios of annual rings from trees grown in different densities.

Material and methods

Site location and description

Study plots were located on Weyerhaeuser Co. land at Twin Harbors Tree Farm South (sites 1 and 2) near Doty, Wash., and Twin Harbors Tree Farm North (site three) near Oakville, Wash. Site 1 is located at 46°38′N, 123°21′W, at an elevation of 61 m; site 2 is located at 46°42′N, 123°29′W, at an elevation of 183 m; and site 3 is located at 46°51′N, and 123°26′W, at an elevation of 122 m. Sites 1 and 2 were planted in 1989 with 1+1 stock. Site 3 was planted in 1985 with 2+1. The estimated growth potential of all three sites is 43 m based on a breast-height age of 50 years (Steinbrenner and Duncan 1969).

The maritime Pacific climate of the region is characterized by a wet winter and dry summer. The mean annual precipitation in Centralia, Wash. (32–42 km from the field sites) is 1200 mm. Approximately 90% of the precipitation falls between October and May, and the small amount of precipitation between June and September (~150 mm) creates potential summer drought conditions. The mean annual snowfall is 170 mm. Mean minimum temperature for January is 0.8°C; mean maximum temperature for July is 26°C (Western Regional Climate Center 1998). Soils of all three sites are derived from parent material of sedimentary sandstone. The soils are classified as Haplohumults (reddish-brown lateritic soils) (Franklin and Dyrness 1988) and "Astoria series" by Weyerhaeuser Co.

Experimental design

Trees were planted by the Weyerhaeuser Co. in a randomized block design with a single replicate of density treatments at each site and plot sizes of approximately 2 ha. Weyerhaeuser Co. randomly assigned treatment densities to plots; for this analysis we used three stocking densities, 300, 1360, and 2960 trees/ha (120, 550, and 1200 trees/acre), referred to hereafter as low-, mid-, and high-density treatments. Within each plot we randomly selected 50 measurement trees. Trees within 10 m of plot boundaries were not considered to avoid edge effects. For statistical analyses, we considered the three sites to be blocks.

Tree measurements

Measurements were conducted during the summer of 1997. We measured stem diameter 30 cm above ground with Spencer diameter tapes. A core sample was taken from each tree with an 8-in. (1 in. = 2.54 cm) Suunto increment borer 30 cm above ground on the north side of trees; additional cores were extracted if necessary until core included the pith. From the cores, annual diameter growth was measured using a Metrics Quick Check QC-1000-M-AR digital readout unit, a 0.001 mm resolution Accu-Rite linear encoder, and a Velmex Unislide measuring stage.

Tree heights were measured with a height pole to a 0.1-m resolution. Annual height growth was determined retrospectively by measuring the distance between branch whorls for each year of growth. Trees in site 3 were 4 years older than those in the other two sites and too large for measurement with a height pole. Weyerhaeuser Co. measured tree heights annually at this site commencing 3 years after planting, and we used these measurements to calculate height growth commencing at year 4. However, these measurements were not included in statistical analyses, because the sampling design was different from the rest of the experiment.

For sites 1 and 2, we calculated a tree biomass index as d^2h, where d is stem diameter at 30 cm above ground and h is height. An analysis of d^2h could not be conducted for site 3, because trees sampled for height growth were different from the trees sampled for diameter growth.

In determining diameter growth of annual rings, we began measuring from the current year and counted inward. For some trees, the number of growth rings was less than the total number of years since planting because the end of the first or second year of growth occurred below the sampling height of 30 cm. Similarly, we measured height growth from the top whorl (current year) down, and for some trees the number of internodes was less than the number of years since planting. Therefore, the sample size during early growth years was less than the 50 trees per plot that we selected for measurement.

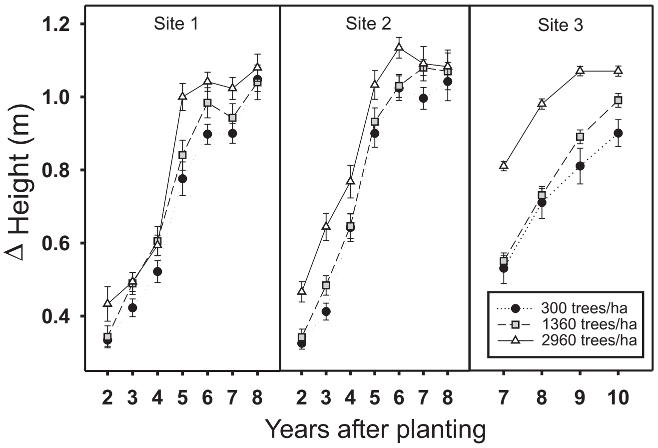
Stable isotope analysis

The growth rings for the second and third years after planting were excised from the core samples with a razor blade. These years were chosen for stable isotope analysis because height and diameter growth was greater in high-density than in low-density treatments in both of these years. The excised xylem was dried at 70°C for at least 72 h. It was then ground with a coffee grinder and pulverized in liquid nitrogen with a mortar and pestle. Cellulose was extracted from pulverized xylem samples according to the procedures described by Wise et al. (1945). Stable carbon isotope ratios of the extracted cellulose were determined at the Stable Isotope Ratio Facility for Environmental Research laboratory at the Biology Department of the University of Utah. All isotope data are expressed in delta notation (δ) and are presented relative to the Pee Dee belemnite standard for $\delta^{13}C$.

Statistical analyses

Height and diameter growth data were analyzed using the SAS statistical package (SAS Institute Inc. 1996) and the mixed-model procedure to determine the effect of initial stocking density on diameter, height, and volume (d^2h) of seedlings. A separate analysis was conducted for each year of growth from year 2 on. Fisher's protected least significant difference (LSD) was used for overall comparisons of all treatments for each year. Data for the analysis of d^2h were positively skewed and, therefore, were transformed (ln), because they violated assumptions of constant variance and normal distribution (Montgomery 1997). Median values were used in back transformation instead of mean values for this reason. The ^{13}C data were analyzed using the SAS statistical package (SAS Institute Inc. 1996) and the mixed-model procedure to determine the effect of initial stocking density on fractionation during the period covering the second and third years after planting. Fisher's protected LSD was used for overall comparison of all treatments.

Fig. 1. Annual height growth for trees in the low-, mid-, and high-density treatments. Error bars are SEs of up to 50 trees for sites 1 and 2 and between 28 and 323 trees for site 3. Sample sizes were lower in the early years; see text.



Results

Analyses of growth

Mean annual height increment was greater in the high-density treatment than in the low-density treatment, and height growth of the mid-density treatment was typically between the other treatments (Fig. 1). Averaged across sites 1 and 2, the greatest absolute difference among treatments in mean annual height increment occurred in year 5. Significant differences in height growth occurred in years 2, 5, and 6 (Table 1). Proportionally, the greatest differences in height increment occurred during years 2 and 3. Mean second and third-year height increment averaged across sites 1 and 2 in the high-density treatment was 133 and 136% of that in the low-density treatment, respectively (Table 1). The positive growth response to density declined over time such that, by the eighth year after planting, height growth in the high-density treatment was only 3% greater than that in the low-density treatment. Differences in mean annual height increment between mid- and high-density treatments were typically greater than those between low- and mid-density treatments. There were no significant differences in mean annual height increment between the low- and mid-density treatments in any single year, although the mean value of height growth was greater for the mid-density treatment at all sites in almost every year (Table 1, Fig. 1).

In years 2–5, mean annual diameter increment was consistently greater in the high-density treatment than the low-density treatment (Fig. 2). Mean annual diameter increment of the mid-density treatment was between that of the low- and high-density treatments. During this period the greatest absolute difference in mean annual diameter increment occurred between the low- and high-density treatments in year 4. Diameter growth in the high-density treatment was significantly greater than that of the low-density treatments in years 2, 3, 4, and 5 (Table 2). Proportionally, the greatest differences in diameter increment occurred during years 2

Table 1. Comparisons of mean annual height increment in low-, mid-, and high-density treatments.

Year	Stand density (trees/ha)	Mean height growth (m)	Treatment comparison	Treatment difference		df	Overall		Treatment comparison	
				Mean	SE		*F*	*p*	*t*	*p*
2	300	0.33	Low vs. mid	–0.01	0.02	2	25.74	0.037	0.60	0.610
2	1360	0.34	Mid vs. high	–0.10	0.02	2			5.89	0.028
2	2960	0.44	Low vs. high	–0.11	0.02	2			6.49	0.023
3	300	0.42	Low vs. high	–0.06	0.06	2	3.45	0.225	0.14	0.372
3	1360	0.48	Mid vs. high	–0.09	0.06	2			1.48	0.278
3	2960	0.57	Low vs. high	–0.15	0.06	2			2.62	0.120
4	300	0.58	Low vs. mid	–0.05	0.04	2	3.33	0.231	1.09	0.390
4	1360	0.63	Mid vs. high	–0.06	0.04	2			1.48	0.277
4	2960	0.69	Low vs. high	–0.11	0.04	2			2.57	0.124
5	300	0.84	Low vs. mid	–0.05	0.03	2	29.21	0.033	2.14	0.166
5	1360	0.89	Mid vs. high	–0.11	0.03	2			5.29	0.034
5	2960	1.00	Low vs. high	–0.16	0.03	2			7.42	0.018
6	300	0.96	Low vs. mid	–0.04	0.03	2	22.02	0.043	1.72	0.228
6	1360	1.00	Mid vs. high	–0.09	0.03	2			4.69	0.043
6	2960	1.09	Low vs. high	–0.13	0.03	2			6.41	0.024
7	300	0.96	Low vs. mid	–0.10	0.05	2	1.30	0.435	1.27	0.331
7	1360	1.06	Mid vs. high	0.04	0.05	2			0.22	0.850
7	2960	1.02	Low vs. high	–0.06	0.05	2			1.49	0.274
8	300	1.05	Low vs. mid	–0.01	0.02	2	3.69	0.213	0.34	0.769
8	1360	1.06	Mid vs. high	–0.02	0.02	2			2.50	0.129
8	2960	1.08	Low vs. high	–0.03	0.02	2			2.17	0.163

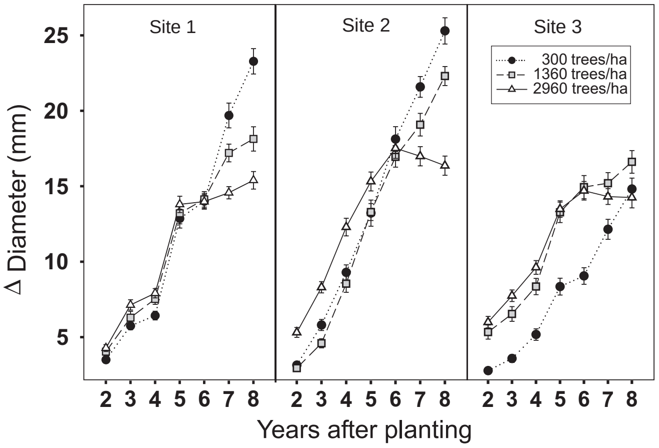
and 3. Averaged across all sites, mean diameter increment in years 2 and 3 in the high-density treatment were 165 and 154% of that in the low-density treatment, respectively (Table 2). This positive growth response to density declined over time such that by the seventh year after planting diameter increment was greatest in the low-density treatment. By the eighth year after planting, diameter increment was significantly greater in the low-density treatment than in the high-density treatment. Averaged across all three sites, mean diameter increment for the eighth year after planting in the high-density treatment was 72% of that in the low-density treatment (Table 2).

For years 2–5, annual median d^2h increment was greater in the high-density treatment than in the low-density treatment (Fig. 3). Proportionally, the greatest observed difference in median annual d^2h increment occurred between the low- and high-density treatments in year 2 (Table 3). Averaged across sites 1 and 2, median second-year d^2h increment in the high-density treatment was 300% of that in the low-density treatment (Table 3). As with the height and diameter increments, the positive growth response to density decreased over time. By year 7, median d^2h increment was significantly greater in the low-density treatment than in the high-density treatment. During the eighth year after planting, median d^2h increment for sites 1 and 2 at the lowest density was more than double that of the highest density.

Stable isotope analysis

There were no significant differences among the three planting densities in carbon isotopic composition of wood cellulose in the second and third years after planting for sites 1 and 2 (Table 4, Fig. 4). Carbon isotopes were not analyzed for samples collected from site 3 because of cost and the very clear lack of significant differences at the other two sites.

Fig. 2. Annual diameter growth for trees in the low-, mid-, and high-density treatments. Error bars are SEs of up to 50 trees. Sample sizes were lower in years 2 and 3; see text.



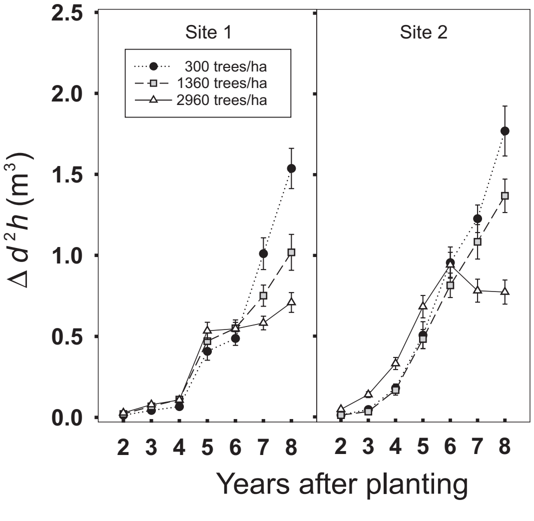
Discussion

Studies of single-species plant populations have shown a relationship between the maximum number of individuals that can occupy a site and the mean size of the individuals (Hiley 1959; Sjolte-Jorgensen 1967; Evert 1971; Dahms 1973; Schmidt et al. 1976; Seidel 1984; Lanner 1985; Clark et al. 1994; Smith et al. 1997). In these studies, the maximum number of plants of any given size that can exist on a site is correlated with the mean individual plant biomass

Table 2. Comparisons of mean annual diameter increment in the low-, mid-, and high-density treatments.

Year	Stand density (trees/ha)	Mean diameter growth (cm)	Treatment comparison	Treatment difference		df	Overall		Treatment comparison	
				Mean	SE		*F*	*p*	*t*	*p*
2	300	0.31	Low vs. mid	–0.09	0.07	4	4.96	0.083	1.33	0.254
2	1360	0.40	Mid vs. high	–0.11	0.07	4			1.81	0.145
2	2960	0.51	Low vs. high	–0.20	0.07	4			3.14	0.035
3	300	0.50	Low vs. mid	–0.07	0.08	4	6.17	0.060	1.01	0.370
3	1360	0.57	Mid vs. high	–0.20	0.08	4			2.41	0.074
3	2960	0.77	Low vs. high	–0.27	0.08	4			3.42	0.027
4	300	0.69	Low vs. mid	–0.12	0.104	4	4.22	0.103	1.03	0.362
4	1360	0.81	Mid vs. high	–0.18	0.104	4			1.84	0.140
4	2960	0.99	Low vs. high	–0.30	0.104	4			2.87	0.046
5	300	1.14	Low vs. mid	–0.18	0.113	4	3.47	0.134	1.75	0.156
5	1360	1.32	Mid vs. high	–0.10	0.113	4			0.84	0.451
5	2960	1.42	Low vs. high	–0.28	0.113	4			2.58	0.061
6	300	1.37	Low vs. mid	–0.16	0.17	4	0.63	0.577	0.95	0.395
6	1360	1.53	Mid vs. high	–0.01	0.17	4			0.04	0.968
6	2960	1.54	Low vs. high	–0.17	0.17	4			0.99	0.376
7	300	1.78	Low vs. mid	0.07	0.17	4	1.12	0.411	0.37	0.732
7	1360	1.71	Mid vs. high	0.18	0.17	4			1.07	0.343
7	2960	1.53	Low vs. high	0.25	0.17	4			1.44	0.223
8	300	2.11	Low vs. mid	0.21	0.063	4	4.16	0.105	1.05	0.352
8	1360	1.90	Mid vs. high	0.37	0.063	4			1.80	0.146
8	2960	1.53	Low vs. high	0.58	0.063	4			2.85	0.046

Fig. 3. Annual increase in d^2h for trees in the low-, mid-, and high-density treatments. Error bars are SEs of up to 50 trees. Sample sizes were lower in years 2 and 3; see text.



raised to the power of –3/2 (Yoda et al. 1963; Westoby 1984). This relation has been termed the "self-thinning rule". This rule suggests that as trees grow larger, the competition for resources increases, and competition will increase with increasing stand density. Once trees of a given density reach a certain mean biomass, the competition for resources is so intense that mortality ensues. The self-thinning rule illustrates that it is generally believed that higher stocking density is correlated with a lower rate of growth at the individual tree level. The research presented in this study provides evidence of a contradiction to this idea. As noted earlier, a possible explanation for this apparent contradiction is that studies that indicate only a negative growth response to density may have missed the early stage of the growth when a positive growth response to density may occur. This again highlights the importance of investigating the early dynamics in the responses of growth to stand density.

In this study, both height and diameter growth of Douglas-fir trees were positively correlated with initial stocking density for the first few years after planting. This trend reversed in later years, resulting in decreased growth (at the individual tree level) in stands of higher initial stocking density. The greatest positive correlation between growth and density occurred in the second and third years after planting. As time progressed, high initial density became less advantageous to growth. By year 8, both diameter and d^2h increments were significantly lower in the high- and mid-density treatments than in the low-density treatment. This suggests two possible scenarios: the positive growth response to density is caused by a mechanism that functions only early in the growth of seedlings, or greater competition from neighboring seedlings in the higher densities negates any growth benefits derived from the still-functioning mechanism.

The lack of any significant differences in stable carbon isotope composition of wood cellulose suggests that growth differences probably were not caused by a mechanism that operates primarily through changes in availability of water or nutrients that affected photosynthetic performance. It is also possible that changes in more than one of these factors canceled each other out.

Among other possible explanations for the positive early growth at high density are increased animal browsing in lower density plots, increased interspecific competition in

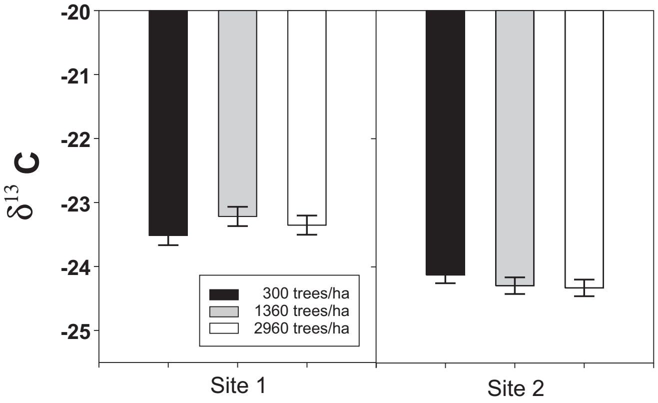
Table 3. Back-transformed comparisons of median annual d^2h increment in the low-, mid-, and high-density treatments.

Year	Stand density (trees/ha)	Median increase in d^2h (cm^3)	Treatment comparison	Ratio of treatments	95% confidence limit for treatment ratio		df	Overall		Treatment comparison	
					Lower	Upper		*F*	*p*	*t*	*p*
2	300	4.75	Low vs. mid	0.80	0.17	3.81	2	5.1	0.164	0.62	0.598
2	1360	5.95	Mid vs. high	0.42	0.09	1.99	2			2.4	0.138
2	2960	14.24	Low vs. high	0.33	0.07	1.59	2			3.02	0.094
3	300	17.03	Low vs. mid	0.91	0.18	4.6	2	3.35	0.23	0.26	0.819
3	1360	18.72	Mid vs. high	0.45	0.09	2.3	2			2.1	0.171
3	2960	41.68	Low vs. high	0.41	0.08	2.08	2			2.36	0.142
4	300	43.38	Low vs. mid	0.86	0.21	3.54	2	1.53	0.396	0.44	0.7
4	1360	50.40	Mid vs. high	0.67	0.16	2.72	2			1.24	0.34
4	2960	75.49	Low vs. high	0.57	0.14	2.36	2			1.69	0.234
5	300	181.64	Low vs. mid	0.95	0.66	1.37	2	6.53	0.133	0.57	0.627
5	1360	190.51	Mid vs. high	0.79	0.55	1.14	2			2.81	0.107
5	2960	241.58	Low vs. high	0.75	0.52	1.08	2			3.37	0.078
6	300	272.82	Low vs. mid	1.03	0.70	1.52	2	0.45	0.69	0.36	0.754
6	1360	264.16	Mid vs. high	0.92	0.62	1.35	2			0.94	0.446
6	2960	287.44	Low vs. high	0.95	0.64	1.40	2			0.58	0.62
7	300	445.32	Low vs. mid	1.21	0.98	1.51	2	50.56	0.019	3.81	0.062
7	1360	367.42	Mid vs. high	1.36	1.10	1.69	2			6.15	0.025
7	2960	269.43	Low vs. high	1.65	1.33	2.05	2			9.96	0.01
8	300	659.64	Low vs. mid	1.40	1.00	1.95	2	52.95	0.019	4.29	0.05
8	1360	472.48	Mid vs. high	1.59	1.14	2.22	2			5.96	0.027
8	2960	296.78	Low vs. high	2.22	1.59	3.11	2			10.25	0.009

Table 4. Comparisons of mean annual $\delta^{13}C$ in the low-, mid-, and high-density treatments.

Stand density (trees/ha)	Mean $\delta^{13}C$	Treatment comparison	Treatment difference		df	Overall		Treatment comparison	
			Mean	SE		*F*	*p*	*t*	*p*
300	–23.8	Mid vs. low	0.06	0.17	2	0.13	0.884	0.37	0.746
1360	–23.8	High vs. mid	–0.09	0.17	2			0.49	0.673
2960	–23.9	High vs. low	–0.03	0.17	2			0.12	0.917

Fig. 4. $\delta^{13}C$ of cellulose extracted from the second and third years of stem growth for low-, mid-, and high-density treatment seedlings. Material from second and third years of growth are pooled. Error bars are SEs of 50 samples.



low-density plots, improved probability of good microsites in high-density plantings, and changes in quality of side light affecting allometry of growing seedlings. Foliage of adjacent trees in the high-density stocking treatment was not touching until 7–10 years after planting. Therefore, it is not likely that the degree of canopy closure during the ages in which we observed the greatest differences in growth between treatments was sufficient enough to result in significant differences in the overall levels of animal browsing. The same can be said for the effects of interspecific competition. Improved probability of good microsites may enhance the growth of some trees in the high-density plantings; however, it is not likely that this would significantly affect the overall mean growth rate within a treatment, as there is an increased probability of trees being planted in poor microsites as well. In a greenhouse study involving individually potted seedlings of Douglas-fir, height, crown biomass, and branch number increased with decreasing growing space (Ritchie 1997). Plant height was inversely correlated with estimated phytochrome photoequilibrium values. This study indicated that light striking the sides of the trees may be altered because of reflectance from green leaves of neighboring individuals, resulting in a decrease in the ratio of red to far red light (R/FR). The change in quality of side light may affect allometry of growing seedlings. In operational plantations such as the ones in our study, there is a great deal of herbaceous and shrubby vegetation between planted trees. One might expect that this interspecific competition could also result in a decreased R/FR of side light reaching crop seedlings. Seedlings may identify different species as potential competitors or noncompetitors by variations in leaf reflectance properties and respond accordingly (Ritchie 1997). Clearly, this is an area that deserves further research.

Potential benefits of increasing stocking density are better understood when considering precommercial thinning. Taking advantage of enhanced growth of seedlings through increased density would necessitate a high initial stocking density. If initial stocking density is high, then a thinning is often desirable (Randall 1971; Smith et al. 1997). Planting a greater number of trees and a thinning both require added expense. Thinning the high- and low-density treatments to an equal density, however, results in retention of a different percentage of the originally planted trees. Precommercial thinning applications often emphasize the retention of the larger and higher quality trees (Smith et al. 1997). The high-density treatment will retain a lower percentage of the originally planted trees, allowing for a greater level of selection of larger and higher quality trees to retain for future harvest.

For seedlings in an exponential growth phase, small changes in biomass partitioning or net carbon gain can lead to large differences in time-integrated growth. If foresters are to take advantage of the positive growth response to density, however, it is important to understand what causes it, how plants respond to it physiologically, when this phenomenon is expressed, and to what extent it is occurring for different stocking densities. As mentioned, several studies have shown a positive correlation of growth with stocking density at a young age for several species of broad-leaved and coniferous trees (Helmers 1948; Cameron et al. 1989; DeBell and Giordano 1994; Gilbert et al. 1995; Knowe and Hibbs 1996; Ritchie 1997; Scott et al. 1998). This study provides a greater amount of information than previously available about the temporal dynamics involved in the observed positive growth response to density and the degree to which this phenomenon is occurring at different stages of growth and in different densities of Douglas-fir plantations. Increases in stocking density are already being implemented in certain areas of the coastal Pacific Northwest as a result of research indicating a positive growth response to density. These prescribed densities are based entirely on empirical information. Improved understanding of the mechanisms behind enhanced growth associated with increased density should allow more thoughtful analysis of the most cost-efficient approach for maximizing early growth. With improved understanding of this phenomenon, thinnings, rotation lengths, and stocking densities could be manipulated to more successfully capture the possible growth benefits of increased stocking density in Douglas-fir plantations. Further research in this area could provide information of possible benefits for plantations of other species as well. Additionally, a greater understanding of this phenomenon could lead to new ways of thinking about the physiology and biology of plant competition and interaction.

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