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Forest Sci., Vol. 30, No. 1, 1984, pp. 259–263

Douglas-fir Stem Growth per Unit of Leaf Area Increased by Interplanted Sitka Alder and Red Alder

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ABSTRACT. Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] stem growth per unit of leaf area was compared in the presence and absence of Sitka alder (*Alnus sinuata*) and red alder (*Alnus rubra*). The apparent effect of the alders differed with the method used to calculate the ratio. When Douglas-fir's rating was calculated from conversion ratios for sapwood area to leaf area as measured at each site, it was increased 40 percent by the presence of Sitka alder and 250 percent by red alder. This increased stem growth per unit of leaf area probably resulted from both greater net photosynthetic rates and a shift in within-tree photosynthate allocation. FOREST SCI. 30:259–263.

ADDITIONAL KEY WORDS. *Pseudotsuga menziesii*, leaf area, net primary production, photosynthesis allocation.

SOIL FERTILITY can affect net primary production in forest ecosystems by limiting stand leaf area and rates of photosynthesis per unit of leaf area (Brix and Ebell 1969, Brix 1981). In addition, the production of stemwood per unit of leaf area depends upon the allocation of photosynthate within trees; fertile soil requires a lower investment in root production, allowing a greater proportional allocation to stemwood production (Keyes and Grier 1981, Waring 1982, Grier 1984). Therefore, the potential interactions between conifer crop trees and interplanted nitrogen-fixing plants should involve tradeoffs between competition for canopy space (leaf area) and effects of soil fertility enhancement on net photosynthesis and photosynthate allocation.

In the present study, I examined Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] stemwood growth per unit of leaf area in three study sites within one 23-year-old Douglas-fir plantation. One site also contained red alder (*Alnus rubra* Bong.); the second site also contained Sitka alder [*Alnus sinuata* (Regel) Rydb.]. The third site lacked alder and served as a control. I hypothesized that red alder with its tree growth form would reduce Douglas-fir leaf area more than would Sitka alder with its shrubby, multiple-stem form but that greater rates of N-fixation by red alder (and increased soil fertility) would result in greater Douglas-fir photosynthate allocation to stemwood growth. Three approaches were used to test this hypothesis. The simplest test involved measuring 5-year stemwood growth relative to stem sapwood area ["tree vigor index" after Waring and others (1980)] on the assumption that sapwood area is linearly correlated to leaf area (Grier and Waring 1974, Snell and Brown 1978, Whitehead 1978, Long and others 1981). The second test involved using biomass regression equations (Gholz and others 1979) to estimate 5-year stemwood growth in kg ha^{-1}, again on the assumption that a linear relation exists between stem sapwood area and leaf area. The last test involved stemwood growth estimates (based on biomass regression equations) in combination with on-site measurements of Douglas-fir leaf area. The use of these three methods allowed me to evaluate the effect of the alders on Douglas-fir stemwood growth per unit of leaf area and to test simplified methods for estimating these parameters.

SITE DESCRIPTION

Three study sites were located within one 23-year-old Douglas-fir plantation in MacMillan Bloedel Limited's Tree Farm 19 on Mt. Benson (510 m elevation) near Nanaimo, British

When this study was conducted, the author was Graduate Research Assistant, Department of Forest Science, School of Forestry, Oregon State University; his present address is School of Forestry and Environmental Studies, Duke University, Durham, NC 27706. Joint publication of Woodlands Services Division, MacMillan Bloedel Limited, and Department of Forest Science, Oregon State University. This project was stimulated by discussions with R. H. Waring. The author thanks V. Heinsalu, J. D. Lousier, and C. McCain for their help and R. McNees for technical editing. Paper 1677 of the Forest Research Laboratory, Oregon State University. Manuscript received 21 June 1982.

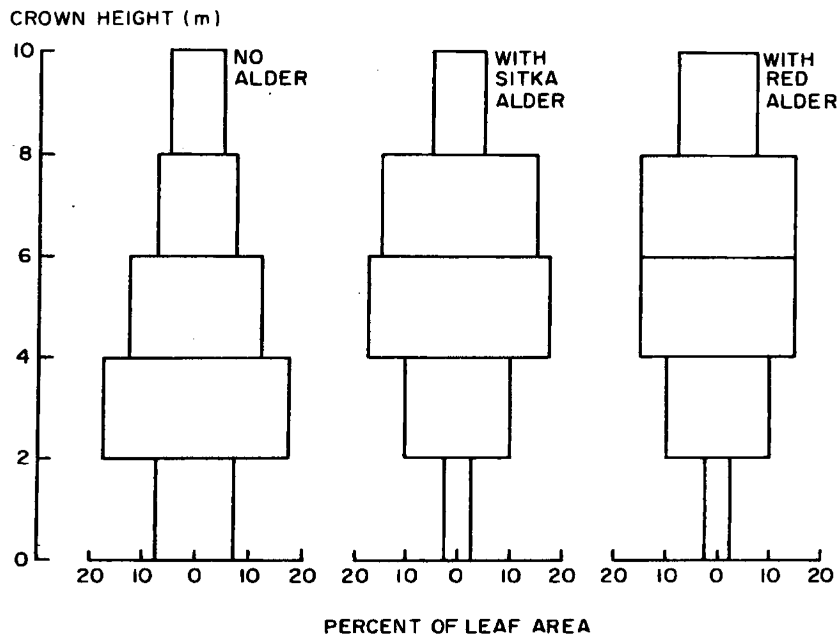

FIGURE 1. Relative distribution of Douglas-fir leaf area by canopy height on sites with and without alder. Averaged from 5 trees/site as described in the Methods section. No significant differences in height were found with this sampling.

Columbia. One site contained no alder, another contained naturally seeded Sitka alder, and the third contained naturally seeded red alder. The area is classified as a *Tsuga heterophylla/Gaultheria shallon-Berberis nervosa* habitat type of the *Tsuga heterophylla* vegetation zone (Franklin and Dyrness 1973). Site index for Douglas-fir without alder is 24 m at 50 years. These ecosystems are described briefly here and in detail in Binkley (1983) and Binkley and others (1984).

Nitrogen accretion was 690 kg ha^{-1} under Sitka alder and 1,490 kg ha^{-1} under red alder. In the absence of alder, the forest floor was a discontinuous 01 layer with a biomass of 7,000 kg ha^{-1}. The site with Sitka alder had a continuous 01 layer with a biomass of 22,100 kg ha^{-1}. Both 01 and 02 layers had developed on the site with red alder, with a combined biomass of 33,600 kg ha^{-1}. Roots were restricted to the mineral soil in the sites without alder or with Sitka alder, but they were present in both the mineral soil and 02 layer on the site with red alder.

The plantation was the result of Douglas-fir seedlings planted in 1958 after the area had been logged and burned between 1952 and 1956. Aerial photographs taken in 1958 indicated that the alder establishment was related to the available seed sources; seeding did not appear to follow any existing soil patterns.

METHODS

Measurements.—In 1981, eight 15-m by 25-m plots were located systematically within the site without alder and eight within the site with Stika alder. The red alder site was large enough to accommodate only four plots. A 10-m buffer separated all plots. Douglas-fir crop trees (exceeding 7 cm dbh) were measured for diameter, sapwood radius, and 5-year diameter increment (1976–80). Five Douglas-firs of average diameter (mean ± 1 cm) were randomly chosen in each site for determinations of leaf area. Each of these trees was divided into 2-m stem sections, and the number of branches per section was recorded. One representative branch was chosen subjectively from each section and returned to the laboratory. All needles were stripped from each sample branch, ovendried, and weighed. Subsamples from each branch were measured with a Li-Cor Model 3100 area meter for projected leaf area.

TABLE 1. Average stocking, size, and 5-year growth of Douglas-fir crop trees on the three sites.[1] *(From Binkley 1983, Binkley and others 1984.)*

Property	Site type		
	No alder	Sitka alder	Red alder
Stocking,			
Crop trees/ha	650b	570ab	540a
Alder stems/ha	—	10,000b	2,200a
Basal area,			
m^2/ha	9.7a	10.9a	10.0a
$cm^2/tree$	149a	191b	185b
Sapwood area,			
m^2/ha	6.7b	6.4b	5.4a
$cm^2/tree$	103a	112a	100a
Leaf area index,[2]			
m^2/m^2	5.4b	5.4b	1.9a
Breast height diameter,			
cm	13.8a	15.6b	15.3b
5-yr basal area growth,			
m^2/ha	4.5a	6.0b	4.6a
$cm^2/tree$	69a	105c	85b

[1] In each row, means followed by the same letter do not differ significantly at $p < 0.05$.
[2] Projected basis, calculated from measured conversion ratios in Table 2. Leaf area indexes for Sitka alder and red alder were 2.2 and 3.5 (Binkley, unpublished data).

Calculations.—The Douglas-fir stem growth per unit of leaf area for each site was calculated by three methods. In Method 1, which was the simplest, basal area growth over the previous 5 years was divided by stem cross-sectional sapwood area at breast height (Waring and others 1980). This method assumes (1) that basal area growth is a suitable measure of stem growth and (2) that ratios of sapwood area to leaf area are the same for all stands being compared. The first assumption would be reasonable for trees of similar size but would introduce bias when average stem sizes differ among stands. Method 2 utilizes stem biomass

TABLE 2. Measured and assumed relationships involving leaf area and leaf biomass of Douglas-fir on the three sites.[1]

Property[2]	Site type		
	No alder	Sitka alder	Red alder
Leaf biomass/sapwood area, g/cm^2			
Assumed	74	74	74
Measured	114b	102b	62a
Leaf area/leaf weight, cm^2/g			
Assumed	60	60	60
Measured[3]	55a	57a	53a
Leaf area/sapwood area, cm^2/cm^2			
Assumed	4,440	4,440	4,440
Measured	6,320b	5,810b	3,290a

[1] For each measured ratio, means followed by the same letter do not differ significantly at $p < 0.05$.
[2] Assumed values from Waring and others (1980).
[3] Weighted average of leaf area/leaf weight ratios for each 2-m canopy section; ovendry basis.

TABLE 3. Douglas-fir indexes calculated by three methods for each of the three sites.[a]

Vigor index (method and basis)	Site type: No alder	Sitka alder	Red alder
1. 5-yr basal area growth/sapwood area, cm^2/cm^2	0.66a	0.71a	0.71a
2. 5-yr stem growth/leaf area; conversion ratios assumed,[b] g/m^2	600a	830b	670a
3. 5-yr stem growth/leaf area; conversion ratios measured, g/m^2	390a	540b	1,360c

[a] In each row, means followed by the same letter do not differ significantly at $p < 0.05$.
[b] Conversion ratios are listed in Table 2.

regression equations (from Gholz and others 1979) to calculate growth of stem biomass and assumed ratios for the conversion of sapwood area to leaf area. Method 2 is, therefore, suitable for situations in which average stem size differs among stands but the ratio of sapwood area to leaf area is consistent. Method 3 uses the same stem growth estimates as Method 2, but conversions of sapwood area to leaf area are based on measured (rather than assumed) values within each stand. This last method is appropriate for comparisons among stands that differ in the ratio of sapwood area to leaf area. The use of one stemwood biomass regression equation for all sites also assumes a constant relationship between tree diameter and height (Gholz and others 1979).

Two-tailed t-tests were used to test for significant differences between means at $p < 0.05$.

Results and Discussion

In 1981, the Douglas-fir canopy on the site without alder was open, with live crowns extending to the ground (Fig. 1). On the site with Sitka alder, the dense alder canopy at 5 to 6 m restricted most of the Douglas-fir crowns to the upper 6 m of the stems. On the site with red alder, Douglas-fir crowns were mixed with the alder crowns for the entire height of the trees.

Although Douglas-fir stocking was similar on the sites with Sitka alder and without alder, the site with red alder contained 15 percent fewer Douglas-fir stems than the site without alder (Table 1). Average Douglas-fir diameter (calculated from average stem basal area) was significantly increased in both sites with alder. Five-year basal area growth was greater on the Sitka alder site than on the other sites.

The measured ratios of leaf area to leaf weight did not differ among the three sites (Table 2) and were very close to the value assumed from Waring and others (1980). However, the measured conversion ratio of leaf biomass to sapwood area on the site with red alder was 65 percent lower than that on the site with Sitka alder and 80 percent lower than that on the site without alder. Consequently, the ratio of leaf area to sapwood area was also much lower for the site with red alder than for the other two sites.

The apparent effects of the alders varied with the method used to calculate the stem growth : leaf area index. Calculations by the first method indicated no difference between sites, whereas the second method indicated highest stem growth : leaf area on the site with Sitka alder (Table 3). However, these two methods revealed no increase in the site with red alder. Calculation by Method 3 resulted in a very different pattern: the rating for the site with Sitka alder was 40 percent higher than, and that for the site with red alder was more than 3 times as high as, the value for the site without alder. The rating by Method 3 was superior for the site with red alder because the ratio of leaf area to sapwood area was lower for this than for the other two sites.

As Method 3 was based on measured (rather than assumed) ratios of leaf area to sapwood area, it provides the most realistic test of my hypothesis regarding the effects of alder on Douglas-fir stem growth per unit of leaf area. Increased soil fertility beneath red alder appeared to compensate for the 65 percent reduction in Douglas-fir leaf area. The 40 to 250 percent increase in stem growth per unit of leaf area on sites with alder is substantially greater than can be explained by increased net rates of photosynthesis. Brix (1981) found that improving Douglas-fir nutrition through fertilization increased net rates of photosynthesis by a maximum of 30 percent. An additional source of photosynthate for stem growth per unit of leaf area might be reallocation within the trees. Several recent studies have documented decreasing belowground photosynthate allocation for fine root production with increasing soil fertility (Santantonio 1979, Keyes and Grier 1981, Waring 1982). Soil enrichment by the nitrogen-fixing alders may have led to decreased fine root production by the Douglas-fir so that a greater proportion of the total photosynthate budget was allocated to stem growth. This proposed mechanism of interaction between nitrogen-fixing plants and associated trees merits direct evaluation.

The application of Waring's tree vigor index to my study sites was complicated by anomalies in conversion ratios of leaf biomass to sapwood area. When based on direct on-site estimates of leaf area, the tree vigor index showed substantial effects of alder on Douglas-fir growth efficiency. This index could be coupled with usual measures of stand growth to manage stands of mixed species for maximum benefit from N-fixation by alder (i.e., minimum reduction in crop tree leaf area and maximum increase in stem growth per unit of leaf area). However, the use of the index for this and other purposes will require a more thorough evaluation of the factors responsible for variations in the sapwood-area-to-leaf-area relationship.

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