IMPORTANCE OF SIZE–DENSITY RELATIONSHIPS IN MIXED STANDS OF DOUGLAS-FIR AND RED ALDER

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(Accepted 21 February 1984)

ABSTRACT


Pairs of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and Douglas-fir and red alder (Alnus rubra Bong.) stands were examined at four locations for patterns in average tree size as a function of stand density. On fertile sites, the mixed stands experienced higher mortality than the pure conifer stands. On infertile sites, the pure conifer stands were well below the maximum tree size and density relationship compared to fertile sites or mixed stands, suggesting under-utilized site resources were available for nitrogen-fixing alder. Planting trials which vary relative densities of these species across gradients in site fertility are needed for a clear assessment of the benefits to be derived from species mixtures.

INTRODUCTION

The performance of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in mixed stands with nitrogen-fixing red alder (Alnus rubra Bong.) varies with site fertility and relative species densities. Binkley and Greene (1984) noted substantial increases in ecosystem production in mixed conifer/alder stands when compared with pure conifer control plots on infertile sites. However, little change was found in mixed stands on fertile sites; conifer growth was reduced proportionately with the addition of alder growth. Relative densities of the conifer and alder may also alter the performance of each species, but experimental density plantings are not available for such evaluations. In this paper I examine the tree size and stocking densities of the stands reported by Binkley and Greene (1984), and focus on the importance of density and mortality in managing forest stands of mixed species.

METHODS

Pairs of stands, each with a pure conifer portion and a mixed alder/conifer portion, were examined at four locations described more fully in Binkley...
(1983) and Binkley and Greene (1984). The Cascade Head, Oregon site was very fertile with a site index of 40 m at 50 years for Douglas-fir. Naturally established red alder and conifer (mostly Douglas-fir, with some Sitka spruce (Picea sitchensis (Bong.) Carr.) and western hemlock (Tsuga heterophylla (Raf.) Sarg.)) saplings were thinned at age 8 (in 1935—1937) to produce 0.2-ha plots of pure alder, pure conifer and mixed alder/conifer (Berntsen, 1961). The second fertile site, located at Skykomish River, WA, had a Douglas-fir site index of 45 m at 50 years. The removal of naturally-seeded alder seedlings from one-half of a 2-year-old plantation in 1960 produced small (0.1 ha) plots of pure conifer and mixed alder/conifer. An infertile site at Wind River, WA (site index 25 m at 50 years) provided an older pair of stands, where a 20 m wide fire break of red alder was planted through a Douglas-fir plantation in 1928 (Tarrant, 1961). A younger pair of stands developed after red alder seedlings established naturally in a 1958 Douglas-fir plantation (site index 25 m at 50 years) on Mt. Benson, Vancouver Island, B.C.

Complete plot tallies of all stems greater than 2.5 cm diameter at breast height were made at Cascade Head at five times between the ages of 19 and 53. The Wind River stands were measured twice, at ages 27 and 48, and the two youngest pairs of stands were assessed once at age 23.

Tree size and stocking density were examined as the average tree biomass relative to the number of stems per hectare. When plotted on logarithmic axes, this ‘self-thinning’, or density-dependent relationship has been found to approximate a −3/2 slope (see Harper, 1977; Mohler et al., 1978; White, 1980; Pickard, 1983).

RESULTS AND DISCUSSION

The thinning treatments which established the Cascade Head plots resulted in a wide range of densities (Fig. 1), from about 1600 stems per ha in the pure conifer plot at age 19 to 4000 stems per ha in the mixed plot. Mortality was heavy in the densely-stocked pure alder and mixed plots, but remained light in the pure conifer plot until about age 30. Net primary production was similar among these stands, but lower mortality in the pure conifer plot resulted in a greater biomass accumulation rate (Binkley and Greene, 1984). The lines in Fig. 1 suggest that these differences in mortality were attributable largely to high stand density and not simply an effect of alder. The maximum size/density relationship appeared similar for the pure conifer and mixed stands but was lower for the pure alder stand.

Expanding the analysis to the other sites (Fig. 2) revealed a size/density pattern coincident with the site fertilities. The fertile Skykomish stands both fell near the ‘−3/2 ceiling’ determined graphically for the Cascade Head stands. The pure conifer stand at Skykomish appeared to exploit site resources fully; the addition of alder therefore reduced Douglas-fir stocking and growth (Binkley and Greene, 1984). Conversely, the pure conifer stands
at Wind River (ages 27 and 48) and Mt. Benson (age 23) fell far below the self-thinning ceiling, indicating a potential availability of space and resources for the added alder. The mixed stand at Wind River carried larger trees at higher densities than did the pure conifer stand.

The maximum tree size-density relationship appeared lower for the pure alder stand at Cascade Head than for the mixed alder/conifer or pure conifer stands, and it appeared lower for the pure conifer stand at Wind River than for the pure conifer stand at Cascade Head site. Greater replication of sites is needed before firm conclusions are warranted, but some speculation can be advanced for the mechanism underlying the observed mortality patterns. Harper (1977) proposed that dominant individuals within a population exploit a disproportionate share of site resources, causing the net assimilation rate of suppressed plants to approach zero. This idea can be expanded to include the energy costs of maintaining aboveground biomass in a manner consistent with the patterns from all sites in this study. Red alder fixes sub-
Fig. 2. Average tree weight as a function of stand density at the fertile Skykomish site and the infertile Wind River and Mt. Benson sites. Ages given at sampling points, b equals slope between samplings.

Substantial amounts of nitrogen at a high energy cost even at the fertile Cascade Head sites (Franklin et al., 1968). Therefore, the lower self-thinning ceiling in the pure alder stand could derive from the energy consumed in N-fixation increasing the total respiration of red alder trees relative to Douglas-fir trees of comparable size. The differences in maximum size-density relationships for the pure conifer stands on infertile and fertile sites could be due to the belowground energy requirements for maintaining aboveground tissues. Keyes and Grier (1981) compared net primary production and allocation in two 40-year-old stands of Douglas-fir. On an infertile site, 50% of a total ecosystem production of 15.4 t ha⁻¹ year⁻¹ was allocated belowground, as compared to a fertile site production of 17.8 t ha⁻¹ year⁻¹ with 25% allocated belowground. If the allocation to roots is viewed as an energy cost of maintaining aboveground tissues, then suppressed trees on infertile sites might approach zero net assimilation rates at a lower size-density relationship than on fertile sites.
Future studies on the yields of conifers in mixtures with alder will need to separate density-related effects from species-interaction effects, and should also account for patterns in energy allocation. Such an approach would allow a clearer examination of the degree of competition and niche differentiation between the species across gradients in site fertility.

ACKNOWLEDGEMENTS

The concepts examined here were outlined in discussions with D. Perry. I thank J. Franklin and S. Greene of the U.S. Forest Service for the use of the Cascade Head records, and D. Perry, S. Hart, N. Christensen and two anonymous reviewers for helpful comments on the manuscript.

REFERENCES