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STAND DEVELOPMENT IN WHITEBARK PINE WOODLANDS

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ABSTRACT

Analysis of density data from stands in the Northern Rocky Mountains shows that, while seedlings establish at the rate of over 1,000/ha x year in whitebark pine-grouse whortleberry (Pinus albicaulis-Vaccinium scoparium) *forests of all ages, stem numbers in the canopy thin to 400 at 30 years, 150 at 200 years, and 100 at 300 to 600 years. Indices of productive potential, cover, and total circumference rise to an asymptote at about 100 years. Total basal area rises from 0 to 60 m^2/ha at about 200 years, the aggregate basal area of trees with diameters over 20 cm rises from 0 to 40 m^2/ha at about 250 years, and tree height maximizes (12 m) at 200 years. It is hypothesized that further growth in productive potential (that is leaf and/or root area) is prevented by limited supplies of water or a nutrient, further growth in basal area is prevented by lack of a nutrient (probably not carbon, hydrogen, oxygen, or nitrogen) and further growth in height is prevented by scarcity of water.*

INTRODUCTION

Ecologists often describe plant succession by comparing communities existing on a series of sites that are considered environmentally identical, but differ widely in age (Boggs and Weaver, in preparation; Cooper 1923; Cowles 1899; Crocker and Major 1955; Olsen 1958). Chronosequence studies in secondary seres in the whitebark pine-grouse whortleberry (*Pinus albicaulis-Vaccinium scoparium*) environments (= habitat types or HT's, Arno and Weaver, this proceedings; Pfister and others 1977; Weaver and Dale 1974) have demonstrated little change in understory vegetation (Weaver and Dale 1974), large increases in biomass (Forcella and Weaver 1977), and small increases in productivity (Forcella and Weaver 1977, 1986). Field data from these studies are reworked here to (1) describe the dynamics of tree establishment, stand closure, and competition and (2) to generate hypotheses to explain the control of productivity, maximum standing crop, and tree height.

METHODS

To characterize succession in whitebark pine woodlands we compared 47 stands of diverse ages in one environmental type (*Pinus albicaulis-Vaccinium scoparium* [Daubenmire and Daubenmire 1968; Pfister and others 1977]). Each stand was aged by coring three trees representative of the dominants, that is, trees that were neither new reproduction nor representatives of an earlier generation; the ages ranged from 29 to 643 years. The stands sampled were broadly representative of stands found in Montana, Wyoming, and Idaho (Forcella 1978; Forcella and Weaver 1977; Weaver and Dale 1974).

Tree densities were estimated by counting individuals in representative areas at each site. Trees in the 19 stands considered in the first study (Weaver and Dale 1974) were sampled with a 500-m^2 circular plot (r = 12.6 m). To guarantee a complete count, we counted seedlings in a 1- by 30-m plot whose center coincided with that of the circle. Trees and seedlings in the 28 stands sampled in the second study were counted in a 600-m^2 area consisting of three 6.67- by 30-m plots (Forcella and Weaver 1977).

Trees in the first and second studies were tallied into 10-cm and 5-cm diameter at breast height (d.b.h.) classes, respectively. These data were used directly in comparison of seedling survival among stands of differing age. Total circumferences were calculated by assuming that all trees in a size class had a diameter equal to the midpoint of the class, multiplying for each individual ($\pi \times D$), and summing across individuals. The use of midpoints introduced a downward bias in the smallest size classes in a stand and an upward bias in the largest size classes. Calculation of total basal areas also involved the use of midpoints, multiplication ($\pi \times r^2$), and summation across all trees in the plot. We did not correct for the additional small error due to the fact that the basal area of a midpoint tree is less than the average basal area of trees at the top and bottom of that size class.

Canopy cover was estimated as the percentage of 30 points, observed overhead through a vertical periscope (Weaver and Dale 1974), which were covered by trees. Tree heights were measured with a Bitterlich "relaskop."

Cone production in the year of observation was estimated by multiplying an estimate of branch tip density

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in the canopy (#/m^2) by the average number of cones on a sample of branch tips. Cone production in earlier years was estimated by multiplying branch tip density by estimates of cone production made from counts of cone scars at nodes representing the previous 4 years (Weaver and Forcella 1986). Seed production was estimated by multiplying cone number by the average number of seeds in a cone (75 ± 28, Weaver and Forcella 1986).

RESULTS AND DISCUSSION

The dynamics of *Pinus albicaulis* in whitebark pine woodlands were studied by examining a chronosequence based on 47 stands with ages ranging from 29 to 650 years. Readers preferring different units will remember that there are 10,000 m^2/ha and 2.47 acres/ha.

Seedling Establishment

Cone production rose from 0 cones/ha in newly established stands to an average of about 10,000 cones/ha in stands over 100 years old. Figure 1a presents 5-year averages of cone production. Cone production was variable among stands (for example, 0.5 to 5 cones/m^2 annually in the 100- to 200-year stage) as well as among years (Weaver and Forcella 1986). If each cone contained 75 seeds (Weaver and Forcella 1986), seed production ranged from 370 to 3,700 seeds/ha annually in stands over 150 years old.

Median seedling density was 1,000 to 1,500 seedlings/ha during the first 300 years of stand development (fig. 1b) and quite variable among stands in any age class (for example, 0 to 5,000 among 100- to 200-year communities). The large seedling number in young stands must be due to long distance dispersal, probably by Clark's nutcracker (Hutchinson and Lanner 1982; Linhart and Tomback 1985), because whitebark pine seeds are both too heavy for wind dispersal and unlikely to have survived in the seed bank since the stand replacing event (Harper 1977). The consistency of seedling densities across stands of increasing age suggests that nutcracker cache density may not vary significantly among stands with different ages.

Competition and Thinning

Total whitebark pine density falls exponentially from 4,000 individuals/ha at 30 years to 1,500 at 200 years and 1,000 at 400 years (fig. 1d). We attribute this decline to self-thinning; while seedlings established with mean areas of 2 to 3 m^2 cannot compete significantly, 200- to 300-year-old trees apparently require mean areas averaging about 10 m^2. The decline in tree density with time is exponential because the growth of young trees is exponential and the area saturated by a tree is proportional to its size.

Seedling fate is a second indicator of the time of resource (that is, space) saturation in developing whitebark pine woodlands. Seedlings establish at rates of 1,000 to 1,500 individuals/ha^2 in stands of all ages (fig. 1b).

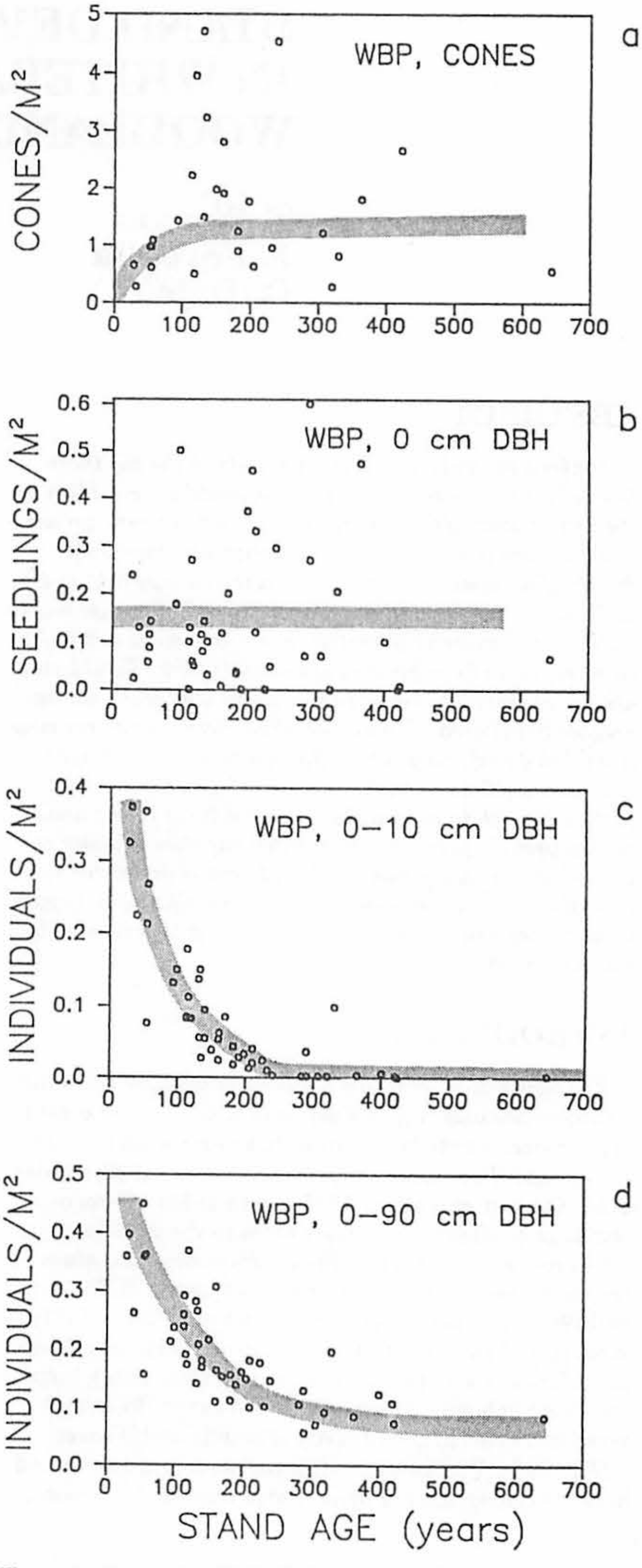

Figure 1—Change in whitebark pine density with stand age (0 to 650 years): (a) cones with an average of 75 seeds, (b) seedlings, (c) 0- to 10-cm d.b.h. saplings, and (d) all individuals. While seedling number remains constant, establishing trees (0 to 10 cm d.b.h.) fail in stands older than 250 years, established trees self-thin through 350 years. The line is hand-fit through medians calculated across centuries.

In stands less than 100 years old many individuals reach heights of 1.5 m, as indicated by tree counts in the 0- to 5- and 0- to 10-cm d.b.h. classes (fig. 1c). The simultaneous presence of seedlings and absence of 0- to 5-cm (and 0- to 10-cm) d.b.h. trees in stands older than 150 (250) years indicates that, while there are noncompetitive "safe sites" for seedlings in all stands, the "safe sites" in stands older than approximately 100 years are not large enough to support growth from the seedling to the sapling stage. Since the probability of reproductive success is diminishingly small for those seedlings that regularly establish in clearings of less than 10 m^2, we conclude that the sites are, in fact, only apparently "safe." That is, tree establishment is only apparent and its appearance is an artifact of the short time period humans easily comprehend.

The sum, across all trees in the stand, of tree circumference is a third indicator that resource use becomes complete in most whitebark pine woodlands at about 100 years. Circumference is a good index of leaf area because it is strongly correlated with the amount of vascular tissue supplying water and nutrients to the leaves (Marshall and Waring 1986; Shinozaki and others 1964). It must be an equally good index of root area because it is strongly correlated with the amount of phloem delivering photosynthate to absorbing organs. Whether saturation is due to canopy closure (full utilization of light) or complete exploitation of the soil resources (water and minerals), we can expect total circumference to grow exponentially (or, at least linearly) from stand establishment to near site saturation and then level out. Our expectation is realized (fig. 2a): initial circumference (even under very high seedling densities) is near 0, rises to about 750 m/ha (= 0.1 m/m^2) soon after 100 years, and remains constant through the next 500 years. Regardless of whether the population is light or water-nutrient limited, growth of one individual after saturation (100 years in whitebark pine) can only occur when resources are released by the death of another individual (Valentine 1988).

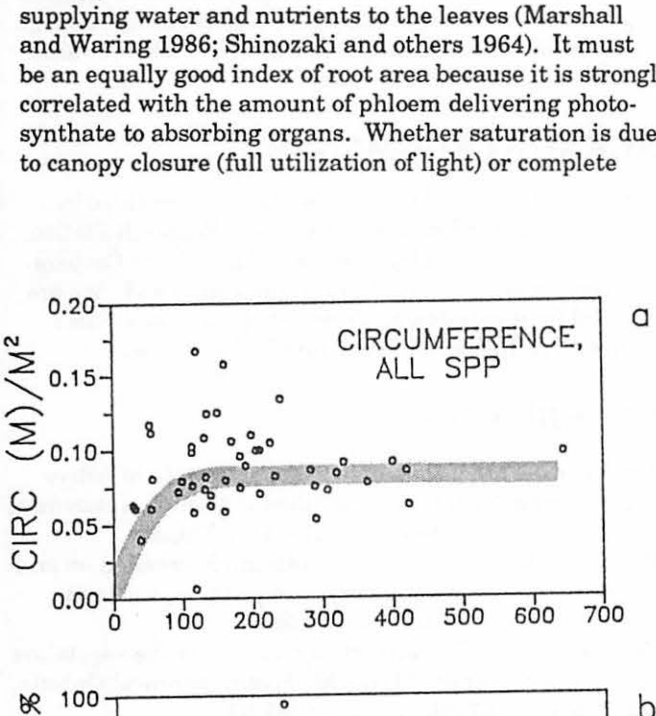

Figure 2—Indices of resource saturation and productive potential (a) aggregate circumference and (b) canopy cover increase to about 150 years and equilibrate there. The line is hand-fit through medians calculated across centuries.

Factors Limiting Production

Community production can be limited by resource availability. Among resources, lack of heat (temperature) surely limits production in the winter through its influence on both water-nutrient availability and enzyme activity. Warmer and moist conditions may result in nutrient limitation in the spring (Weaver and Forcella 1979), and relatively dry conditions probably cause water limitation in the summer (Weaver 1980).

The productive potential of a community also depends on its "factory size"—its leaf or root area. Factory size might be limited by either light or a soil (water or a nutrient) resource. While the former is often assumed (and as a result, trees are often ranked according to their "shade tolerance"), ditching tests suggest that root competition is often the actual controlling factor (Watt and Fraser 1933). Whitebark pine woodlands consist of open stands with an initial canopy cover of 0 percent, which grows to a limit of 60 percent in 100 to 150 years, and remains constant at that level for the next 200 to 300 years (fig. 2). Since, in saturated stands, canopy coverages are only 60 percent and since forest floor light levels (200 to 1,600 $uEm^{-2}s^{-1}$) are well above those required for whitebark pine photosynthesis (200 $uEm^{-2}s^{-1}$ at compensation and 1,000 $uEm^{-2}s^{-1}$ at saturation, Jacobs and Weaver [this proceedings]), we deduce that stand saturation in whitebark pine is more likely due to complete exploitation of a soil resource (water or a nutrient element) than to exhaustion of the light supply.

Factors Limiting Maximum Standing Crop

The rate of production is initially low, grows with increases in foliage cover, and halts at stand saturation (about 100 years), because leaf or root surfaces are maximized. In contrast, basal area accumulation continues to a maximum (60 m^2/ha) at 200 to 250 years and levels there (fig. 3a). The upper limit for standing crop must be due to one of three factors: excessive respiratory mass, a resource limit, or a structural limit. First, the most immediate limiting factor is probably the accumulation of a respiratory mass sufficient to consume all current photosynthesis (Odum 1969). Second, since the canopy is not saturated at maturity, however, the ultimate limiting factor must be either a nonlight resource or a structural deficiency. The limiting factor cannot be temperature

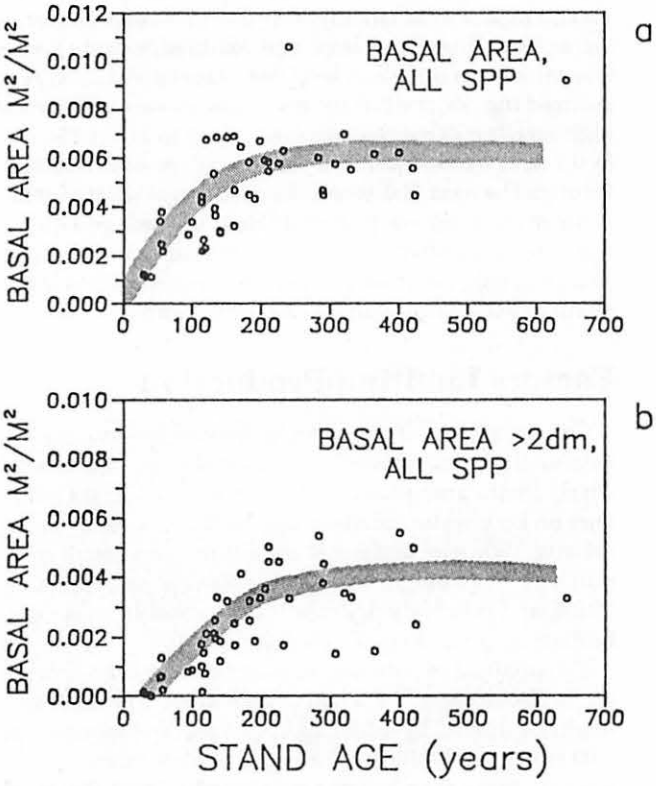

Figure 3—Standing crop, indexed by basal area (a) total and (b) trees larger than 20 cm d.b.h., increases to about 250 years and equilibrates. Tree heights equilibrate at about 200 years (12 M, Weaver and Dale 1974). The line is hand-fit through medians calculated across centuries.

because air temperature does not change systematically during stand development and, while soil temperature might be reduced by canopy shading, if this effect were controlling it should be maximized at canopy closure (100 years, not 250 years). The limiting factor cannot be water, because, while drought may stop growth each summer, precipitation in the following winter and spring will allow resumption of growth (not observed) if no other factor limits. The limiting resource is most likely the supply of an important nutrient—and probably not carbon, hydrogen, oxygen, or nitrogen, because supplies of these elements are constantly delivered from the atmosphere. The reader may question the inclusion of nitrogen in the list of elements available from the atmosphere; we do so because we believe researchers underestimate both nitrogen losses (production of decomposition-recalcitrant organic matter, and fire) and compensating nitrogen imports (Aradottir 1984; Boggs and Weaver, in preparation; Johnson and others 1983; Weaver and others 1978). Third, a structural limit would exist if nutrient supplies were sufficient to allow the growth of larger trees with the consolidation of more productive potential, but physical damage prohibited it. We doubt that it is physical control because the trees in whitebark pine woodlands can be relatively large, because little wind deformation occurs, because wind-snow breakage is uncommon, and because seedlings occupying openings fail to establish.

Total biomass depends on tree height as well as basal area. Tree heights increase linearly to 12 m at 200 years and then level off (Weaver and Dale 1974). Maximum tree height is most likely determined by water availability at the shoot tip and is therefore a product of the drying power of the air, the conductivity of the stem, and the water supplying power of the soil.

Harvestable Production

With few exceptions (Losensky, this proceedings), the height and form of whitebark pine trees encourage the reservation of forests dominated by it for wildlife, watershed cover, recreational, and esthetic purposes rather than timber production. If logging is contemplated, the manager needs a measure of basal area against time for trees large enough to log (for example, over 20-cm d.b.h.). Figure 3b shows that the basal area of trees large enough to log levels later (about 250 years) and at a lower value (40 m^2/ha) than total basal area.

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Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from R. Brown)—Do you know of studies of water relations—for example, the diurnal course of plant water status or transpiration rates—for whitebark pine?

A.—While Tranquillini (1979) provided extensive discussion of water relations in closely related *Pinus cembra*, I know of no studies of water relations in whitebark pine. In this paper I have speculated that water stress limits late summer production, but not maximum standing crop, in whitebark pine woodlands. In answering your question (of my climate paper) about factors limiting the distribution of whitebark pine I speculated that the southern limit of the tree's range might be set by summer drought.

Q. (from M. Cole)—According to your basal area graphs, standing crop is initially zero and increases asymptotically with time. The graphs also show considerable variance. Do you think the variance could be explained by plotting a series of site class curves in each graph?

A.—The variance you observe strongly suggests that while we selected stands representative of the *Pinus albicaulis-Vaccinium scoparium* woodland climax there is "site class" variance in the indicated habitat type. While it would be well represented by site class curves, I have no independent site class data to enable me to draw such curves; can you suggest an approach I haven't thought of?