BIOMASS AND PRODUCTIVITY OF THE SUBALPINE *PINUS ALBICAULIS* – *VACCINIUM SCOPARIUM* ASSOCIATION IN MONTANA, USA*

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Keywords:

Biomass, *Pinus albicaulis*, Productivity (net primary), Root mass, Subalpine forest, *Vaccinium scoparium*, Woodland

Introduction

Natural resource management has been and remains a significant problem in the western United States of America. In at least some geographic areas, vegetation classification is a constructive precursor to effective management. The values of a classification lie, in part, in their applicability to estimation of 'site potential', i.e. the potential taxa, productivity and stability of specific communities within the classificatory scheme. A significant portion of the Pacific Northwest's climax vegetation has recently been classified. Pfister (1976) lists all completed and on-going classifications (excepting Hickman 1976) in the western USA.

Now that these classifications are more or less complete, and with a management perspective in mind, what are the current and near future research priorities? In conjunction with continual reassessments of the classifications, we believe that they might include studies of (1) vegetation mapping, (2) vegetation change, (3) biomass and productivity and (4) nutrient cycling. That resource managers need immediate, coherent data, or at least 'best guesses' from the research groups on these subjects has been

* Idiotaxonomy follows that of Hitchcock & Cronquist (1973). There presently is no formal, Latinized syntaxonomical system for the Pacific N.W. of the USA.

The summer field work was funded by the Intermountain forest and Range Experiment Station, U.S. Forest Service, under Contract No. 12-11-204-12, Suppl. No. 33. Funds for computer analyses were generously provided by the Dept. of Biology, Montana State University, and S. Holland (University of California).

The authors thank J. V. Basile, J. Major, R. H. Rumely, the editors H. Lieth and R. H. Whittaker, and a reviewer for *Vegetatio* for their helpful comments.

clearly stated in a recent Institute of Ecology Report [1974, 4(3): 3].

Relatively little research has been published on the biomass and productivity of Rocky Mountain forests (Moir 1972, Johnstone 1971, Whittaker & Niering 1975, Landis & Mogren 1975, and Hanley 1976). This paper deals with the above- and belowground biomass and productivity of the *Pinus albicaulis* Engelm.-*Vaccinium scoparium* Leiberg association. Since we studied 14 stands, we were able to determine the range of values expected in typical stands, and relate some of the variance to stand basal area and age. The mass and production of each stand was not, however, studied in depth. Samples of stand components were taken from each stand and regression equations developed for prediction of mass and productivity (ultimately on a unit area basis). The validity of this approach is a function of the initial regression equation statistics. Though error is of course present in the equations, we feel that accurate predictions of biomass and reasonable estimates of productivity are possible. We hope that the results reported here will contribute to a basis for the management of these forests.

The Pinus albicaulis-Vaccinium scoparium association

An association, as we have used the word here, is the sum of easily recognized, floristically and structurally repetitive stands of vegetation. The term 'habitat type' has been adopted as a classificatory unit for land by several researchers in the Pacific Northwest. Though the inclusion of habitat into the definition of association (Flahault & Schröter 1910, in Braun-Blanquet 1964) is appealing, we have avoided its use in this report because the abiotic factors of an organism's environment are not easily documented by field observations – except circularly through floristics

and physiognomy.

The *P. albicaulis*-*V. scoparium* association is an easily recognized, geographically repeatable, subalpine forest of noncalcareous substrates in the northern Rocky Mountains. Its vegetation, soil, soil parent material and climate have been characterized by Weaver & Dale (1974). The stands of this association are normally even-aged and may attain relatively great ages (600 years +). The site index (tree height from time of establishment) is about 8 m at 100 years age. The understory is typically dominated by the low-growing (10–30 cm) *V. scoparium* (Figure 1). Vegetational change appears to be cataclysmic rather than 'successional' (cf. Loucks 1970). Fire scarred stumps and/or soil charcoal are always found in the stands. Avalanches and wind-throwing may also affect vegetation cycling in this association.

Tree seedling establishment under the arboreal canopy

Fig. 1. A 150 year old *Pinus albicaulis*-*Vaccinium scoparium* community. The trees are about 10 m in height and 20 cm dbh. Note the carpet of *V. scoparium*, and the absence of prominent herbs. The height of the shovel above the ground is about 1 m.

is meager. Occasionally, the few *Abies lasiocarpa* individuals in the understory outnumber those of *P. albicaulis*. These small *Abies* often result from the layering of an older tree. Both Daubenmire & Daubenmire (1968) and Pfister et al. (1974) recognize an *A. lasiocarpa* (*P. albicaulis*)-*V. scoparium* habitat type. The dominance of *P. albicaulis* in our stands might be due to (1) a very slow (600 years +) successional replacement of *P. albicaulis* by *A. lasiocarpa*, (2) physical (eg. climatic) limitation of *Abies* on *P. albicaulis* sites, or (3) biological limitations to *Abies* such as ubiquity (100%, constancy) of the *Abies* pathogen *Pucciniastrum geoppertianum* (Boyce 1961, Faull 1939) in the *P. albicaulis*-*V. scoparium* association.

Though *P. albicaulis* is not generally recognized for its merchantable qualities (until recently, see Day 1967, Kaspar & Szabo 1970, Keenam et al. 1970), the *P. albicaulis*-*V. scoparium* association is valuable for its aesthetic qualities, for wildlife food (large edible pine seeds, *Vaccinium* fruit and assorted forages; see Weckwerth 1971, Mealey 1975) and for watershed protection.

Sampling methods

Vegetation

Fourteen stands of the *P. albicaulis*-*V. scoparium* association were sampled in 7 mountain ranges throughout southwestern Montana (the Madison, Tobacco Root, Elkhorn, Big Belt, Little Belt, Castle and Absaroka Mountain Ranges). Each stand was sampled with three 6.67 × 30 m (0.06 ha) plots which were placed parallel to the slope of the stand. All trees within these 200 sq.m plots were tallied by species into 5 cm dbh size-classes (trees less than 1.35 m height were considered seedlings). Shrub and herb coverages were estimated in 10% classes in sixty 1 sq.m quadrats which were placed in two contiguous 1 × 30 m transects along the axis of each plot. These transects were large enough to encompass the contagious distribution of the shrubs (Forcella 1975). The canopy coverage of the tree layer was measured with a vertical periscope and was considered to be equal to the percentage of 30 points (at 1 m intervals) covered along the axis of each plot. The vascular plant species encountered within each plot were recorded, collected and filed at the Herbarium, Montana State University.

Biomass and productivity

The aboveground portions of 34 *P. albicaulis* trees, 1–37 cm dbh, 1.35–18.0 m height and representative of the

stands in which they grew, were felled, sectioned into component parts, and weighed in the field with hand-held scales. The roots wider than 1 cm diameter of 9 trees were excavated and weighed also. Sections of each component part of the tree were wrapped in polyethylene and transported to the laboratory for annual ring width, ring number and wet weight/dry weight analyses. Samples were oven dried at 60 °C to constant weight. Wood (xylem) production of 26 of the trees was estimated by calculation of the mean annual parabolic volume increment and conversion to mass increment by the density factor of 0.42 g/cm³ (Peattie 1953, Keenam et al. 1970). Radial increments used in calculating volume increment were the annual (1969–1973) means measured at 8 equidistant circumferential points, perpendicular to the axis of growth on dbh cross-sections. Radial increments of bole cross-sections above breast height were not analyzed consistently; where they were measured, they compared favorably with those at 1.35 m. A sample of leafy twigs from each of 16 trees was divided into annual increments for determination of leaf production and longevity. Phloem and bark production were not measured directly. The combined production of these two tissues was estimated through a series of assumptions described in Appendix 1. Briefly, there appears to be a linear relationship between bark mass and tree basal area (BA). Hence changes in BA (annual increment) will have corresponding increments in bark mass (annual production).

At the end of the 1974 growing season, twenty-nine 0.5 sq.m quadrats of the understory vegetation were clipped from several of the stands to estimate understory biomass and production. Twig and leaf production of *V. scoparium* were estimated by separation of the leaves and current twigs from the main shoots; these plant parts were then dried at 60 °C and weighed. Diameter increments of the numerous small (less than 2 mm diameter) woody shoots of this shrub are small; and because of the shrub's low stature (10–30 cm), the mass increment of these stems is probably minute (cf. Andreyashkina & Gorchakovskii 1972) and was not measured, but it was estimated from the work of Whittaker & Woodwell (1969) as described later. The dead twig mass of *V. scoparium* was measured separately. Herbaceous production was considered equal to its standing crop, though some ephemerals were senescent at the sampling date.

For a simple estimate of biomass of roots and rhizomes less than 1 cm diameter, eleven 1 sq.m quadrats from 5 stands were excavated to 0–10 and 10–40 cm depths. These soil depth-intervals were chosen because the rhizomes of

V. scoparium are confined entirely to the upper 10 cm of soil, and root material was not readily apparent below 40 cm. All roots and/or rhizomes greater than 1 mm diameter were sieved from the soil and separated by species. To estimate the mass of fine roots (< 1 mm) the sieved soil was evenly redistributed throughout the excavation and 1/16 of it (to both 10 and 40 cm depths) was transported to the laboratory for further sieving and washing; these roots were not separated by species.

Regressions, estimates and stand totals

Untransformed and logarithmic (base 10) transformations of the biomass and production data were regressed against the easily measured plant parameters, dbh and shrub coverage. The estimates obtained from the resulting regression equations were substituted for original stand data (tree density by size class, or shrub coverage) to determine mass and production on a unit area basis. For tree species other than *P. albicaulis*, and for the few individuals of *P. albicaulis* greater than 37 cm dbh in the samples plots, the biomass regression equations of Weaver & Forcella (1977) were used. The productivity-dbh equations were extended somewhat beyond their data limits (*P. albicaulis*, 1–37 cm dbh) to account for the trees mentioned above.

The independent variables used in the regressions were chosen for their ease of field and laboratory measurement and were not necessarily those that gave the best fit to the data. For example, the independent variable 'dbh × tree height' gives a slightly better fit to regressions of mass and production than simple 'dbh'. However, dbh was used for correlation with these data because it was not feasible to make height measurements for every tree in every stand.

After unit area mass and production were calculated for each stand, the two sets of variables were regressed against stand basal area and arboreal canopy coverage, and median shrub coverage for the tree and shrub synusiae respectively.

There is an inherent bias in logarithmic, sum of least squares regressions due to the skewed distribution of the (arithmetic) squared deviates around the mean regression line (Baskerville 1972, Beauchamp & Olson 1973). The antilogarithmic conversion of the regression equation to arithmetic units should thus result in systematic underestimation. Brownlee (1967, as cited by Baskerville 1972) provides a method for correcting the arithmetic estimates. 'Corrected' estimates of *P. albicaulis* data were graphically compared to the original regression estimates and to the original data. The degree of difference between the cor-

rected and original estimates is a function of the magnitude of the squared deviations of the original data. In poorly correlated regressions (leaf mass-dbh) the difference between the corrected and original estimates is large, but this is likely due to the high variation in mass of component parts of the largest sampled trees (Whittaker et al. 1974). In highly correlated regressions (aboveground mass-dbh), corrected estimates appear to overestimate the original data significantly. Madgwick & Satoo (1975) compared the actual standing crops to 'corrected - unbiased' logarithmic regression estimates, of very small forest stands. The corrected regression estimates consistently overestimated the actual standing crop (ibid., Table 3, p. 1449).

Corrected logarithmic regression estimates have not been used in this report and the resulting calculations might therefore be considered mean to minimal estimates.

Results and discussion

Vegetation

P. albicaulis always provided over 75% (usually 85–100%) of the basal area (BA) in the stands studied; other contributors were old 'wolf' trees of *Pinus contorta latifolia* and infrequent individuals of *Abies lasiocarpa* and *Picea engelmannii*. Mean BA's for the stands (3 plots/stand) range from 25 to 108 sq.m/ha (c.v. 20% or less). This range of BA is similar to that of many mature Rocky Mountain forests studied by Daubenmire & Daubenmire (1968) and Whittaker & Niering (1975), but smaller than stands of the *Tsuga heterophylla* series (100–500 sq.m/ha, Daubenmire & Daubenmire 1968) and of the Pacific Coast forests (100–300+ sq.m/ha, Franklin & Dyrness 1973, Westman & Whittaker 1975). Canopy coverage of the

Table 1. Individual tree and stand biomass and productivity regression statistics for *Pinus albicaulis* and associated species. Equations are in the forms: $y = a + bx$ and $y = a + b \log_{10} x$.

REGRESSION STATISTICS							
Dependent variable (y)	r	e	E	n	Slope (b)	Y-intercept (a)	Independent variables (x)
Tree Mass (kg):							
Leaves	0.9174		1.499	32	0.8755	-1.429	Log [dbh(cm)] ²
Wood 1-10 cm	0.8522		1.555	32	0.6742	-0.431	" "
Wood 10+ cm	0.9592		1.375	28	1.4170	-1.850	" "
Wood 1+ cm	0.9872		1.238	32	1.2350	-1.244	" "
Aboveground	0.9876		1.224	32	1.1890	-1.082	" "
Belowground 1+ cm	0.9971		1.151	09	2.1070	-1.285	Log dbh (cm)
Wood Volume (m ³):	0.9916		1.194	26	2.9010	-4.576	" "
Tree Productivity (kg/yr):							
Leaves	0.9613		1.330	17	1.6750	-1.966	Log dbh (cm)
Bole	0.7271		2.956	26	2.4420	-3.564	" "
Bole Volume (m ³):	0.7271		2.956	26	2.4420	-6.183	" "
Stand Mass (kg/m ²):							
Leaves	0.9474	0.0027		14	0.0270	-0.132	Stand Basal Area (m ² /ha)
Wood 10+ cm	0.9437	0.0386		14	0.3820	-7.029	" " " "
Bark	0.8479	0.2273		14	0.0161	0.401	" " " "
Belowground	0.9911	0.0039		14	0.1010	-0.453	" " " "
Total Tree	0.9678	0.0446		14	0.5940	-7.152	" " " "
Stand Bole Volume (m ³ /m ²):	0.9437	0.0071		14	0.0009	-0.016	" " " "
Stand productivity (kg/m ² /yr):							
Leaves	0.9815	0.0003		14	0.0045	0.2069	Stand Basal Area (m ² /ha)
Wood 10+ cm	0.9543	0.0002		14	0.0019	-0.2570	" " " "
Belowground	0.9106	0.0002		14	0.0013	0.2825	" " " "
Total Tree	0.9917	0.0003		14	0.0077	0.2321	" " " "
Wood	0.9659	0.0115		14	0.0678	-0.1210	Leaf Mass (kg/m ²)
Stand Basal Area (m ² /ha)	0.8113	13.5000		28	0.9620	0.1710	Canopy Coverage (%)

tree layer ranged from 36 to 95% (c.v. 25% or less) and was correlated with BA ($r = 0.81$, Table 1). Such open canopies suggest 'woodland' conditions, but as will be shown later, tree densities and biomasses are suggestive of a forest association.

Median coverage of *Vaccinium scoparium* ranged from 12 to 67% (cf. Weaver & Dale 1974). These shrubs are distributed in patches on the forest floor (Forcella 1975), and stands on steep (35%+) slopes support considerably less *V. scoparium* than those of more level topography (slope vs. coverage, $r = -0.50$). This lack of shrub coverage, in small patches or entire stands, may be due to snow drifts (Knight 1975), snow movement, or solifluction.

Herb coverage was generally less than 5% and was not noticeably correlated with shrub coverage, though the differing phenologies of the taxa may obscure any relationship. Herbaceous species with high constancies were: *Arnica latifolia* 93%, *Carex rossii* 71%, *Lupinus argentea* 64%, *C. geyeri* 57%, *Poa nervosa* 57%, *Hieracium gracile* 57%, *Epilobium angustifolium* 57%, *Potentilla diversifolia* ssp. *diversifolia* 50% and *A. cordifolia* 50%. The shrub, *Juniperus communis* ssp. *montana*, with negligible cover, occurred in 57% of the stands. No annual species were observed in our stands.

Regressions

The biomass and productivity regressions generated for *P. albicaulis* are remarkably similar to those of taxa presented by Whittaker et al. (1974), Whittaker & Woodwell (1968) and Weaver & Forcella (1977). The regression statistics, independent variables and number of data points for all regressions used are listed in Tables 1 and 2. The correlation coefficients range from 0.72 to 0.99 and all are significant at the 99% level. Better evaluations of regression error are made with the standard error 'e' for simple regressions and the relative error of the estimate 'E' for logarithmic regressions (Whittaker & Woodwell 1968).

Tree mass

Tree size within our stands ranged from seedlings to individuals with breast height diameters of 55–60 cm. The biomass of the largest tree was: aboveground 1367 kg, belowground 266 kg, leaves 112 kg and merchantable bole (10 cm+ diameter) 961 kg.

The arboreal masses per sq.m were calculated by summing the estimated masses of individual trees in the sample plots. The resulting summations were well correlated with stand basal area (Figure 2, Table 1). The fact that basal area is also correlated with canopy coverage (Table 1) suggests that aerial photographs might be used

Table 2. Individual quadrat (1 m²) and stand biomass and productivity regression statistics for *Vaccinium scoparium*. Equations are in the form: $y = a + bx$

REGRESSION STATISTICS						
Dependent variable (y)		r	e	n	Slope (b) Y-intercept (a)	Independent variable (x)
M ² Quadrats	Mass (g/m ²):					
	Aboveground	0.9387	20.100	29	2.1980 -28.9500	% Coverage
	Belowground	0.7473	95.850	11	4.2800 2.7513	"
	Dead Twigs	0.8904	4.868	29	0.3647 -6.3730	"
	Productivity (g/m ² /yr):					
	Leaves	0.8951	2.674	29	0.2157 -1.5330	% Coverage
	Current Twigs	0.8303	2.837	29	0.1698 -0.5528	"
(to be proportional to aboveground production)						
STAND	Mass (g/m ²):					
	Aboveground	0.9889	4.553	14	1.5790 -4.0180	Median % Coverage
	Belowground	0.9921	9.665	14	3.9880 -7.6440	"
	Total Shrub	0.9953	10.380	14	5.5680 -11.7200	"
	Productivity (g/m ² /yr):					
	Leaves	0.9961	0.298	14	0.1750 -0.3174	Median % Coverage
	Current Twigs	0.9963	0.229	14	0.1390 0.2205	"
	Belowground	0.9850	2.682	14	0.7975 0.3714	"
	Total Shrub	0.9928	2.583	14	1.1120 0.2440	"

Fig. 2. The biomass and productivity of *P. albicaulis* stands in relation to stand basal area.

to estimate biomass (and productivity), at least in arboreal vegetation with relatively open canopies.

The range of arboreal aboveground mass in the 14 stands was 8.4 to 47.2 kg/sq.m. The ranges of stand volume, merchantable (10 cm+) bole mass, bark mass and leaf mass were 12.3–80.8 dm³/m², 5.0–33.7 kg/m², 0.7–2.0 kg/m² and 0.7–2.8 kg/m² respectively (Figure 2).

The variation (or e) of the 'leaf mass/m² of basal area' regression is small compared to those of total tree or bole wood regressions (Table 1), but simple 'leaf mass/dbh' regressions for individual trees have typically high variability. Might this indicate that the forest canopy is more internally consistent than, and somewhat independent of, its supporting woody structures? Leaf mass is well correlated with the current functional vascular tissue of single plants and stands (Shinozaki et al. 1964). Leaf mass and wood production are correlated in *P. albicaulis* stands also (Table 1).

The mass of major roots (1 cm+) range from 2.6–10.4 kg/m². The mean mass of *P. albicaulis* roots 0.1–1.0 cm diameter in the eleven 1 m² × 0.4 m excavations was 0.4 kg/m² (s.d. = 0.18). The mean mass of fine roots (less than 1 mm, species composition unknown) was 0.5 kg/m² (s.d. = 0.18). The root mass of the two finer diameter classes was approximately evenly distributed between the two soil depths (0–10 and 10–40 cm). There was no correlation of root mass with the distance of the excavation to the nearest tree, or with the above- or belowground mass of *V. scoparium*. The root to shoot biomass ratio is consistently 1:4 for the tree synusia. Temperate forest ratios are generally 1:5, and woodlands 1:4 (Rodin & Bazilevich 1967, Whittaker & Marks 1975).

Fig. 3. The biomass and productivity of *V. scoparium* in *P. albicaulis* stands in relation to median shrub coverage. Aboveground wood productivity has been estimated as described in the text.

Understory biomass

Shrub coverage in the sq.m quadrats ranged from 0 to 100%. Above- and belowground mass for a quadrat with 100% coverage was 191 and 425 g/m² respectively. Herbaceous standing crops (= production) varied, but were small and averaged less than 10 g/m².

The mass of the shrub-herb layer (the mean of the averages for three plots per stand) ranged from 23–109 g/m² for the aboveground parts, and 20–264 g/m² for the belowground (> 1 mm diameter) portions (Figure 3). The regression equations used for the mass of *V. scoparium* appear to also predict the aboveground weight of *V. myrtillus*, a similar species, in Finland (Mälköne 1975). The below- to aboveground ratio for this synusia is 2.0–2.5:1.0, which is nearly identical to the ratios for *V. vacillans* and *Gaylussacia baccata* (Whittaker & Marks 1975). This ratio for the understory, however, is strikingly different from that of the tree layer; one might speculate that selection for these contrasting 'storage' strategies involved ground fire, animal browsing and competition for light.

Total masses

Total aboveground biomass for both the arboreal and shrub-herb synusia ranged from 8.5–47.4 kg/m². Total belowground mass was 3.7–11.3 kg/m². Total stand biomass ranged from 12.2–58.8 kg/m². Our older stands are surprisingly massive. Published reports of forest stands with greater masses of which we are aware are: Appalachian cove forests (Whittaker 1966) with 60 kg/m² aboveground; tropical rain forests (Rodin & Bazilevich 1967) with 75+ kg/cm² total; *Thuja plicata* and *Abies grandis* stands in northern Idaho (U.S.A.; maritime

influence) with up to 93 kg/m² (Hanley 1976); and mesic northeastern Pacific Coast *Tsuga heterophylla*-*Picea sitchensis* (Grier & Logan 1975), *Pseudotsuga menziesii* and *Sequoia sempervirens* (Franklin & Dyrness 1973) forests with aboveground weights of 87, 177, and 270 kg/m² respectively.

Tree productivity

Annual productivity for the largest trees in our stands (55–60 cm dbh) was: bole wood, 6 kg (14 dm³); leaves, 10 kg; and belowground (estimated to be directly proportional to aboveground production on a biomass basis), 3 kg.

Annual leaf production was normally 12% of the total leaf mass for individual trees. Leaves lived for more than 13 years in many cases. About 30% of the leaf mass had dropped after 6 years age, and 85% after 8 years. Similar leaf longevity was reported for a subalpine stand of *Abies mariesii* and *A. veitchii* in Hokaido (Kimura 1963). Grime (1966) suggests that long leaf persistence is correlated with high environmental stress.

Stand wood production, found by summing the productivities of trees present in sample plots, was 32–180 g/m²/yr (= 0.08–0.42 dm³/m²/yr). Bark production of *P. albicaulis* was about 1–7 g/m²/yr (Appendix 1). Leaf productivity for the tree layer ranged from 133–475 g/m²/yr, and the belowground productivity estimates were from 50–144 g/m²/yr (Figure 1).

We have estimated a 6–8 year ovulate cone and seed production sequence in 28 *P. albicaulis* stands which include the 14 stands discussed here (Forcella & Weaver 1977). Average cone and seed production for the 14 stands considered here range from 25–84 and from 8–27 g/m²/yr respectively. Average annual cone production is better correlated with (and is probably a function of) stand canopy coverage than with any other stand characteristic measured. Though there is wide variation among the stands, cone and seed productivity represent about 9 and 3% of total tree production.

Of total tree production (229–890 g/m²/yr), about 55% (s.d. = 3.6) is devoted to the leaves; the leaf production to aboveground wood production ratio is about 3.5, and smaller stands have a slightly greater ratio than the larger stands. The funnelling of photosynthate to new leaves was also observed in *Betula pubescens* (60%) in Greenland (Elkington & Jones 1974), and the phenomenon may be characteristic for treeline forests. In contrast to the stress environment species, the generally slow growth of woody plant seedlings may be due to channelling of

photosynthate to wood rather than leaf production (Grime & Hunt 1975). In temperate forest trees the photosynthetic product channelled into wood production also equals or exceeds that which is used for leaf production (Weaver 1975, Rodin & Bazilevich 1967).

Understory productivity

Maximum shrub productivity for a sq.m quadrat (100% coverage) was: leaves and twigs, 37 g/yr; and belowground (estimated as with tree roots), 81 g/yr.

The range of average productivities for the shrub synusia was: leaves, 3–12 g/m²/yr; and current twigs, 2–10 g/m²/yr. (Figure 3). Stem wood increment was not measured in *V. scoparium*, but since biomass and productivity ratios for *Gaylussacia baccata* (Whittaker & Woodwell 1969) and *V. scoparium* are nearly identical for organ systems measured on each, we based our stem productivity estimates on the branch wood and bark production to aboveground mass ratio of *G. baccata* (0.086). Productivity of stem tissue in *V. scoparium*, which lacks a main stem, would then be 2–9 g/m²/yr. Total aboveground woody production for the shrub is 4–19 g/m²/yr. The belowground productivity estimates for the shrub layer range from 4–79 g/m²/yr.

Total productivity

Total aboveground productivity of all synusiae ranged from 208–752 g/m²/yr. Fine root productivity, not considered above, was assumed to equal 10% of its mass, i.e. 51 g/m²/yr. The range of total belowground productivity was 168–267 g/m²/yr. Thus total stand productivity ranges from 381–951 g/m²/yr (the above figures are not additive). Such productivities are relatively low for temperate forests, but are probably typical for temperate woodlands (Whittaker & Marks 1975, Rodin & Bazilevich 1967). Kimura's (1963) subalpine *Abies* stand produced 1100 g/m²/yr, and the arctic treeline *Betula pubescens* 207 g/m²/yr (Elkington & Jones 1974).

The mean below- to aboveground productivity ratio for *P. albicaulis* trees is 0.25 (s.d. = 0.03); the more massive stands have ratios less than the mean. Weaver (1975) has shown that root-shoot ratios decline as oak trees age. Kimura (1963) reports a productivity ratio of 0.30 for a single *Abies* stand, and Bray (1963) calculates a ratio of 0.21 for arboreal species in general. The belowground/aboveground productivity ratio for all stand components, including shrubs, fine roots, etc., is 0.50 (± 0.12); again, the more massive stands, especially those with little *V. scoparium* cover, are those with ratios less than the mean.

The shrub-herb and fine root components play a significant role in stand dynamics. In young stands the productivity of the shrub-herb layer may approach 25% of total stand production, though its corresponding biomass is normally less than 2% of the stand total.

Stand age vs. mass and productivity

In contrast to the good empirical 'mass or productivity - basal area' relationship (Figure 2), stand age is a relatively poor predictor of arboreal mass and production (Figure 4). Cone production of *P. albicaulis* fluctuates widely between years (Forcella & Weaver 1977), and variable seed crops

Fig. 4. The biomass and annual productivity of *P. albicaulis* stands in relation to the age of the stand.

Fig. 5. The density of trees (> 1 cm dbh) in *P. albicaulis* stands in relation to the age of the stand. Data for 19 of these stands were taken from Weaver & Dale (1974).

may play an important role in the initial establishment of a stand. Extremely high variation of tree density in stands of similar age may be a result of this: Figure 5 incorporates the field data of Weaver & Dale (1974) with that of our study to show the possibility of 5-fold differences in stand densities of trees greater than 1.0 cm dbh in 50 year old stands. Figure 5 also indicates that high density variations persist, though they progressively decrease to an age of about 400 years. Basal area, biomass and productivity are in part a function of tree density (Spurr 1952), and the high variation in density may partially explain the poor mass - age relationship. The great mass of Stand 2 (240 years old) cannot, however, be explained by density alone. Analysis of increment cores from this stand reveal a high growth rate (annual radial increment greater than 1.5 mm) until the year 1850. At that time there was an abrupt reduction in growth (annual radial increment 0.27 mm, s.d. 0.08 mm) that has continued to the present; growth is now similar to that of trees in older *P. albicaulis* stands. Productivity estimates for this stand are therefore probably reasonable.

Conclusions

Within the *Pinus albicaulis*-*Vaccinium scoparium* association one may estimate the biomass and productivity of individual trees or shrubs within quadrats from measurements of their dbh or coverage respectively. Similarly, mass and production on a unit-area basis can be estimated from measurements of stand basal area and median shrub coverage.

Considering the physiographic position of the stands, their short frost-free season (32 days, Weaver & Dale 1974) and data available in the literature for 'temperate' forests, it is surprising that *P. albicaulis* forests accumulate standing crops up to 58.8 kg/m² with annual productivities as large as 951 g/m². Forest biomass usually tends to peak at mesothermal elevations in mountainous systems (Whittaker 1963, Whittaker & Niering 1975, Yoda 1968). We have relatively little data for systematic comparisons of our stands to lower forests in the northern Rockies (Weaver & Forcella 1977), but in conjunction with our field observations, these data suggest to us that *P. albicaulis* forests have the potential, under existing conditions, of being the oldest and most massive forests in the area (excepting giant *Thuja-Tsuga* and *Abies* forests, Hanley 1976). How and why such immense masses accumulate remains an enigma for us. *P. albicaulis* forests do not exist in

Fig. 6. A comparison of biomass accumulation ratios both within the *P. albicaulis*-*V. scoparium* association and between several vegetation types. The area between the two oblique parallel lines represents the biomass accumulation ratio range for temperate vegetation (from Whittaker et al. 1974). *P. albicaulis*-*V. scoparium* 1-14; *P. contorta*-*V. myrtilloides* PV, *P. contorta*-*Geranium fremontii* PG (Moir 1972); *Alnus rubra* AR (Zavitkowski & Stevens 1972); *Quercus* sp. QQ (Johnson & Risser 1975); *Typha* TY, *Pteridium* PT (Westlake 1963); *Tsuga-Picea* TP (Grier & Logan 1975); *Pinus-Rhododendron* PR, *Cupressus-Arcostaphylos* CA, *Acer-Betula* AB, *Picea-Abies* PA, *Tsuga-Acer* TA, *Liriodendron tulipifera* LT, *Acer-Aesculus* AA, *Abies-Picea* AP, *Quercus-Vaccinium* QV (Whittaker et al. 1974); *Thuja plicata*-*Pachistima myrsinites* TH (17500 and 13800 g/m²/yr, Henley 1976).

especially favorable sites; they are often on ridge tops and their psammepic soils are not particularly fertile (Weaver & Dale 1974). The high and relatively moist sites of these forests do not exclude them entirely from forest fires, but they may reduce the frequency of the holocausts sufficiently to allow attainment of great age and biomass.

Inter- and intravegetational comparisons of above-ground biomass accumulation ratios (Figure 6) suggest: (1) relatively low production in the *P. albicaulis* stands, (2) the necessary increase in biomass accumulation ratios (32 to 69) from the least to most massive stands, and (3) a wide range in the data. The third suggestion requires elaboration. The biomass and production of forest stands within one vegetation type (association) vary greatly among themselves, due to age, disturbances, slight habitat differences etc. Thus statements about forest masses and production based on the analysis of a single 'mature (near) climax' stand, no matter how detailed the analysis may be, are as inconclusive as statements concerning any other population based on a sample number of one. Our stands, all of which came from what we believe to be the same plant association, may serve as an example;

omitting the three youngest, they were originally chosen as mature representatives of the *P. albicaulis*-*V. scoparium* association, but they varied widely in age ($\times 4$), biomass ($\times 3$) and productivity ($\times 2$).

Neither the traditional (hypothesized) logistic biomass - age curve nor the optimal yield (rise and decline) productivity - age relationship is apparent in our data. On a unit-area basis, plant biomass continually increases with age, to at least an age of 640 years, whereas net primary productivity reaches a nearly stable level after about 150 years.

Appendix I

Up to an age of 75 years the bark of *P. albicaulis* remains smooth and about 3 mm thick over the entire surface of the bole. Assuming that a smooth bark indicates a lack of bark shedding, then all the bark produced by a tree remains on that tree. The mass of a tree's bark is easily measured by estimating its volume from the difference of total bole volume and bole wood volume, and multiplying by bark density (about 0.8 g/cm³, c.v. 14%).

The mass of bark in a stand is linearly related to stand basal area (BA, Table 1), and ranges from 0.69 to 2.03 kg/m² in the 14 stands studied. The regression coefficient or slope (b) of this relationship is the increase of bark mass per unit area increase of BA. If the yearly basal area increment (BAI) is known, then annual bark mass increment (= production) may be calculated:

$$\text{BAI} \times b = \text{bark production}$$

Annual BA increment is calculated by dividing the annual wood volume increment by the slope of the stand bole volume over BA regression (Table 1); this slope is essentially a weighted mean height increment per unit BA increment. Annual BA increments in the stands range from 0.09 to 0.48 m²/ha/yr with a corresponding bark production of 1 to 7 g/m²/yr. These production figures appear small, though if they are multiplied by the age of the stand, the products are often twice the calculated bark mass; about what one would expect considering that when a stand was younger, it probably produced less than it currently does. In some instances the 'production $\times$ age' products are about equal to bark mass, thus the production estimates are certainly biased toward the low side in such cases. Of course, these bark production figures are also skewed toward low values due to our assumed absence of bark shedding. All in all, these values likely represent minimal but reasonable estimates.

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Accepted 2 March 1977