



Flora, chorology, biomass and productivity of the *Pinus albicaulis*-*Vaccinium scoparium* association
by Frank Forcella

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE
in BOTANY

Montana State University

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Abstract:

The *Pinus albicaulis* - *Vaccinium scoparium* association is restricted to noncalcareous sites in the subalpine zone of the northern Rocky Mountains (USA). The flora of the association changes clinally with latitude. Stands of this association may annually produce a total (above- and belowground) of 950 grams of dry matter per square meter and may obtain biomasses of nearly 60 kg per square meter. General productivity and biomass may be accurately estimated from simple measurements of stand basal area and median shrub coverage for the tree and shrub synusiae respectively. Mean cone and seed productivities range up to 84 and 25 grams per square meter per year respectively, and these productivities are correlated with percent canopy coverage (another easily measured stand parameter). Edible food production of typical stands of this association is sufficient to support 1000 red squirrels, 20 black bears or 50 humans on a square km basis. The spatial and temporal fluctuations of *Pinus albicaulis* seed production suggests that strategies for seed predator avoidance may have been selected for in this taxon.

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Date 31 May 1977

FLORA, CHOROLOGY, BIOMASS AND PRODUCTIVITY OF THE

PINUS ALBICAULIS - VACCINIUM SCOPARIUM

ASSOCIATION

by

FRANK FORCELLA

A thesis submitted in partial fulfillment
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BOTANY

Approved:

T. WFAVER

Chairperson, Graduate Committee

James M. Pickett

Head, Major Department

Henry L. Parsons

Graduate Dean

MONTANA STATE UNIVERSITY

Bozeman, Montana

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PREFACE

This thesis has been divided into four segments or chapters. Though all chapters are interrelated, each has been written as an individual entity with its own Introduction, Methods etc. Such a format has been followed for the convenience of the reader. Plant taxonomists and geographers will be interested mostly in Chap. 1; interests of forest mensurationists lie entirely in Chap. 2; silviculturists and ecologists will find Chap. 3 useful, if not amusing; lastly, Chap. 4 is oriented toward wildlife biologists and general biologists. Within this thesis, retrieval of specific information by 'special interest groups' will be greatly facilitated by the format used.

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The Department of Biology at Montana State University, under the chairmanship of Dr. J. Pickett, provided me with the following: a financially lucrative 'teaching assistantship' for 7 academic quarters (with options for two more); computer time; travelling expenses for field research, field trips and for the presentation of research papers at annual scientific gatherings; and lastly, general hospitality. The research presented in this paper was *initiated* through a \$5000 grant from the U.S. Forest Service to Dr. T.W. Weaver. In turn, Dr. Weaver gave me nearly full, unhindered responsibility for the appropriate use of these funds.

Beginning with my parents, there are several individuals who have greatly affected my personal development. Those who have contributed academically (and in other ways) include: Arthur Johnson, Fred A. Barkley, J.H. Rumely, H.N. Metcalf, S.J. Harvey and J. Major. I thank all these individuals. Of course in this same regard, T.W. Weaver deserves special mention. If I have any (good) scientific/analytic qualities, a very large proportion of them can be attributed to my association with Dr. Weaver. Though ones' initial boyhood enthusiasum in the natural sciences may often have been spontaneous, its maintainence into adulthood is

not necessarily self-perpetuating; Dr. Weaver has the uncanny ability to sustain, in another individual, an insatiable enthusiasm -- through his very own, perhaps.

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ABSTRACT

FLORA, CHOROLOGY, BIOMASS AND PRODUCTIVITY OF THE

PINUS ALBICAULIS - *VACCINIUM SCOPARIUM*

ASSOCIATION

The *Pinus albicaulis* - *Vaccinium scoparium* association is restricted to noncalcareous sites in the subalpine zone of the northern Rocky Mountains (USA). The flora of the association changes clinally with latitude. Stands of this association may annually produce a total (above- and belowground) of 950 grams of dry matter per square meter and may obtain biomasses of nearly 60 kg per square meter. General productivity and biomass may be accurately estimated from simple measurements of stand basal area and median shrub coverage for the tree and shrub synusiae respectively. Mean cone and seed productivities range up to 84 and 25 grams per square meter per year respectively, and these productivities are correlated with percent canopy coverage (another easily measured stand parameter). Edible food production of typical stands of this association is sufficient to support 1000 red squirrels, 20 black bears or 50 humans on a square km basis. The spatial and temporal fluctuations of *Pinus albicaulis* seed production suggests that strategies for seed predator avoidance may have been selected for in this taxon.

CHAPTER 1

THE FLORA AND CHOROLOGY OF THE *PINUS ALBICAULIS* -
VACCINIUM SCOPARIUM ASSOCIATION

INTRODUCTION

Floristic variation within a plant association may indicate that the habitat of the association is not uniform throughout, and that two or more plant associations are being considered as one, the extreme case being that each community is an individual, an association unto itself. Other interpretations exist; summaries can be found in Major and Pyott (1965) and in several texts dealing with vegetation. In this chapter I shall describe the compositional variation of the *Pinus albicaulis* - *Vaccinium scoparium* association, and relate some of the variation to one factor of vegetation formation (Major 1951), i.e., the flora from which the vegetation may have originated.

The suggestion that a single plant association varies according to the flora available to it suggests that this association may exist in more than one floristic region. If regional climate and events during historical time determine floristic regions, one might conclude that these factors could act differentially within the association and thereby affect its variation. Alternatively, if one assumes that a recurring mixture of plant species indicates a particular set of environmental conditions, and that the probability of two or more of these species concurrently evolving the same degree of ecotypic variation is low, then it follows that the

habitat within which this association of plant species exists is more or less equivalent throughout (if it is integrated over ecologic time). Thus floristic differences of communities with "identical" habitats must be a result of either the availability of their flora at the time of their establishment (Egler 1953) and/or through the remainder of their existence (Major 1951).

METHODS

Stands in Wyoming, Idaho and Montana (U.S.A.) with overstories dominated by *Pinus albicaulis*, understories dominated by *Vaccinium scoparium* and lacking conspicuous populations of *Abies lasiocarpa* seedlings and/or layered shoots (i.e., *Abies* reproduction less than that of *P. albicaulis*), and soils not stony or rocky (Soil Survey Staff 1976) enough to obviously affect the growth and distribution of plants, were sampled. Within a 600 m² area (three, 6.67 x 30 m) in each of 29 stands, all vascular plant species were collected (identified and filed at the Herbarium, Montana State University; Bozeman, Montana); and within ninety 2 x 5 dm frames in each 600 m² area, the coverage of each vascular plant taxon was estimated. Foliose arboreal lichens were also collected, but not systematically. Nomenclature follows that of Hitchcock and Cronquist (1973) for the Pacific

Northwest vascular plants, Munz and Keck (1968) for other vascular plants, and Hale (1969) for lichens. Taxonomic authorities not in the text are listed in Table 1.

RESULTS

Four species other than *Pinus albicaulis* and *Vaccinium scoparium* were nearly ubiquitous in the sampled stands: the widespread *Carex rossii*, *Abies lasiocarpa* and *Poa nervosa* with constancies of 80, 90 and 70% respectively, and *Arnica latifolia* (80% constancy, though absent from most Wyoming stands). The presence of these taxa lends some support (or degrees of freedom in a statistical sense) to the initial assumption of the improbability of two or more species concurrently evolving associated ecotypes.

In Table 1, the flora and some other stand characteristics are provided in relevé form. This table lists the stands in a latitudinal sequence, with adjustments to accommodate latitudinally-similar stands with widely separated longitudinal ordinates (cf. Fig. 1). Stands have not been sorted according to their floristic similarities as is usually done in relevé analyses (Mueller-Dombois and Ellenberg 1974). However, the taxa have been arranged to give the maximum impression of latitudinal change to

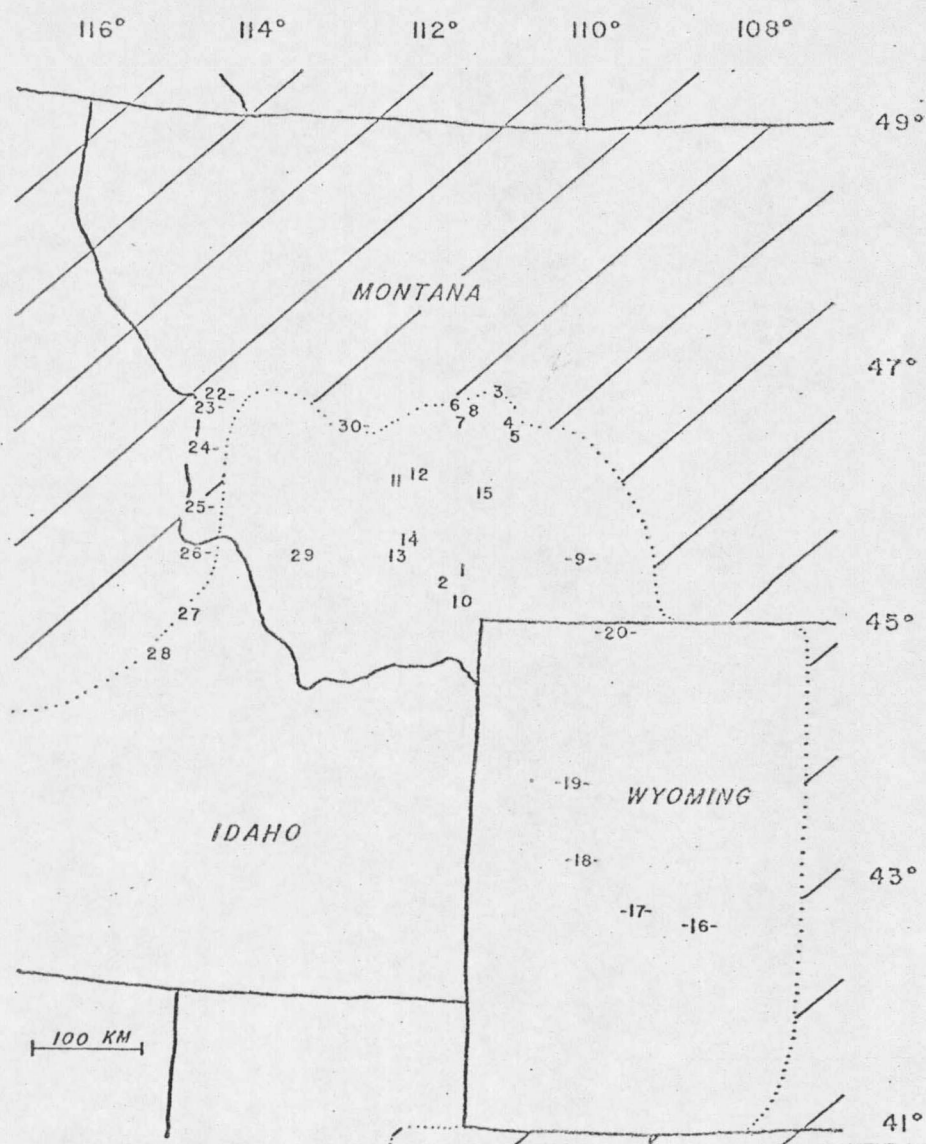


Figure 1. The distribution of the *Pinus albicaulis* - *Vaccinium scoparium* association. The numbers and their associated characters (e.g. n-, -n-) represent stand numbers and the three geographic/floristic regions referred to in the text. The geographical extent of the stands is thought to represent the range of the association. The unhatched area inside the dotted line represents the gap in the distribution of *Pinus ponderosa* (from Little 1971). (There is no Stand 21.)

Table 1a. Flora of the *Pinus albicaulis* - *Vaccinium scoparium* association. Stand age (years), % arboreal canopy coverage, % *V. scoparium* coverage are shown along with the taxa of the association with constancies greater than 15% (and which show limited distributions in the association). The stands have been arranged in a latitudinal sequence from south to north (cf. Fig. 1.). Assume varietal status of each taxon to be common Rocky Mt. variety or equivalent to specific epithet unless stated otherwise. Taxa with limited distributions in the association due to their actual narrow regional distributions are denoted by asterisks (*). Simple presence in the 600 m² sampling area is represented by a '+', whereas '1-5' represent frequency classes from low to high.

Stand Age	188	161	214	131	210	307	205	150	240	188	94	182	643	160	320	53	135	364	120	55	55	330	132	59	115	32	29	423	
Percent Arboreal Coverage	63	63	71	63	49	54	52	73	97	31	30	69	47	56	53	40	73	51	61	54	37	70	66	--	32	22	13	18	50
Percent Vaccinium Coverage	7	21	16	5	25	59	14	45	10	9	27	29	46	54	55	43	64	75	75	74	59	36	37	16	23	23	30	32	
Stand Number	16	17	18	19	20	09	10	01	02	28	27	29	13	14	15	11	12	06	07	08	04	05	03	30	26	25	24	23	22
<i>Sedum lanceolatum</i> Torr.	1	1	+	1	.	+	1	+
<i>Achillea millefolium</i> L.	.	1	+	1	.	.	.	1	.	1	1
<i>Claytonia lanceolata</i> Pursh	.	1	+	.	.	1	1	1
<i>Solidago multiradiata</i> Ait.	.	+	1	+	.	+	1	1	1	1	1	+	.	.	.	1	.	.	.
<i>Castilleja verticillata</i> Rydb.	.	.	.	+	.	1	.	1	+	.	+	.	.	.	+	1
<i>Agoseris glauca</i> (Pursh) Raf.	.	+	.	1	.	+	1	1	.	+	1	+	.	.
<i>Pinus contorta latifolia</i> Engelm.	.	.	.	+	+	.	+	+	+	+	.
* <i>Aster foliaceus apricus</i> Gray	.	.	+	.	.	.	1	1	1	1
<i>Trisetum spicatum</i> (L.) Richter	.	.	1	+	.	1	1	1	.	+	2	.
<i>Lupinus argenteus</i> Pursh	1	+	+	1	.	.	1	+	.	2	1	+	.	1	.	1	.	1	+	1
<i>Potentilla diversifolia</i> Lehm.	+	1	.	.	1	+	1	.	.	+	.	.	+	.	+	.	1	+	+
<i>Arnica cordifolia</i> Hook.	.	2	2	3	+	1	2	1	2	+	.	1	.	1	1	+	1	.	1
<i>A. latifolia</i> Bong	1	3	1	2	3	+	2	2	.	1	1	1	2	2	2	2	3	+	1	1	2	+	1	.	+
<i>Rhynchospora grandiflora</i> Pursh	2	.	.	.	1	1	.	+	.	.	.	+	+	+
<i>Carex geyeri</i> Boott	1	1	+	.	+	.	.	3	3	2	2	3	1	1	2	.	.	+
* <i>Lomatium ovisokii</i> (Wats.) Coult. & Rose	1	1	1	.	.	.	+
<i>Pedicularis groenlandica</i> Retz.	1	1	+	1	.	.
<i>Juncus parryi</i> Engelm.	.	+	1	1	+	1	1	+
<i>Antennaria lanata</i> (Hook.) Greene	+	+	.	.	1	.	.	1	+
* <i>Lumula hitchookii</i> Hamet-Ahti	1	1	2	2	4

demonstrate that the flora of the association changes clinally with latitude, and that the flora of any stand is at least a partial consequence of the floristic region in which the stand exists.

Table 1a consists of those taxa with constancies $> 15\%$, and whose presence appears to be nonrandomly distributed within the association. When the within-association distributions of these taxa are compared to their general distributions listed in standard Floras for the Pacific Northwest (Hitchcock and Cronquist 1973, Davis 1952, Booth and Wright 1966, Shaw 1976 and Despain 1975), approximately 15% of them are distributionally restricted from attaining 100% constancy in the *P. albicaulis* - *V. scoparium* association. Similarly, of those taxa with between 5 and 15% constancies, and those with $< 5\%$ constancy (Table 1b, 1c), about 1/2 of the former and 1/3 of the latter are distributionally restricted from ubiquity in the association. Taxa which exhibit no latitudinal affinities (Table 1c) are characteristically widespread in their general distributions.

A few of the taxa in Table 1 deserve special mention. The low glandular shrub, *Leptodactylon pungens*, and the similar but more cushion-like *Arenaria aculeata* both have stiff spinulose leaves often found in desert-region plants, as indeed both are. In *P.*

	16	17	18	19	20	09	10	01	02	28	27	29	13	14	15	11	12	06	07	08	04	05	03	30	26	25	24	23	22
<i>Abies lasiocarpa</i> (Hook.) Nutt.	.	.	1	.	+	1	+	1	1	+	1	+	1	1	.	1	+	+	1	+	.	1	1	+	1	1	1	1	+
<i>Carex rossii</i> Boott	+	1	1	+	1	1	.	1	1	.	1	1	1	.	+	1	1	1	+	+	.	.	+	1	1	+	+	2	.
<i>Poa nervosa</i> (Hook.) Vasey	1	2	2	1	2	1	1	.	1	1	.	1	+	.	1	.	.	.	+	+	+	+	.	.	1	+	+	+	.
<i>Hieracium gracile</i> Hook.	.	+	.	.	+	1	.	1	.	.	.	2	2	+	1	1	2	+	.	1	1	+	1	1
<i>Epilobium angustifolium</i> L.	.	.	+	2	.	.	1	.	+	1	+	.	.	1	+	+	+	+	1	+	.	.	.	1	+
<i>Juniperus communis montana</i> Ait.	.	.	+	.	.	+	1	+	+	.	+	+	+	1	.	.	.	+	1	+
<i>Antennaria umbrinella</i> Rydb.	+	1	.	+	1	.	.	.	+	1	+	+	+	+
<i>Picea engelmannii</i> Parry	.	.	.	1	+	+	+	+	+
<i>Pyrola secunda obtusata</i> Turcz.	+	1	.	+	1	1	.	+	.	.	+	.
<i>Penstemon rydbergii</i> A. Nels.	.	.	.	+	2	+
<i>Oryzopsis exigua</i> Thurb.	+	1	+	1
<i>Arenaria congesta cephaloidea</i> (Rydb.) Maguire	.	1	+	+	+	1	+
<i>Erigeron peregrinus</i> (Pursh) Greene	.	+	+	1	+	.	.
<i>Polygonum bistortoides</i> Pursh	.	+	+	1	.	+
<i>Fragaria virginiana platypetala</i> (Rydb.) Hall	.	.	.	1	+	1
<i>Ribes lacustre</i> (Pers.) Poir.	+	+	.

Thirty-two taxa have only single occurrences in the stands (constancy < 5%). In the latitudinal sequence shown above, the stands with their respective taxa are: 17 *Erigeron pumilus* Nutt.; 19 **Mertensia ciliata* (Torr.) G. Don., *Gentiana amarella* L.; 20 *Arenaria obtusiloba* (Rydb.) Fern., *Selaginella densa scopulorum* (Maxon) Tryon, *Saxifraga bronchialis* L.; 10 *Penstemon fruticosus fruticosus* (Pursh) Greene; 2 **Trifolium haydenii* Porter; 28 *Stipa occidentalis* Thurb., **Happlopappus suffruticosus* (Nutt.) Gray; 27 *Silene repens* Pers.; 15 *Goodyera oblongifolia* Raf.; 7 *Poa alpina* L.; 5 **Vaccinium membranaceum* Dougl.; 3 *Valeriana edulis* Nutt., *Lloydia serotina* (L.) Sweet; 30 *Hypopitys monotropa* Crantz; 26 **Aster stenomerus* Gray, *Bromus carinatus* H. & A.; 25 **Leptodaetylon pungens* (Torr.) Nutt.; 24 *Rumex paucifolius* Nutt., *Salix phyllifolia* L., **Veronica cusickii* Gray, **Linanthastrum nuttallii* (Gray) Ewan., **Penstemon flavescens* Pennell, *Hieracium albiflorum* Hook., *Danthonia intermedia* Vasey, *Hypericum formosum nortoniae* (Jones) Hitchc., *Agoseris auriantica* (Hook.) Greene, **Spiraea densifolia* Pall., *Anaphalis margaritacea* (L.) B. & H.; 23 *Carex paysonis* Clokey, *Poa sandbergii* Vasey, *Festuca ovina brevifolia* (R. Br.) Wats.; 22 *Campanula parryi* Gray.

Table 1c. Flora of the *Pinus albicaulis* - *Vaccinium scoparium* association; the taxa of the association exhibiting no latitudinal affinities. Table specifications follow those in Table 1a.

albicaulis forests these species are found in the southern Bitterroot Mountains and the Salmon River Mountains of east and central Idaho. The dry finger-like intermountain valleys (Lemhi, Pahsimeroi and Lost River Valleys) which extend from the northern edge of the Great Basin and abut these mountain ranges probably supplied the migratory path for these species from the deserts to *P. albicaulis* forests. To find either taxon in a mesic subalpine forest is surprising, but would have been much more so if that forest had been in central Montana, rather than east-central Idaho with its direct connection to the Great Basin.

Three species of the *P. albicaulis* - *V. scoparium* association are relatively narrow endemics: *Penstemon flavescens* (Idaho Co., Idaho and Ravalli Co., Montana), *Chionophila tweedyi* (central Idaho and adjacent Montana) and *Aster stenomerus* (central Idaho and adjacent Montana to northeastern Washington and southeastern British Columbia). Similarly, the typically alpine *Trifolium haydenii* extends only as far north as southern Montana. It occurs in a whitebark pine stand immediately adjacent to alpine meadows and scree in the Madison Range (Gallatin Co., Montana) and would not be expected in *P. albicaulis* forests further north.

Though the general regional occurrences of the above taxa are easily obtained from standard Floras, their equally important

intra-regional distributions are not so readily available. For example, *Arnica latifolia* and *Carex geyeri*, which are prominent in many Montana whitebark pine stands, are absent from the stands in the Wind River Mountains of Wyoming. This mountain range does support both taxa, but their populations are not as extensive as elsewhere. In such cases, the chance of limited taxa reaching *P. albicaulis* forests is low. King (1977) has noted this same phenomenon, but on a much smaller scale; the ability of a plant to colonize ant mounds in British pastures is determined by its relative abundance and distance from the mounds.

Superficially at least, in some regions of *P. albicaulis* forests there appears to be an "ecological" replacement of one taxon (life form) by another. *Arnica cordifolia* is generally prominent in those stands in which *A. latifolia* is not, and *Luzula hitchcockii* is relatively important in the Bitterroot Mountains where *Carex geyeri* is not.

Lichens

Both *Letharia vulpina* (L.) Hue and *Hypogymnia vittata* (Ach.) Gas. were widespread throughout the association; the former being much more prominent. *Alectoria oregana* Tuck. and *A. americana* Mot. were confined to the northern-most stands. Both

Alectorias have limited distributions in the Rocky Mountains which correlate with their presence in the whitebark pine forests.

Disjunctions

Daubenmire (1975) has applied the term "oceanic element" to taxa with distributions largely restricted to maritime-influenced climates of the Pacific Northwest (NW Montana, N Idaho, W Oregon, W and NE Washington and the adjacent parts of Alberta and British Columbia). I had considered both *Xerophyllum tenax* and *Luzula hitchcockii* to be strict oceanic elements, but their actual distributions are in fact more extensive. Widely disjunct populations of both species occur as far south as Teton Co., Wyoming (Shaw 1976, Pfister et al. 1974, Maule 1959). *Menziesia ferruginea* Smith and *Pinus monticola* Dougl. (not in whitebark pine forests) are other oceanic elements often found close to or associated with *X. tenax* and *L. hitchcockii*. They also have disjunct distributions nearly identical to the others (Hickman and Johnson 1969 and personal observations). Perhaps in past times, the paleoclimate was sufficiently different to support an "oceanic" vegetation throughout the northern Rocky Mountains, as presently exists in NW Montana and N Idaho. Additional evidence for such a maritime paleoclimate is the discovery of *Taxus brevifolia* Nutt. (an unquestionably oceanic species) wood remnants during archaeological

excavations in the Yellowstone Valley, SW Montana (Arthur 1966; the same valley presently supports very localized populations of *X. tenax* and *M. ferruginea*). Radiocarbon dates for the *Taxus* material were 5000 years BP. The early Holocene epoch in the Rocky Mountains is thought to have been cool and wet (Hansen 1947); the Xero- or Altithermal interval began about 7500 BP and lasted until the onset of Neoglaciation, ca. 4000 BP (Richmond 1970). Wells (1970) has suggested that the "Xerothermal" interval in the Laramie Basin of Wyoming was wetter, not dryer, than present. Unless these plant disjunctions and excavations represent relict vegetation from the pre-Pinedale Glacial times, with the recession of Cordilleran ice (12,000 BP; Richmond 1970), a Pacific maritime climate and vegetation *may* have pervaded the entire northern Rocky Mountains. A subsequent cooling and drying trend in W Wyoming and SW Montana could not support a maritime vegetation, and extinctions and disjunctions resulted. High elevation bog pollen-profiles in Yellowstone National Park (Waddington and Wright 1974) are dominated by *Pinus contorta* from ca. 11,600 BP to present; an increase of *Picea engelmannii* pollen at 5000 BP implies climatic cooling. That the W Wyoming - SW Montana area is still subjected to a relatively cold climate can be seen by the present gap in the distribution of *Pinus*

ponderosa Laws. (Fig. 1), a typically "warm" pine (Mirov 1967). Curiously, the absence of *P. ponderosa* from this area correlates generally with the occurrence of the *P. albicaulis* - *V. scoparium* association. If those whitebark pine stands with oceanic elements are omitted, then the correlation is nearly perfect.

Species Number

The number of species in the whitebark pine stands ranged from 6 in the oldest stand (640 years) to 33 in one of the youngest (33 years). There was a general trend in decreasing species number with stand age, but stands that were proximal tended to have similar species numbers despite age differences.

Management Implications

Although whitebark pine forests receive relatively little resource management attention at the present time, it can be expected to increase rapidly. *P. albicaulis* produce exceptionally large mast crops (Chapters 3, 4), and such production may significantly affect the habits of wildlife. (Craighead 1976, Chapters 3, 4). Total net primary productivity in these forests may exceed $900 \text{ g/m}^2/\text{yr}$, and standing crops may approach 60 kg/m^2 (Chapter 2); economically, these figures are substantial.

There are also some practical aspects involved with the floristic distributional anomalies of whitebark pine forests.

The three dominant herbaceous species of the association are: *Carex geyeri*, *Arnica latifolia* and *A. cordifolia*. These taxa all have known forage value for both domestic and wild ungulates. The biomass and energy (kcal) per unit-area of each species can be readily predicted from their canopy coverages (measured separately; Chapter 4). Further, as can be seen in Table 1, the species are distributionally limited within the association. If the 29 stands are split into three geographic/floristic regions (Fig. 1; separations based on plant distributions and agglomerative cluster analysis), the mean energy value per m² for each species differs significantly between at least two regions (t-test, p = 0.01; Chapter 4). In vegetation mapping, the *P. albicaulis* - *V. scoparium* association, as a whole, would probably comprise a single cartographic unit. Knowledge of regional differences in forage availability within associations might prove valuable to resource managers.

Chorology

The stands shown in Fig. 1 essentially outline the distribution of the *P. albicaulis* - *V. scoparium* association. To the north and northwest, *Abies lasiocarpa*, *Larix lyalli* and *Vaccinium membranaceum* gain importance in whitebark pine forests. In Alberta, Canada (on acidic substrates), *P. albicaulis* occurs with

equal amounts of *Picea engelmannii* and *A. lasiocarpa* in the over-story. Understory components always contain *V. scoparium*, but it may be accompanied or dominated by *Vaccinium caespitosum* Michx., *Empetrum nigrum* L., *Dryas octopetala* L., *Salix arctica* Pall. or *Spiraea* sp. In Banff National Park, I found one stand on dolostone totally dominated by *P. albicaulis*; its understory, in order of importance, consisted of *Betula glandulosa* Michx., *Potentilla fruticosa* L., *Linnaea borealis* L., *Shepherdia canadensis* (L.) Nutt., *Juniperus communis* and *Dryas octopetala*. There were no *Vacciniums* in this stand, probably due to its basic substrate.

The eastern limit of the *P. albicaulis* - *V. scoparium* association is correlated with the eastern extent of acid-rock mountain ranges in Alberta and Montana. Limestone ranges such as the Big Snowy Mountains (Montana) do not contain this association. The eastern limit in Wyoming is the Absaroka and Wind River Mountains; the granitic Big Horn Mountains, 170 km eastward, do have scattered populations of *P. albicaulis* (Hoffman 1976, D. Despain *per. comm.*).

To the south, the Medicine Bow Mountains (Wyoming), the Colorado Rockies and the Uinta Mountains of Utah all lack whitebark pine. That the southern limit of *P. albicaulis* coincides with the northern boundary of other edible large-seeded, grove-forming pines (*P. edulis* Engelm., S Wyoming; *P. monophylla* Torr. & Frem.,

S Idaho to California) may be more than coincidental. Forcella and Rumely (in prep.) hypothesize that prehistoric man carried seed of *P. sibirica* L. (= *P. albicaulis*) across Beringia. His dispersal of the energy-rich seed ceased when contact was made with native large-seeded pines.

In far western Wyoming (the Wyoming Range), *P. albicaulis* forests contain an understory of *Ribes montigenum* McClatchie (which forms conspicuous closed circles under the canopies of the rather widely spaced trees) and *Bromus carinatus*. To the northwest, in the White Cloud Peaks and Sawtooth Mountains of central Idaho, *P. albicaulis* stands often support an understory of *Artemisia tridentata* Nutt. and/or a carpet of forbs, *Lupinus argenteus* being the most prominent.

Within the distributional limits of the *P. albicaulis* - *V. scoparium* association, there may be other associations which contain *P. albicaulis*. On limestone outcrops, Weaver and Dale (1974) mention a stand in which *P. flexilis* James and various forbs associate with whitebark pine. I have seen such stands and others similar, but always including *Arctostaphylos uva-ursi* (L.) Spreng. This type of community, with a distinctly different habitat (limestone), appears to have lumped with the *P. albicaulis* - *V. scoparium* association in the "habitat-type" classification of

Pfister et al. (1974) and Reed (1976). Also, on what may be more mesic sites, *Abies lasiocarpa* shares the overstory with whitebark pine, and *V. membranaceum* is often present in the understory. It is possible that alternate plant associations (*Abies* vs. *Pinus*) may exist on the same site at different times, the occurrence of either possibly being a function of its seed crop size at the time of stand establishment. Seed production of *P. albicaulis* varies significantly from year to year (Chapter 3). Treeline form(s) of whitebark pine community occurs too; its distinguishing feature is, of course, the stunted growth and flagged structure of the trees (Daubenmire and Daubenmire 1968). Clausen (1965) speculates a genetic basis for the stunted *P. albicaulis* of the Sierra Nevada krummholz.

CONCLUSIONS

The *Pinus albicaulis* - *Vaccinium scoparium* association is limited to subalpine sites on non-calcareous substrates in western Wyoming, southwestern Montana and east-central Idaho. Its floristic composition changes clinally with latitude; this does not necessarily imply a change in habitat. Nearly 25% of the taxa which comprise the association are distributionally restricted from occurring in all stands of the association.

This suggests that to some degree, the floristic composition of a stand is a function of the local flora available to it.

CHAPTER 2

THE BIOMASS AND PRODUCTIVITY OF THE *PINUS ALBICAULIS* -
VACCINIUM SCOPARIUM ASSOCIATION

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 U.S.A.

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, I 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 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 and Niering 1975, Landis and Mogrén 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 I studied 14 stands (stands 1-14, Fig. 1), I was 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, I feel that accurate predictions of biomass and reasonable estimates of productivity are possible. I 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 I 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 and Schröter 1910, in Braun-Blanquet 1964)

is appealing, I 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 non-calcareous substrates in the northern Rocky Mountains. Its vegetation, soil, soil parent material and climate have been characterized by Weaver and 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 meters at 100 years of age. The understory is typically dominated by the low-growing (10-30 cm) *V. scoparium*. 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 is meager. Occasionally, the few *Abies lasiocarpa* Hook. individuals in the understory outnumber those of *P. albicaulis*. These small *Abies* often result from the layering of an older tree. Both Daubenmire and Daubenmire (1968) and Pfister et al. (1974) recognize an *A.*

lasiocarpa (*P. albicaulis*) - *V. scoparium* habitat type. The dominance of *P. albicaulis* in my stands might be due to (1) a very slow (600 years +) successional replacement of *P. albicaulis* by *A. lasiocarpa*, (2) physical (e.g., climatic) limitation to *Abies* on *P. albicaulis* sites, or (3) biological limitations to *Abies* due to the 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 and 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 x 30 meter (0.06 ha) plots which were placed parallel to the

slope of the stand. All trees within these 200 m² 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 m² quadrats which were placed in two contiguous 1 x 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 25 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/cm^3 (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 m^2 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 and Gorchakovskii 1972) and was not measured, but it was estimated from the work of Whittaker and 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 m² 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 sample plots, the biomass regression equations of Weaver and 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 x 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 and Olson 1973). The antilogarithmic conversion of the regression equation to arithmetic units should thus result in systematic underestimation. Brownlee (1967, as cited by Baskerville 1973) 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. 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 and 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* Engelm. and infrequent individuals of *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* Parry. Mean BA's for the stands (3 plots/stand) range from 25 to 108 m²/ha (c.v. 20% or less). This range of BA is similar to that of many mature Rocky Mountain forests studied by Daubenmire and Daubenmire (1968) and Whittaker and Niering (1975), but smaller than stands of the *Tsuga heterophylla* series (100-500 m²/ha, Daubenmire and Daubenmire 1968) and of the Pacific Coast forests (100-300+ m²/ha, Franklin and Dyrness 1973, Westman and Whittaker 1975). Canopy coverage of the 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 and Dale 1974). These shrubs are distributed in patches on the forest floor (Forcella 1975), and stands on steep (32%+) slopes support considerably less *V. scoparium* than those of more level topography (slope vs. coverage, $r = -0.5$). 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* Bong 93%, *Carex rossii* Boott 71%, *Lupinus argentrus* Pursh 64%, *C. geyeri* Boott 57%, *Poa nervosa* Vasey 57%, *Hieracium gracile* Hook. 57%, *Epilobium angustifolium* L. 57%, *Potentilla diversifolia diversifolia* Lehm. 50% and *A. cordifolia* Hook. 50%. The shrub, *Juniperus communis montana* Ait., with negligible cover, occurred in 57% of the stands. No annual species were observed in the 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 and Woodwell (1968) and Weaver and Forcella (1977). The regression statistics, independent variables and number of data points for all regressions used are listed in Tables 2 and 3. 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"

Table 2. 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 (%)

Table 3. Individual quadrat (1 m^2) 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	"	

for simple regressions and the relative error of the estimate "E" for logarithmic regressions (Whittaker and Woodwell 1968).

Tree Mass

Tree size within the 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 m^2 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 2). The fact that basal area is also correlated with canopy coverage (Table 2) suggests that aerial photographs might be used 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/m^2 . The ranges of stand volume, merchantable (10 cm +) bole mass, bark mass and leaf mass were 12.3-80.8 dm^3/m^2 , 5.0-33.7 kg/m^2 , 0.7-2.0 kg/m^2 and 0.7-2.8 kg/m^2 , respectively (Figure 2).

The variation (or e) of the "leaf mass/ m^2 - basal area" regression is small compared to those of total tree or bole wood regressions (Table 2), but simple "leaf mass/tree - dbh" regressions have typically high variability. Might this indicate that the

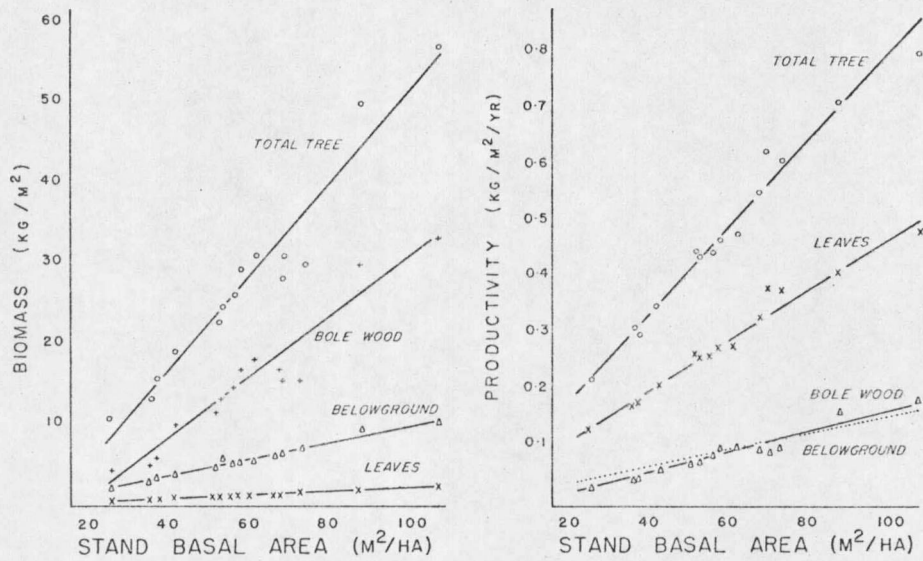


Figure 2. Arboreal biomass and productivity in relation to stand basal area in 14 *Pinus albicaulis* - *Vaccinium scoparium* communities.

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 2).

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 x 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 synthesis. Temperate forest ratios are generally 1:5, and woodlands 1:4 (Rodin and Bazilevich 1967, Whittaker and Marks 1975).

Understory Biomass

Shrub coverage in the m² quadrats ranged from 0 to 100%. Above- and belowground mass for a quadrat with 100% coverage was 191 and

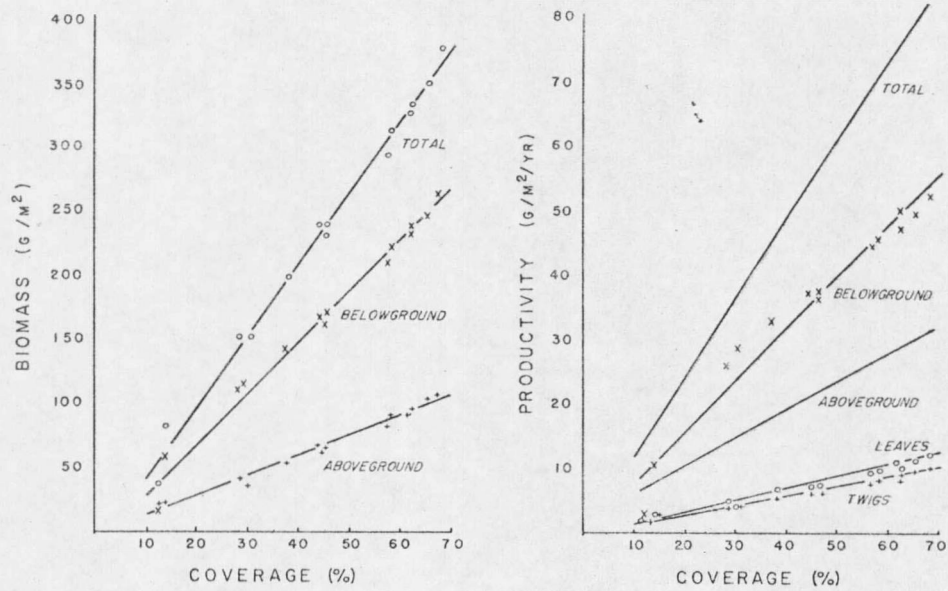


Figure 3. The biomass and productivity of *Vaccinium scoparium* in relation to median shrub coverage in 14 *Pinus albicaulis* - *Vaccinium scoparium* communities. Aboveground wood productivity has been estimated as described in the text.

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 (Mälköene 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. vaccillans* and *Gaylussacia baccata* (Whittaker and 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 synusiae 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. The 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 and Bazilevich 1967) with $75 + \text{kg/m}^2$ total; *Thuja plicata* and *Abies grandis* stands in northern Idaho (U.S.A.; maritime influence) with up to 93 kg/m^2 (Hanley 1976); and mesic northeastern Pacific Coast *Tsuga heterophylla* - *Picea sitchensis* (Grier and Logan 1975), *Pseudotsuga menziesii* and *Sequoia sempervirens* (Franklin and Dyrness 1973) forests with aboveground weights of 87, 177, and 270 kg/m^2 , respectively.

Tree Productivity

Annual productivity for the largest trees in the stands (55-60 cm dbh) was: bole wood, $6 \text{ kg} (14 \text{ dm}^3)$; leaves, 10 kg ; and below-ground (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 $32-180 \text{ g/m}^2/\text{yr}$ ($= 0.08-0.42 \text{ dm}^3/\text{m}^2/\text{yr}$). Bark production of *P. albicaulis* was about $1-7 \text{ g/m}^2/\text{yr}$.

(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 2).

I have estimated a 6-8 year pistillate cone and seed production sequence in 28 *P. albicaulis* stands which include the 14 stands discussed here (Chapter 3). 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 and 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 and 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 and Bazilevich 1967).

Understory Productivity

Maximum shrub productivity for a m^2 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 $g/m^2/yr$; and current twigs, 2-10 $g/m^2/yr$ (Figure 3). Stem wood increment was not measured in *V. scoparium*, but since biomass and productivity ratios for *Gaylussacia baccata* (Whittaker and Woodwell 1969) and *V. scoparium* are nearly identical for organ systems measured on each, I based the 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 $g/m^2/yr$. Total aboveground woody production for the shrub is 4-19 $g/m^2/yr$. The belowground productivity estimates for the shrub layer range from 4-79 $g/m^2/yr$.

Total Productivity

Total aboveground productivity of all synusiae ranged from 208-752 $g/m^2/yr$. Fine root productivity, not considered above, was

assumed to equal 10% of its mass, i.e., $51 \text{ g/m}^2/\text{yr}$. The range of total belowground productivity was $168\text{--}267 \text{ g/m}^2/\text{yr}$. Thus total stand productivity ranges from $381\text{--}951 \text{ g/m}^2/\text{yr}$ (the above figures are not additive). Such productivities are relatively low for temperate forests, but are probably typical for temperate woodlands (Whittaker and Marks 1975, Rodin and Bazilevich 1967). Kimura's (1963) subalpine *Abies* stand produced $1100 \text{ g/m}^2/\text{yr}$, and the arctic treeline *Betula pubescens* $207 \text{ g/m}^2/\text{yr}$ (Elkington and 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 $0.50 (\pm 0.12)$; 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 (Chapter 3) and variable seed crops 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 and Dale (1974) with that of this 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

