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

Abstract:

The Pinus dlbieaulis - Vacoinium seoparium 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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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

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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.

ACKNOWLEDGEMENTS

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 [illegible] primarily [illegible] encouragement [illegible] not neccessarily self-perpetuating; Dr. Weaver has the uncanny ability to sustain, in another individual, an insatiable enthusiasum -- through his very own, perhaps.

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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 m^2 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 m^2 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

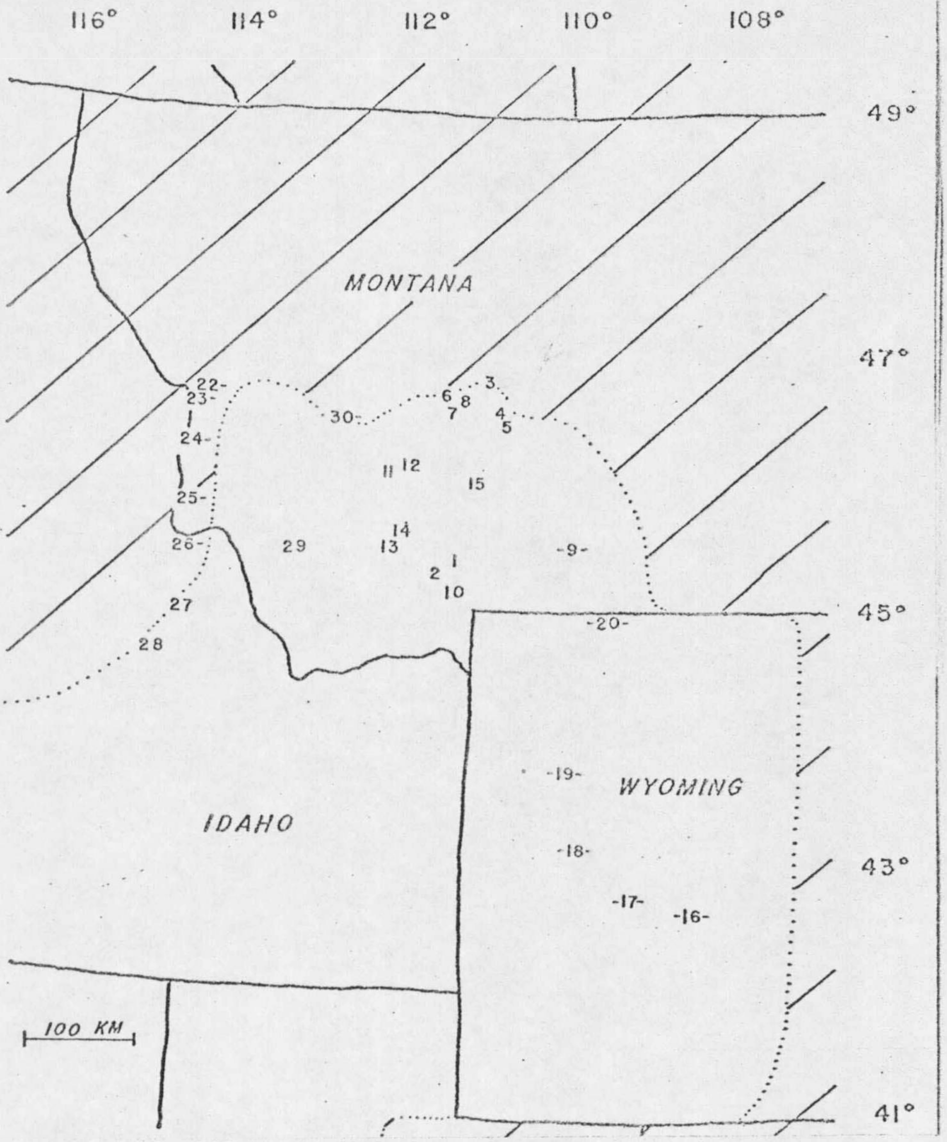

Figure 1. The distribution of the *Pinus albicaulis - Vaccinium scoparium* association. The numbers and their associated characters (e.g. n-, -n-) represent stand numbers and the three geographic/floristic regions referred to in the text. The geographical extent of the stands is thought to represent 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 1*a*. 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 m^2 sampling area is represented by a '+', whereas '1-5' represent frequency classes from low to high.

Stand Age	198	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
Sedum lanceolatum Torr.	1	1	+	.	1	.	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Achillea millefolium L.	.	1	+	1	+	.	+	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Claytonia lanceolata Pursh	.	1	+	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Solidago multiradiata Ait.	.	+	1	+	.	+	1	1	1	1	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	.	.	.
-- *Castilleja rexifolia* Rydb.	.	.	.	+	.	1	.	1	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Agoseris glauca (Pursh) Raf.	.	+	.	1	.	.	+	1	1	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Pinus contorta latifolia Engelm.	.	.	.	.	+	+	.	+	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.
**Aster foliaceus apricus* Gray	.	.	+	.	.	.	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trisetum spicatum (L.) Richter	.	.	1	+	.	1	1	1	.	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	2	.
Lupinus argenteus Pursh	1	+	+	1	.	+	.	1	+	.	2	.	.	.	.	1	+	.	1	.	1	+	1	.	.	.	.	.	.
Potentilla diversifolia Lehm.	+	1	.	.	1	+	.	.	.	.	1	.	.	+	.	.	+	+	.	1	+	.	+	.	.	.	.	.	.
Arnica cordifolia Hook.	.	2	2	3	+	1	2	1	2	+	.	1	.	1	1	+	.	.	.	1	.	.	1	.	.	.	.	.	.
A. latifolia Bong	.	.	.	.	1	3	1	2	3	+	2	2	.	1	1	1	2	2	2	2	3	+	1	1	2	+	1	.	+
Erythronium grandiflorum Pursh	.	.	.	.	.	2	.	2	1	.	1	1	.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+
Carex geyeri Boott	.	.	.	.	.	.	1	1	+	+	.	.	+	3	3	.	.	.	.	.	2	2	3	1	1	2	.	.	+
**Lomatium cusickii* (Wats.) Coult. & Rose	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	+
Pedicularis groenlandica Retz.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	+	.	.	+	.	1	+	1	.	.
Juncus parryi Engelm.	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	1	+	1	1	+
Antennaria lanata (Hook.) Greene	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	1	.	.	1	+
**Luzula hitchcockii* 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.*

Table 1*b*. Flora of the *Pinus albicaulis* - *Vaccinium scoparium* association; the taxa of the association with constancies between 5 and 15% (and which show limited distributions within the association). Table specifications follow those in Table 1*a*.

	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
Lewesia pygmaea (Gray) Robbins.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aquilegia flavescens Wats.	.	+	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola nutallii Pursh	.	+	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla gracilis brunnescens (Rydb.) Hitchc	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lomatium dissectum (Nutt.) Math. & Const.	.	.	+	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antennaria racemosa Hook.	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
*_Osmorhiza purpurea_ (Coult. & Rose) Suksd.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*_Senecio crassulus_ Gray	.	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Valeriana dioica L.	.	.	.	.	.	.	1	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sitanion hystrix (Nutt.) Smith	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
*_Chinophila tweedyi_ (Canby & Rose) Hend.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
*_Arenaria aculeata_ Wats.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sibbaldia procumbens L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.
Heuchera cylindrica Dougl.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.
Spiraea betulifolia Pall.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	+	.	.	.	+	.
*_Xerophyllum tenax_ (Pursh) Nutt.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	1	.	1
*_Arabis hirsuta_ (L.) Scop.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.
Antennaria microphylla Rydb.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	1	.
*_Larix lyallii_ Parl.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
*_Penstemon fruticosus serratus_ (Keck) Cronq.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Phyllodoce empetriformis (Sw.) D. Don.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	+

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 1*a*.

	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
Abies lasiocarpa (Hook.) Nutt.	.	.	1	.	+	1	+	1	1	+	1	+	1	1	.	1	+	+	1	+	.	1	1	+	1	1	1	1	+
Carex rossii Boott	+	1	1	+	1	1	.	1	1	.	1	1	1	.	+	1	1	1	+	+	.	.	+	1	1	+	+	2	.
Poa nervosa (Hook.) Vasey	1	2	2	1	2	1	1	.	1	1	.	1	+	.	1	.	.	.	.	+	+	+	+	.	1	+	+	+	.
Hieracium gracile Hook.	.	+	+	.	+	1	.	1	.	.	2	2	.	.	.	.	+	1	1	2	+	.	1	.	1	+	1	1	.
Epilobium angustifolium L.	.	.	+	2	.	.	1	.	+	1	+	.	.	1	+	+	+	.	.	.	+	1	+	.	.	.	1	+	.
Juniperus communis montana Ait.	.	.	+	.	.	+	1	+	.	.	+	.	.	+	.	+	+	.	.	.	+	1	.	+	.	+	1	+	.
Antennaria umbrinella Rydb.	+	1	.	+	1	.	.	.	.	+	1	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	+	.
Picea engelmannii Parry	.	.	.	1	+	+	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+	+	.
Pyrola secunda obtusata Turcz.	+	.	.	.	.	.	1	.	+	.	.	.	.	.	.	1	.	.	.	.	.	1	.	+	.	.	+	.	+
Penstemon rydbergii A. Nels.	.	.	.	+	.	.	.	.	.	.	2	.	.	.	.	+	.	.	.	.	.	.	.	.	2	2	.	.	.
Oryzopsis exigua Thurb.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	1
Arenaria congesta cephaloidea (Rydb.) Maguire	.	1	+	.	.	.	.	+	.	+	1	+	.	.	.	.	.	+	.	.	.	+	.	.	+	+	.	.	.
Erigeron peregrinus (Pursh) Greene	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.
Polygonum bistortoides Pursh	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.
Fragaria virginiana platypetala (Rydb.) Hall	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.
Ribes lacustre (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 *_Trifloium 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 stenomeres_ Gray, _Bromus carinatus_ H. & A.; 25 *_Leptodactylon pungens_ (Torr.) Nutt.; 24 _Rumex paucifolius_ Nutt., _Salix phylicifolia_ L., *_Veronica cusickii_ Gray, *_Linanthastrum nuttallii_ (Gray) Ewan., *_Penstemon flavescens_ Pennell, _Hieracium albiflorum_ Hook., _Danthonia intermedia_ Vasey, _Hypericum formosum nortoniae_ (Jones) Hitchc., _Agoseris auriantiaca_ (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.

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, Pahsimsroi 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 stenomeres* (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 g/m^2/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 m^2 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 lyallii* 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 overstory. 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 Nevadan 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 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 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 noncalcareous 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 m^2 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 m^2 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 m^2 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 m^2/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 m^2/ha, Daubenmire and Daubenmire 1968) and of the Pacific Coast forests (100-300+ m^2/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

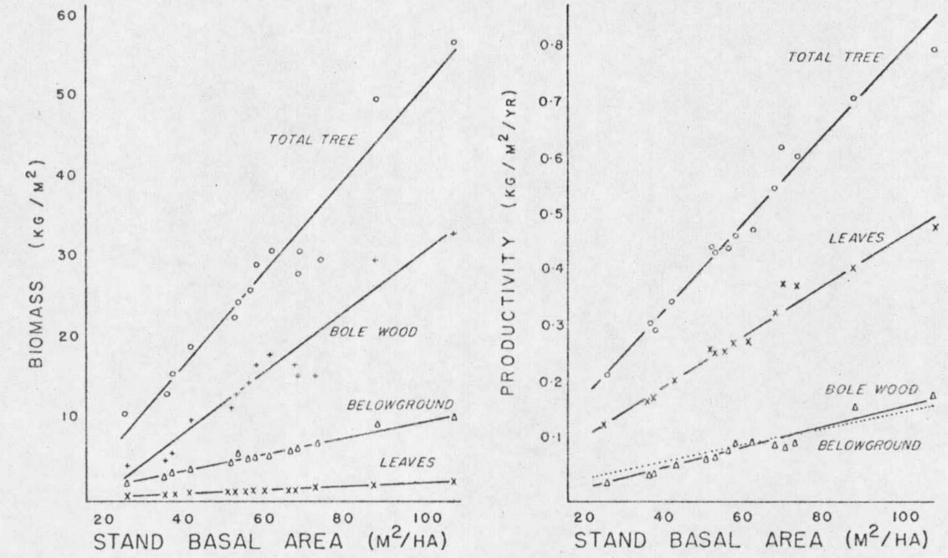

Figure 2. Arboreal biomass and productivity in relation to stand basal area in 14 *Pinus albicaulis* - *Vaccinium scoparium* communities.

forest canopy is more internally consistent then, 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/m^2. The mean mass of *P. albicaulis* roots 0.1-1.0 cm diameter in the eleven 1 m^2 x 0.4 m excavations was 0.4 kg/m^2 (s.d. = 0.18). The mean mass of fine roots (less than 1 mm, species composition unknown) was 0.5 kg/m^2 (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 m^2 quadrats ranged from 0 to 100%. Above- and belowground mass for a quadrat with 100% coverage was 191 and

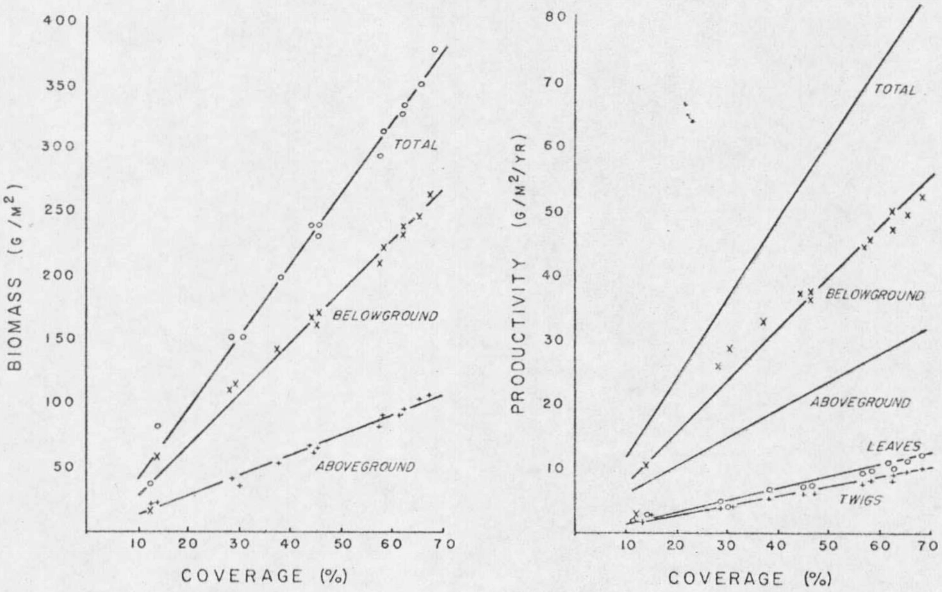

Figure 3. The biomass and productivity of *Vaccinium scoparium* in relation to median shrub coverage in 14 *Pinus albicaulis* - *Vaccinium scoparium* communities. Aboveground wood productivity has been estimated as described in the text.

425 g/m^2, respectively. Herbaceous standing crops (= production) varied, but were small and averaged less than 10 g/m^2.

The mass of the shrub-herb layer (the mean of the averages for three plots per stand) ranged from 23-109 g/m^2 for the aboveground parts, and 20-264 g/m^2 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. vacillans* 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/m^2. Total belowground mass was 3.7-11.3 kg/m^2. Total stand biomass ranged from 12.2-58.8 kg/m^2. 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/m^2 aboveground;

tropical rain forests (Rodin and Bazilevich 1967) with 75 + 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 kg (14 dm^3); 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 $g/m^2/yr$ (= 0.08-0.42 $dm^3/m^2/yr$). Bark production of *P. albicaulis* was about 1-7 $g/m^2/yr$

(Appendix 1). Leaf productivity for the tree layer ranged from 133-475 $g/m^2/yr$, and the belowground productivity estimates were from 50-144 $g/m^2/yr$ (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 $g/m^2/yr$, 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 $g/m^2/yr$), 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 $g/m^2/yr$. The range of total belowground productivity was 168-267 $g/m^2/yr$. Thus total stand productivity ranges from 381-951 $g/m^2/yr$ (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 $g/m^2/yr$, and the arctic treeline *Betula pubescens* 207 $g/m^2/yr$ (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 (±.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

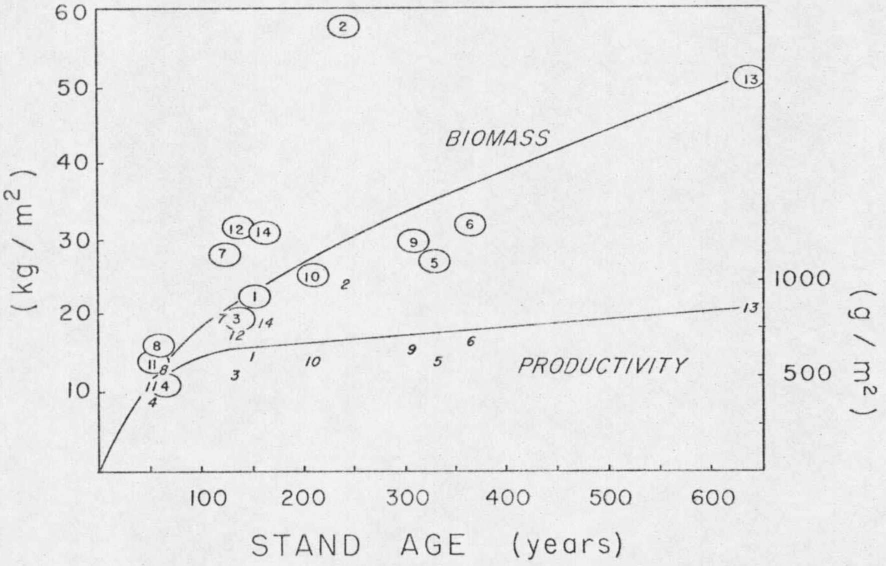

Figure 4. The biomass and productivity of 14 *Pinus albicaulis* - *Vaccinium scoparium* communities in relation to the age of the stand. The left and right Y-axes represent biomass and annual productivity respectively.

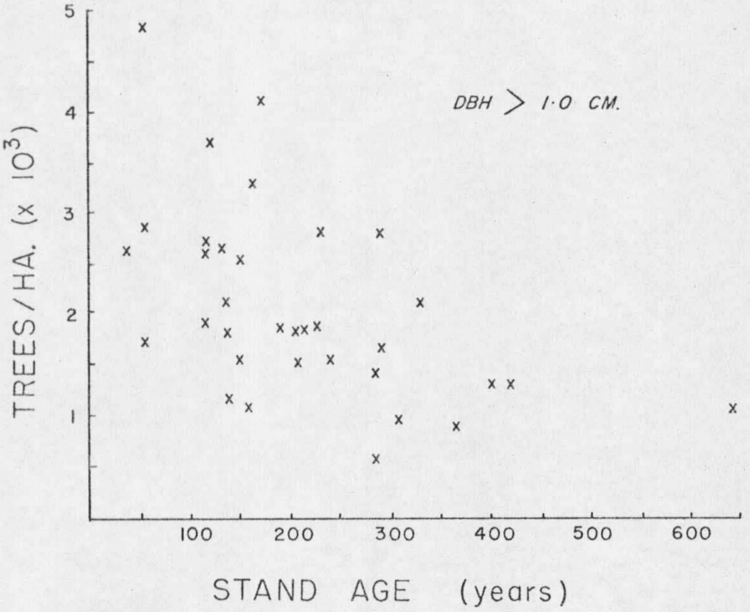

Figure 5. The density of trees (greater than 1 cm dbh) in 33 *Pinus albicaulis - Vaccinium scoparium* communities. Data for 19 of these stands is that of Weaver and Dale (1974).

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 and 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/m^2 with annual productivities as large as 951 g/m^2. Forest biomass usually tend to peak at mesothermal elevations in mountainous systems (Whittaker 1963, Whittaker and Neiring 1975). I have relatively little data for systematic comparisons of my stands to lower forests in the northern Rockies (Weaver and Forcella 1977), but in conjunction with my field observations, these data suggest 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 me. *P. albicaulis* forests do not exist in especially favorable sites; they are often on ridge tops and their psammeptic soils are not particularly fertile (Weaver and 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 aboveground 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

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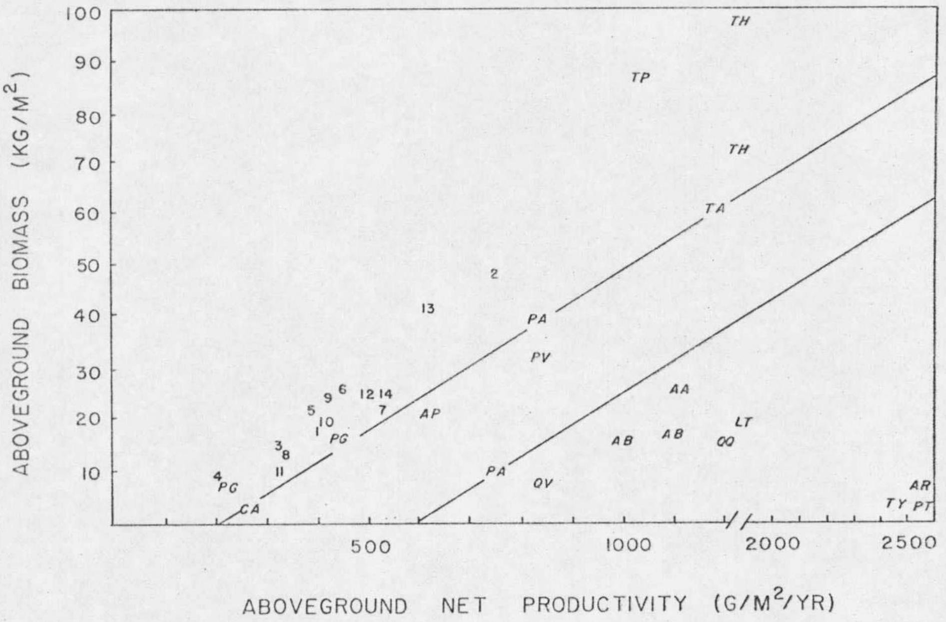

Figure 6. A comparison of biomass accumulation ratios both within the *Pinus albicaulis - Vaccinium scoparium* association and between several vegetation types. The area between the two oblique parallel lines represents the biomass accumulation range for typical temperate vegetation (from Whittaker et al. 1974). *P. albicaulis - Vaccinium scoparium* 1-14; *P. contorta - V. myrtillus* PV, *P. contorta - Geranium fremontii* PG (Moir 1972); *Alnus rubra* AR (Zavitkowskii and Stevens 1972); *Quercus spp.* QQ (Johnson and Risser 1975); *Typha* TY, *Pteridium* PT (Westlake 1963); *Tsuga-Picea* TP (Grier and Logan 1975); *Pinus - Rhododendron* PR, *Cupressus - Arctostaphylos* CA, *Acer - Betula* AB, *Picea - Abies* PA, *Tsuga - Acer* TA, *Lireodendron tulipifera* LT, *Acer - Picea* AP, *Quercus - Vaccinium* QV (Whittaker et al. 1974); *Thuja plicata - Pachistima myrsinites* TH (17500 and 13800 g/m^2/yr, Henley 1976).

of one. My stands, all of which came from what I 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 (x 4), biomass (x 3) and productivity (x 2).

Neither the traditional (hypothesized) logistic biomass - age curve nor the optimal yield (rise and decline) productivity - age relationship is apparent in my 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.

CHAPTER 3

CONE AND SEED CROPS IN THE *PINUS ALBICAULIS* - *VACCINIUM SCOPARIUM* ASSOCIATION

INTRODUCTION

Most investigations of coniferous seed crops depend on either relative estimates of cone production (good year vs. poor year) or quantitative data for single trees. For predictive or etiological models, attempts are often made to correlate either of these two types of data with "causal" factors such as (1) climate, including: temperature, moisture, wind and solar radiation; and (2) silvicultural practices, including: soil fertilization, stand thinning and root and shoot pruning (reviews by Matthews 1963, 1970 and Lahde and Pahkala 1974). Autocorrelation may be used when inherent cyclic variations in cone crops are thought to occur (Rehfeldt et al. 1971). And finally, animal predation may significantly affect the current seed crop and possibly future crops (review by Janzen 1971).

For nearly a century Russian foresters have quantified forest seed production on a unit-area basis with seed traps (Sarvas 1962). Western European researchers and others have since followed and improved this method. Because the actual number and mass of seed produced is of utmost importance to the resource manager, as well as to general biologists, I attempted to quantify: (1) the number of seed produced, (2) the mass of seed produced, and (3) the variation of production on a yearly unit-area basis throughout an age and size spectrum of whitebark pine forests (the *Pinus albicaulis* - *Vaccinium scoparium* association).

PRELIMINARY OBSERVATIONS OF CONE CROPS

Preliminary observations of ovulate cone production in *Pinus albicaulis* Englm. trees, made in 1974 in several SW Montana mountain ranges, led me to the conclusion that current cone number of single trees is poorly correlated with tree dimensions such as: age, dbh, height, tree mass, canopy volume or canopy area ($r^2 < 0.1$ for each). Nor was current cone production (per unit-area) of forests correlated with stand dimensions (age, basal area, canopy coverage and mass).

Whitebark pine cones, like those of other coniferous species (Waring 1958, Baradat 1967, and Matthews 1970) are produced on actively growing leader shoots in the upper portions of the canopy. The greater the areal extent of the canopy, and the greater its exposure to incident radiation, the more numerous will be the leader shoots—the potential sites for cone production. Despite the poor correlation of canopy coverage with cone production in 1974, I believed that the canopy area of a single tree and the canopy coverage of a stand should be correlated with cone production if the yearly fluctuations of production are not considered. Thus, canopy coverage should be correlated with *mean* cone production.

Fortunately, the number of cones produced on a particular leader shoot in past years can be easily estimated by counting the number of scars left by the abscission of cones at the yearly nodes (cf. Gorchakovskii 1958 and Boichenko 1970). Thus, by examination of the nodes of all leader shoots, or a selection of these shoots from individual trees, yearly and mean cone crops should be estimable. In one whitebark pine stand, all leader shoots of 16 trees, each with more than 10 leader shoots/tree, were analyzed for immature first-year cones, mature cones and cone scars. Five leader shoots were then arbitrarily selected from each tree. The data gathered from these groups of 5 were compared (after appropriate extrapolation) to the total leader shoot data of their respective trees. There was no significant difference (t-test, $p = 0.01$) between the sample and the full enumeration data in 13 (81%) of the 16 trees. With these observations, the basis for the 1975 summer sampling procedures was established.

METHODS

In each of 28 stands (Figure 1, excepting stand 30) of the *Pinus albicaulis - Vaccinium scoparium* association, from SW Wyoming to SC Montana to EC Idaho, three 200 m^2 plots (6.67 x 30 m) were selected perpendicular to the slope of the stand. In each plot, the number, dbh, total basal area, total canopy coverage and species of trees in the overstory were determined. Canopy coverage was measured with a vertical periscope at 1 meter intervals along the longitudinal axis of each plot (= 90 points/stand). The composition and coverage of the understory vegetation was estimated with a 2 x 5 dm frame at 2 meter intervals also along the axis of each plot (= 45 frames/stand). Counts were also made of all fallen cones in each plot. These cones were separated into "new" (from the previous year's cone crop) and "old" cones. Cone counts of this type were made for two consecutive years in the same plots in stands 1-14 (Figure 1).

In each stand the canopy area of 5 individual trees was determined from their greatest and least diameters. In each of these trees, I climbed to the top of the canopy where the total number of "potential cone-bearing" leader shoots was counted; 5 of these were also clipped for immature cone, cone and cone scar analyses. Generally cone scars could be detected with some assurance for the previous 4-6 years. Scars left by cones produced prior to this period were often obliterated by diameter growth of the shoot. Thus, by counting the total number of potential cone-bearing shoots, calculating the canopy area of 5 sampled trees and the canopy coverage of the entire stand, together with the yearly cone or cone scar counts on the 25 shoots/5 trees, it was possible to estimate a 6-8 year cone production sequence on a yearly unit-area basis.

An inherent problem of this method is the inability to sample random trees within the stands and random leader shoots within those trees. Specific reasons for these difficulties include the following: 1) Animal devastation of cone-bearing shoots occurs frequently, rendering the remaining shoots a biased sample. *Ursus americanus* (black bear), the normal culprit, usually leaves telltale claw-marks in the tree's trunk and a carpet of broken pine boughs at the base of the tree. Trees with these characteristics were avoided during sampling. *Tamiasciurus hudsonicus* (red squirrel) is ubiquitous in the whitebark pine forests and is probably the cause of the leader shoots found severed near their termini (Squillace 1953, Adams 1955, Schmidt and Shearer 1971). It is not unlikely that these animals are enhancing cone production through their "pruning" action. 2) There were occasional trees which I simply was not able to ascend, hence, sample. 3) Some leader shoots in a sampled tree were in inaccessible portions of the canopy, making attempts at their retrieval somewhat precarious. 4) Shoots bearing cones at the time of sampling were considerably more apparent, and differential sampling may have been a consequence. Another problem, not related to random sampling, is that after immature cone counts were made, abortion could have taken place (cf. Allen 1941, Sarvas 1962, Finnis 1953), though it appeared to be negligible in 1975.

RESULTS

Vegetation

The vegetation of the subalpine *P. albicaulis* - *V. scoparium* association in SW Montana has been described by Weaver and Dale (1974). Vegetational parameters, including net primary productivity, are provided by Forcella and Weaver (1977) and in Chapter 2. Briefly, for the 28 stands sampled for cone production, the overstory of the stands is dominated exclusively by *Pinus albicaulis* Engelm. with basal areas ranging from 12 to 108 m^2/ha, canopy coverage from 10 to 95% and age, at dbh, from 30-640 years (about 10 years can be added for age at base height). Site index at 100 years is 8.0 meters. Net productivity, less cone, is low (ca. 200-850 $g/m^2/yr$) but still in the range of temperate forests.

The understory is dominated by the low-growing (10-30 cm) *Vaccinium scoparium* Leiberg. The mean coverage of this shrub ranges from 5 to 75% between the stands. Herbaceous vegetation and other occasional shrubs only infrequently reach high coverage values. The more common taxa involved include: *Arnica latifolia* Bong., *A. cordifolia* Hook., *Carex geyeri* Boott. and *Luzula* *hitchcockii* Hamet-Ahti. Their presence in the understory appears to vary directly with the stand's geographic position and they might be best described as "local or territorial character" species as discussed by Westhoff and Maarel (1973), Mueller-Dombois and Ellenberg (1974) and in Chapter 1.

Cone Phenology

Ovulate cone primordia normally develop during the late summer to autumn period in most temperate pine species (Mirov 1967). In *P. albicaulis* the immature cones emerge from the buds from early to mid July (about the time of snow melt). They are purple, about 5 mm long and are readily distinguished. Pollinate strobili mature in early July and pollination occurs at this time. For management purposes, this may be the most efficient period for leader shoot analysis and prediction of the two forthcoming cone crops (cf. Allen 1941). By the end of the growing season (mid September) the immature cones are approximately 1.5 x 0.9 cm dimensionally, and they remain in this condition until the following spring (July). One year old cones begin rapid growth in early July and have essentially completed their enlargement by mid August (6.3 x 4.7 cm). Cone maturity continues until mid September to early October when abscission occurs (though abscission may begin as early as mid August). If left unmolested, the cones abscise and fall to the ground intact. Frequently, however, the everpresent *Nucifraga columbiana* (Clark's Nutcracker) will devastate the cones before abscission, leaving only the cone axis with a few basal scales attached to the leader shoots. These axes may remain on the shoots for several years; up to 10 years in some cases. This phenomenon has led to at least one speculation that some populations of *P. albicaulis* have dehiscent cones (Ericson 1965). A more plausible explanation might be that abscising hormones are produced in the cones immediately before abscission. If the cones are destroyed prior to hormone synthesis, abscission fails to occur.

The cones exude and are entirely coated with a viscous, aromatic resin. Resin apparently inhibits seed predation by *Tamiasciurus* (Smith 1970) and *N. columbiana.* As in other pines, the scales appear to be fused by a resin bond (Clements 1910). After abscission, and after the resin has either crystallized or been utilized as a substrate by certain fungi, the scales and large wingless seeds simply fall away from the axis. Small collections of seed and small clusters of seedlings can often be found in the forest litter. They probably result from this *in situ* disarticulation.

Predicting Cone Crops from Stand Characteristics

Cone crops varied greatly both between stands in any given year and between years in any given stand. Generally there were about an equal number of good and poor cone crop years within each stand. The magnitude of the variation was from zero up to 8 cones/m^2/yr between the stands (and between years in the most productive stand). The mean cone productivity/m^2/yr ($\overline{C}$) was found to be correlated with % stand canopy coverage (A, $r^2 = 0.42$, Figure 7):

$$\overline{C} = 0.470 + 0.00032\ (A^2) \qquad \text{Eq. 1}$$

Because A was also used for the initial calculation of cone production, some circular reasoning exists in this regression. However, since both the total number of leader shoots and the estimated mean annual cone production for individual trees is correlated with the canopy area of individual trees (r^2s = 0.69 and 0.58, respectively), I feel that stand canopy coverage is a justifiable "independent" variable.

Stand basal area (BA) and the number of total fallen cones/m^2 (F) are also correlated with $\overline{C}$ (r's = 0.28 and 0.32, respectively):

$$\overline{C} = 0.288 + 0.023\ (BA) \qquad \text{Eq. 2}$$

$$\overline{C} = 0.812 + 0.439\ (F) \qquad \text{Eq. 3}$$

Sarvas (1962) found that ovulate cone production in the *Pinus sylvestris* forests of Finland was correlated (via pollination success) with the areal extent of the stand. He calculated a 2 hectare minimum area for "pollination normal" stands. Topography and time limitations made it difficult to determine the areas for whitebark pine forests, but the 28 stands investigated were subjectively scaled in three general classes: 0.75 ha (= 1), 0.75-1.25 ha (= 2) and 1.25 ha (= 3). Considering that both canopy coverage and stand area (S) may be determined from aerial photographs, and that such photos are often available to land managers, I felt it reasonable to construct a multiple regression equation using both A^2 and S as independent variables. The resultant equation (attributal variability 52%) is:

$$\overline{C} = -0.430 + .00032\ (A^2) + 0.470\ (S) \qquad \text{Eq. 4}$$

Since there appears to be more or less good and poor yearly cone crops, the yearly cone data was divided into these categories (division was generally at the median). The mean of the good and poor yearly cone crops was regressed over stand canopy coverage and stand area (r^2's = 49% and 32%, respectively). The regression equations are:

$$\overline{C}_g = -0.517 + 0.00039\ (A^2) + 0.734\ (S) \qquad \text{Eq. 5}$$

$$\overline{C}_p = 0.269 + 0.00011\ (A^2) - 0.001\ (S) \qquad \text{Eq. 6}$$

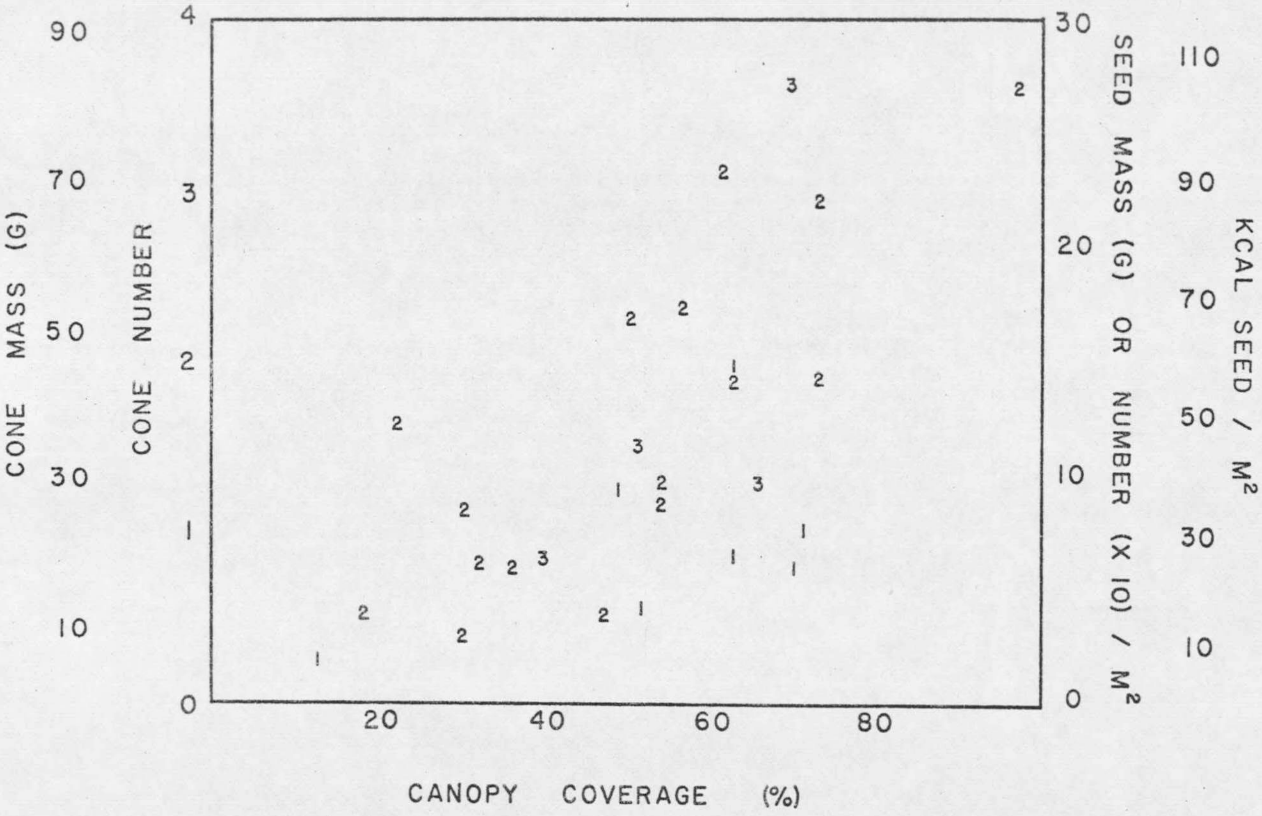

Figure 7. Cone mass and number per m^2 and seed mass, number and energy (endosperm and embryo) per m^2 in relation to stand canopy coverage of 28 stands (Stands 1-29; there is no Stand 21) of the *Pinus albicaulis - Vaccinium scoparium* association. The numbers 1-3 refer to stand areas of less than 0.75 ha, 0.75-1.25 ha and greater than 1.25 ha respectively.

As stated above, the number of fallen cones (F) was correlated with $\overline{C}$ (cf. Sarvas 1962). A multiple regression of $\overline{C}$ over A^2 and F provided the equation ($r^2 = 46\%$):

$$\overline{C} = 0.450 + 0.00023\ (A^2) + 0.206\ (F) \qquad \text{Eq. 7}$$

Though possibly not as useful as Eq. 5, this regression might be beneficial for field surveys.

Further multiple regression analyses employing BA, stand age, stand slope, elevation, aspect, etc. increased attributal variability up to 60%. However, such complicated regressions soon become intangible and make data collection unwieldy.

Originally I had expected that the counts of newly-fallen cones (or remnant cone axes) to equal the actual cone production of the previous year. I also expected that the "leader shoot cone production estimates" would equal the newly-fallen cone counts for the appropriate year. The two methods were not equal in their estimates, but they were correlated (both nonparametrically, r_s = 0.71 [Mosteller and Rourke 1973] and parametrically, $r = 0.72$). Newly-fallen cone counts underestimated the leader shoot estimates (though not badly) as can be seen from the regression coefficient and equation for cone production in 1974:

$$C_{(1974)} = 0.305 + 1.314\ (F_{new}) \qquad \text{Eq. 8}$$

Mounds of old cone scales can often be found at the entrances of rodent dens. This suggests that newly fallen cones may, at least temporarily, be buried underground; thus: 1) making fallen cone counts an underestimate of actual production, and 2) partially explaining the inequality of the two cone production methods.

Biomass and Seed Number

An average mature ovulate cone weighs about 23 grams (range 10-50 g); cones produced in good years tend to be larger than those of poor cone crop years. Single cones support about 75 scales of which a third are infertile (generally the apical and basal scales only). Typical cones contain 75 seeds; each with a mass of about 0.1 g. Within a cone, seed mass is generally 30% of the total, but it may occasionally (and consistently) reach as high as 50% within a stand in a good cone year. Either of these two values is quite high when compared to the reproductive effort in cones of other coniferous species (Smith 1970).

On a unit area basis, average cone production ranges from 6 to 84 $g/m^2/yr$, with seed mass being 2 to 25 $g/m^2/yr$ (= 20-250 seeds) between stands. Previously in Chapter 2, I determined net above- and belowground annual primary productivity (less cones) of 14 of the stands studied here; cone and seed production represent about 10 and 3%, respectively, of the total tree production.

Comparisons With Other Forests

Comparing cone and seed crops of various forests is difficult. Few investigations have asked the same initial question, used the same method for data collection, reported the same "type" of data or in the same units. However, Table 4 presents average cone and seed crops for several *Pinus* forest types. Schopmeyer (1974) was consulted for masses of seeds and cones when not provided by the specific reference.

The number of cones produced by *P. albicaulis* forests appears to be smaller than that of other pine types, especially Diploxylons. However, cone mass, seed mass, seed number and the % seed mass of total cone mass, are all greater for *P. albicaulis*. *P. cembra siberica*, whose individual seed mass is 2-3 times that of *P. albicaulis*, may be an exception. Its seed crops are of sufficient quantity that they are annually harvested for human consumption, but the only seed mass per unit-area figures available are those of Formosof (1933), and these appear to be misprints. If Formosof's figures should read "grams" rather than "kilograms", they would then be 25-30 g/m^2; which is at the upper limit of the *P. albicaulis* range.

Table 4. Comparison of cone and seed crops of several *Pinus* forest types.1/

Forest Type	Average Cones/m^2/yr			Average Seeds/m^2/yr				Reference
	#	grams	%2/	#	grams	%3/	%2/	
Pinus contorta	4.7	28	--	268	0.6	2	-	Smith 1968, -70
P. *contorta* - *Purshia tridentata*	4.8	24	--	120	0.4	2	-	Lotan 1967
P. *contorta* - *Geranium fremontii*	8.0	40	13	---	---	-	-	Moir 1972
P. *contorta* - *Vaccinium myrtillus*	8.0	40	5	---	---	-	-	Moir 1972
P. *contorta bolanderi*	---	52	20	---	---	-	-	West.&Whit. 1975
P. *sibirica*	---	--	--	100	30	-	-	Formosof 1933
P. *sibirica* - *Vaccinium myrtillus*	0.1-2.4	--	--	---	---	-	-	Boichenko 1970
P. *sylvestris* - *Calluna vulgaris*	1.5	9	--	30	0.2	2	-	Sarvas 1962
P. *sylvestris* - *Vaccinium myrtillus*	3.0	18	--	60	0.4	2	-	Sarvas 1962
P. *sylvestris* - *Oxalis acetosella*	4.5	27	--	90	0.6	2	-	Sarvas 1962
P. *monophylla* - *Juniperus osteosperma*	0.1-1.8	2-34	--	1-26	1-9	28	-	Forcella *unpubl.*
P. *edulis* - *Juniperus osteosperma*	0.8	--	--	8	---	-	-	Forcella *unpubl.*
P. *cembroides* - *Juniperus deppeanna*	7.3	17	--	35	6	35	-	Forcella *unpubl.*
P. *albicaulis* - *Vaccinium scoparium*	0.3-3.6	6-84	10	20-250	2-25	30	3	

1/ Ranges in figures represent smallest and largest data provided. 2/ Percent total productivity except third and fourth forest types which are % aboveground productivity only. 3/ Percent total cone mass.

Localizing Cone Crop Variability

As stated earlier, extreme variation in cone crops occurs between years in any stand. But variation may also be expressed between: 1) branches within a tree, 2) trees within a stand, 3) stands within a geographic region, and 4) stands within the entire *P. albicaulis* - *V. scoparium* association (assuming the stands are representative).

To localize the source of variation in cone production, I performed a nested analysis of variance, using the 5-branch/tree samples as the basic data, thereby allowing the comparison between large and small trees, young and old stands, etc. Annual variation of production was tested as an interaction in each "nest" of the analysis.

Cone crops per branch within the 5-branch/tree samples were not significantly different ($p > 0.05$) in 71% of the trees, but annual production was significantly different in 60% of the same trees. Differences in cone production of individual trees within a stand were not significant ($p > 0.05$) in 52% of the stands, but annual production was in 78%.

The stands were divided into 3 geographic regions; though the divisions were subjective, the floristics of the stands substantiate the separations. The regions are: 1) the Wind River and Absaroka Mountains, 2) SW Montana, and 3) the Bitterroot and Salmon River

Mountains (see Chapter 1). Cone production of stands within each region was not significantly different ($p > 0.05$), but yearly production was in each region. An overall analysis of variance (the final nest) of all stands sampled within the *P. albicaulis* - *V. scoparium* association showed no significant difference ($p > 0.05$) both between stands and between years.

It must be recalled that the analyses did not include the entire cone crops of the trees or stands, only the 5 potential cone-producing leader shoots per tree for 5 trees in each stand. With this in mind, the above results suggest that the ability to produce strobili: 1) is inherently similar in branches of the same tree, 2) becomes dissimilar in trees of the same stand, 3) is similar among stands within and between geographic regions (i.e., all stands have equal potential), and 4) the actual cone crops of trees and stands are subjected to annual fluctuations in cone productivity; the non-significant difference between years of stands within the entire association is probably due to compensating variations between geographic regions. This can be shown with factorial analysis where the geographic regions are "blocks" in the analysis. Again, there is no significant difference between stands or years, but there is between geographic regions.

CONCLUSION AND DISCUSSION

The actual number of cones produced over a number of years in the *Pinus albicaulis* - *Vaccinium scoparium* association is probably a function of the number of leader shoots possessed by a tree or a stand. In turn, canopy coverage is in part a description of the numerical and areal extent of the leader shoots; and it is moderately correlated with mean cone productivity. I used a relatively crude method of estimating stand canopy coverage (verticle periscope, 90 points/stand). The summation of canopy areas of all trees in a stand would have been more appropriate--but time consuming. Air-photo interpretation (where possible) of stand canopy coverage may prove an even more useful technique for estimating potential cone crops in whitebark pine forests. When twenty-five leader shoots from each of 28 stands were analyzed for a six to eight year cone production sequence, there was no statistical difference between the stands (except temporally); suggesting that all stands, regardless of their age, size, etc., have similar potentials for cone production. A further suggestion is that the actual difference in total cone production between the stands is a consequence of total leader shoot number (canopy coverage).

With regard to the management of these forests for cone production, whether for silvicultural or wildlife measures, large (but not necessarily old) stands with high canopy coverage (canopy surface area may be even more appropriate) should be encouraged. Older stands (200 + years) often do have more extensive canopies, and in conjunction with the fact that P. *albicaulis* forests are slow growing but long-lived, older stands become even more valuable. Indeed, it may take a young 50-100 year old stand one hundred to two hundred years to simply double its mean short-term annual cone productivity.

Pinus albicaulis cone and seed production varied greatly both between stands and between years. Cone crops varied from zero to eight (0-184 g) per m^2/yr and seed crops from zero to 600 (0-60 g) per m^2/yr. There were approximately an equal number of good and poor cone producing years in the stands sampled. The mean cone and seed crops, from a 6-8 year cone production sequence, ranged from 0.25-3.4 cones (6-84 g) per m^2/yr and 20-250 seeds (2-25 g) per m^2/yr.

Pinus albicaulis cone and seed crops are as great or greater in both mass and number than those of many other pine species. The large, often wingless seed of P. *albicaulis* and other Haploxylon pines (Mirov 1967), which occur in "stress" environments, not only provide a large energy source for their respective embryos but also for their predators (Maley 1975, Formosof 1933), some of whom may function in diaspore dispersal. Thus, for successful colonization and recolonization, trees such as *P. albicaulis* may not only have to produce large energy-rich seeds, but also great numbers of them. This will: 1) attract dispersal agents, 2) mitigate the destructive influence of the dispersal agents and other predators, and 3) insure successful germination and seedling establishment.

Trophic levels are probably essential for the continual functioning of communities and their indigenous species. Yet large consumer populations, if not controlled, could be devastating to producers. It seems reasonable (and often obvious) that strategies for predator avoidance to have been selected for in prey species. Several insects are obligate seed predators of coniferous trees (Mattson 1971, Abrahamson and Kraft 1965, Radcliffe 1952). Mattson (1971) found the populations of seed-consuming insects in *Pinus resinosa* to be correlated to the cone crop size of the previous year regardless of current cone abundance. Perhaps, one strategy for a tree, to avoid seed predation, is to fluctuate cone production (Smith 1970, Janzen 1971). Fluctuations should be of sufficient magnitude as to intermittently "over-" and "under-provision" the predator population. If *P. albicaulis* seed crops are classified and defined as: 1) "excellent", greater than one s.d. unit above the mean, 2) "good", more than average, and 3) "poor", less than average; then excellent seed years should be preceded by an equal number of good and poor years. In my data, excellent seed years were preceded by a significantly greater and lower than expected number of poor (21) and good (9) seed years, respectively ($X^2 = 4.8$, $p < 0.05$).

Variation in seed crops may be both spatial and temporal; they may be inherent within the tree (Rehfeldt et al. 1971, Shoulders 1967, Varnel et al. 1967), climatically induced, or both. The particular strategy or group of strategies employed by a tree species is probably regulated in part by the number of predators and the degree of predation.

CHAPTER 4

FOOD PRODUCTIVITY IN A SUBALPINE ROCKY MOUNTAIN FOREST ASSOCIATION

INTRODUCTION

One of the benefits of considering vegetation as existing in discrete, more or less homogeneous repeatable units, is the ability to make generalizations about them. These generalizations can take the form of management recommendations such as: cattle grazing potentials, timber harvests, road building and maintenance, recreation feasibility and many others. The abstract vegetation units, or plant associations, are also prerequisite for constructing vegetation maps - which further facilitate management decisions.

Some plant associations of a given region are particularly and consistently more valuable for certain uses than are others. For instance, the subalpine *Pinus albicaulis* - *Vaccinium scoparium* association (whitebark pine - grouse whortleberry forests) of the northern Rocky Mountains is an important component of the array of plant associations which comprise the environment of *Ursus arctos* (grizzly bear), *U. americanus* (black bear) and numerous other animals. The importance of this association to wildlife stems from its high production of high energy foods. If quantitative generalizations concerning the annual production of these foods within this association can be made, then 1) the potential annual diet of the animal(s) is known, and 2) approximation of wildlife demographics are possible.

The vegetational characteristics of the *P. albicaulis - V. scoparium* association have been generally described by Weaver and Dale (1974); as have above- and belowground productivity (Chapter 2), the spatial distribution of the understory shrubs (Forcella 1975), the annual production (and its variability) of ovulate cones and seeds (Chapter 3) and the distribution of the association with its floristic variation (Chapter 1).

In this chapter I shall report production and calorific value summations for all plant foods, known to be of importance for wildlife, taken from 28 stands of *P. albicaulis - V. scoparium* association (Figure 1, excepting stand 30). The geographic range of these stands and of the association itself, extends from west-central Wyoming, through southwestern Montana to east-central Idaho.

METHODS

Canopy coverage, the percent of ground surface covered by a vertical projection of the aerial parts of plants (Daubenmire 1959), makes an efficient parameter of plant biomass when it is estimated separately for each species occurring within a given habitat. Such estimates were made in 10% classes for each vascular plant species encountered within forty-five 2 x 5 dm frames in each of the 28 sampled stands. Further sampling details are given in Chapters 1, 2 and 3. From several of these 2 x 5 dm plots, the aboveground portions of all plants which were of known forage value and of sufficient quantity to be of importance, were also clipped, oven-dryed (60°C) and weighed. (For sample numbers, see caption of Figure 8). Fruit production of *V. scoparium* was determined by picking, drying (60°C) and weighing all berries which occurred in several 1 m^2 plots. The coverage of this shrub was additionally estimated as above in each of these plots. Calorific values were obtained for all plant parts through standard bomb calorimetric procedures (Chem. Stn. Analytic Lab., M.S.U.).

Simple linear regressions were developed for both mass and kilocalories (annual production) of each species per m^2 using their respective canopy coverages (including square or square root transformations) as the independent variables. The resultant regression equations were then used to calculate total mass and calorific values for each species from their respective *mean* coverages in each stand.

Nomenclature follows that of Hitchcock and Cronquist (1973), for plants, Hoffman and Pattie (1968) for mammals, the American Ornithologist's Union (1957) for birds, or the specific reference cited.

RESULTS AND DISCUSSION

The annual production of edible mass and energy of all known and important wildlife foods which occurred in the *P. albicaulis* stands are shown in Figure 8, where they are plotted against their respective canopy coverage values.

The data for *P. albicaulis* mast (seeds) for the stands, which is by far the most important food source, were taken from Chapter 3 and are reported as mean annual seed productivities. There are, however, substantial yearly fluctuations of cone crops in whitebark pine forests, and this likely has significant consequences for the animals dependent on them., e.g., grizzly bears (Craighead 1976). Yearly cone crops can be separated into "good" and "poor" crops, and the mean good and poor cone crops are also correlated with arboreal canopy coverage, (Chapter 3). These correlations of good and poor cone crops with canopy coverage may be of greater importance to wildlife and wildlife managers than are correlations with average crops. It is also of management significance that since ovulate pine cones require 2 years for maturity, the resultant mast crops can be predicted by more than a year in advance of their ripened edible state (Allen 1941, Chapter 3). Conceivably, animals other than forest researchers might also be able to predict future cone crops and thereby regulate their populations accordingly. For

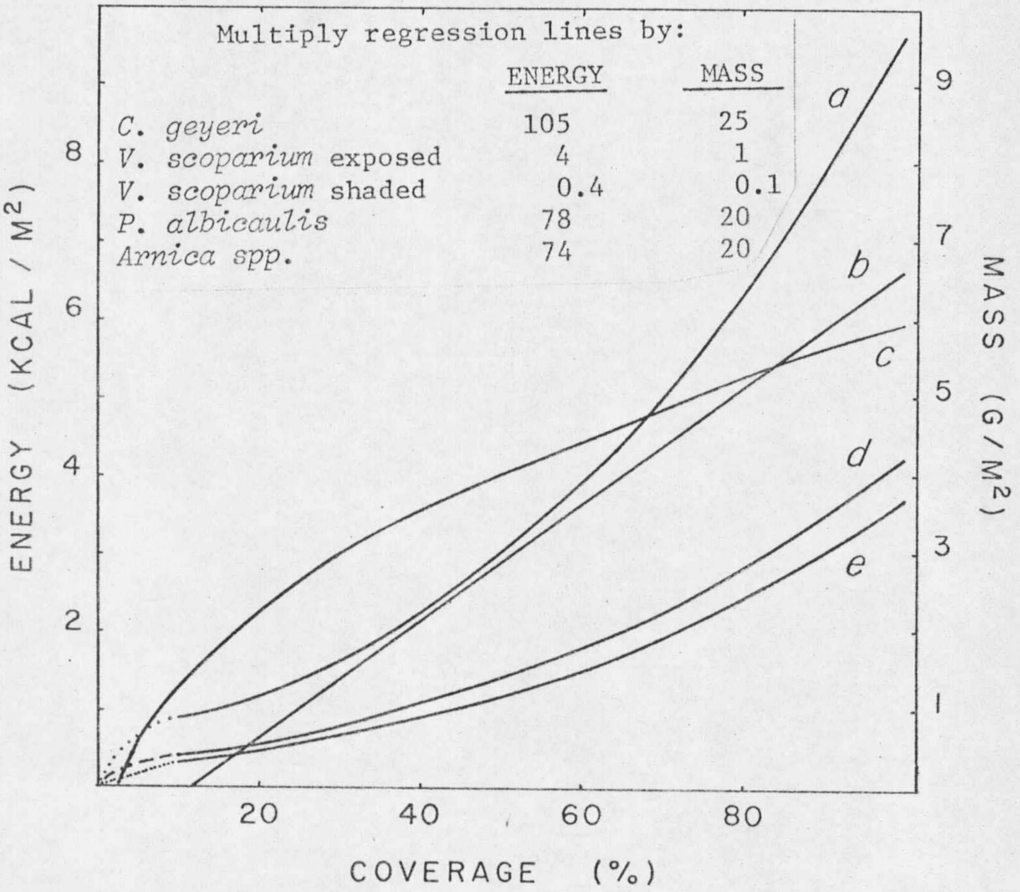

Figure 8. The annual available mass and energy of plant foods as a function of the canopy coverage of the taxa which produced them: The lettered regression lines, the corresponding taxa and the correlation coefficients for the regressions are as follows: *a) Carex geyeri* foliage, r=0.85 (n=27); *b) Vaccinium scoparium* fruit, 'exposed plots', r=0.81 (n=27); *c) V. scoparium* fruit, 'shaded plots', r=0.84 (n=10, ≠ 187 see text); *Pinus albicaulis* seed, r=0.65 (n=28); *e) Arnica latifolia* and *A. cordifolia* foliage combined (kcal/m^2 are identical), r=0.98 (n=24). Values for lines *a*,*d* and *e* below 10% coverage have been estimated and do not follow the generated regression equations. Energy of *P. albicaulis* is for seed endosperm and embryo only. Note the different scales for each function.

example, conception and the number of births of *Tamiasciurus douglasii* (Douglas squirrel) in British Columbian conifer forests, are correlated with the size of the forthcoming mast crop (Smith 1970). A similar mast crop - fertility pattern exists for *Sciurus carolinensis* (gray squirrel) in Ohio (Nixon et al. 1975). This seeming ability of the squirrels to "second guess" mast crops becomes less improbable when one considers the ready visibility of the young cone buds (and/or first year cones in *Pinus*) and the longstanding relationship of the squirrels with the trees and their seeds.

Berry production of *V. scoparium* and its calorific content is slight in comparison with mast on a unit-area basis. Since the berry data recorded for 187 one m^2 plots within the whitebark pine stands was extremely variable, the means for each 10% coverage class (c.v. 's = 100%) were used in the regression shown in Figure 8*c*. The relationship shown here indicates that with increasing canopy coverage of *V. scoparium*, a saturation point for fruit production occurs (at about 40%). This is probably due to the shading effect of the increasingly dense foliage. The high light requirement for fruit production in *Vaccinium* spp. is well known (Hall 1958, Aalders et al. 1969). This light requirement for *V. scoparium* is alluded to when comparing fruit production under a forest canopy with that at the edges of clear cuts or natural openings (Figures 8*c* and *b*, respectively). Fruit production in the exposed sites is considerably greater (x 10) than that of the shaded areas, and it is much less variable (c.v. = 30%) and a saturation point is not evident. Measurements of light intensities were made in 10 of the stands for 24-hour periods with 5-10 integrating light meters (Friend 1961) in each stand. The mean light intensity for the stands was 84±10% full sunlight; the lowest recorded intensity for any single light meter was 66% full sunlight. Apparently, fruit production in *V. scoparium* is comparatively light sensitive (cf. Hall 1958, Aalders et al. 1969). Management decisions which include disturbance of the overstory in whitebark pine forests will increase *V. scoparium* fruit production.

The dominant and edible herbaceous species: *Carex geyeri*, *Arnica latifolia* and *A. cordifolia* (Figures 8*a*, *e*), only rarely obtain mean coverage values greater than 10%; cumulative interspecific herbaceous coverage rarely exceeds 15%. These herbs do, however, contribute substantially to the forage mass and energy of the association; for ungulates they may be of singular importance.

The between stand range (and mean ± s.d.) of kcal/m^2/yr for each plant mentioned above is: *P. albicaulis* seed 8-105 (42±28), *V. scoparium* fruit 0.2-2 (1.2±0.5), *C. geyeri* foliage 0-105 (21±35), *A. latifolia* foliage 0-33 (8±10) and *A. cordifolia* foliage 0-27 (4±7). The high variation of energy of the 3 herbs is partially a consequence of the floristic and compositional variation of the association. The presence and abundance of these and other herbs in the understory of whitebark pine forests is directly related to the geographic (floristic) region in which the stands are located (Chapter 1). For example, if the 28 stands are separated into 3 regions (Wyoming, Idaho and SW Montana, and W Montana; see Figure 1), the differing quantities of each of the three herbs in these regions are clearly distinguishable (t-test, $p = 0.01$). Knowledge of such phenomena may be useful in natural resource management (including domestic stock grazing), when interpreting vegetation maps, for example.

The total food energy available per year in the 28 stands ranges from 11-178 (76±46) kcal/m^2. Assuming that the median of the stands represents the typical whitebark pine forest, then such a forest produces 75 kcal of food energy per m^2 annually. In comparison with other temperate coniferous forests, *P. albicaulis* appears to be significantly more productive (Smith 1968, Chapter 3); *P. sibirica* forests in the U.S.S.R. may be an exception (Formosof 1933, Pravdin 1963, Chapter 3). Agricultural systems may be as much as 9 times more productive than whitebark pine forests: from 1970-1974, typical highly-managed North American wheat fields annually produced 693 kcal/m^2 of food energy (= 0.21 kg/m^2; U.S.D.A. 1974; for conversions see Revelle 1966). If the "cultural energy" used to produce the wheat crop is considered (about 1/3 the total crop; Heichel 1976), then the net energy production difference between *P. albicaulis* and wheat fields is reduced to a factor of 6. One might assume that cultural energy is not used in pine cone production; however, in the procurement of seeds, red squirrels (*Tamiasciurus hudsonicus*) and black bears climb the trees and often destroy the leader shoots on which the strobili are maturing. Such leader shoot damage may well be analogous to the endergonic pruning practices of silviculturists and horticulturists.

A high primary production of food energy in any type of vegetation should also be reflected in its secondary productivity. In reference to forests of *P. sibirica* (a taxon closely related to *P. albicaulis*), Formosof (1933) states that mice, voles, chipmunks, squirrels, sables, brown bears, boars, deer and many species of birds "have constant recourse to this food (pine nuts)." Formosof also points out that: 1) it is only during years of mast failures in Siberia that the nutcracker (*Nucifraga caryocatactes macrorynchus*) mass-migrates west, as far as Britain, 2) the annual marketing of squirrel (*Sciurus vulgaris*) pelts is clearly correlated with the magnitude of the mast crop, and 3) during good mast years, the seeds are regularly collected for human consumption. Pravdin (1963) states that Siberian villagers have even selected for high-yielding trees in their local village plantations.

There are no supportive data for the dependence of secondary production on plant food availability in *P. albicaulis* forests, but there is speculation: for grizzly bears (Craighead 1976) and my own observations suggest it for red squirrels and *Nucifraga columbiana* (Clark's nutcracker). If these speculated dependencies are not for population number *per se*, they are at least for population distribution within a mountain range. The frequency of *Cervus canadensis* (elk), *Odocoileus hemionus* (mule deer) and *Canachites* spp. (grouse) scat in *P. albicaulis* stands attests to even more possible and partial dependencies.

Except for the present on-going "Interagency Grizzly Bear Study" (U.S.F.S., U.S.N.P.S. and local state agencies) there are no data concerning animal demographics in the *P. albicaulis* - *V. scoparium* association. However, if the energetics of individuals are known, it is possible to speculate maximum potential population densities. The best pertinent example that I know of is for *T. hudsonicus*: the average annual energy content of food available in individual red squirrel territories in *Pinus contorta* (lodgepole pine) forests is about 40,000 kcal (Smith 1968; for a deciduous forest see Montgomery 1975). The areal extent of these territories fluctuates with the size of the mast crop, but they average about one hectare. With respect to seeds and berries only, the same kcal-territory needed to fulfill the energy requirements of red squirrels in whitebark pine forests would be 0.1 ha (= 10 squirrels/ha).

Black bears annually consume about 3.4×10^6 kcal in research pens (*per. comm.* with Dr. R.A. Nelson, Mayo Clinic, Rochester, Minnesota 1976). Assuming (naively) that these bears consume only and all whitebark pine forest foods, then such forests could potentially support 0.2 bears/ha (= 20 bears/km^2) in average years. Usual ursine densities encountered within typically high bear density areas in North America range from 0.03-0.5 bears/km^2 (Martinka 1974, Jonkel et al. 1971, Murphy and Floor 1973, Cole 1967).

Blankinship (1905) has listed *P. albicaulis* seed as a common item in Montana Indian diets. The average extant (U.S.A.) citizen eats about 1/3 as much as a bear--about 1.15×10^6 kcal/hr; the average World citizen consumes 0.87×10^6 kcal/yr (U.S.D.A. 1974). *P. albicaulis* forests (seeds and berries only) could potentially support about twice as many U.S. citizens as bears, or 2.5 x as many average humans. For comparison, 1 ha of the wheat fields previously referred to (gross yield; x 2/3 for net yield) could conceivably feed 173 squirrels, 8 World citizens, 6 Americans, 2 bears or a combination thereof.

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APPENDIX 1

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/cm^3, 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/m^2 in the 14 stands studied. The regression coefficient of 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 2); 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 m^2/ha/yr with a corresponding bark production of 1 to 7 g/m^2/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 x 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.

Appendix 2. Locations of the 29 *Pinus albicaulis* - *Vaccinium scoparium* communities.

Stand	Mountain Range	County	State	Longitude	Latitude
01	Madison	Madison	Mont.	111 27	45 17
02	Madison	Madison	Mont.	111 27	45 17
03	Little Belt	Meagher	Mont.	110 41	46 51
04	Castle	Meagher	Mont.	110 46	46 29
05	Castle	Meagher	Mont.	110 46	46 29
06	Big Belt	Broadwater	Mont.	111 15	46 27
07	Big Belt	Broadwater	Mont.	111 16	46 27
08	Big Belt	Broadwater	Mont.	111 16	46 27
09	Absaroka	Park	Mont.	110 15	45 10
10	Madison	Gallatin	Mont.	111 24	45 11
11	Elkhorn	Broadwater	Mont.	111 56	46 18
12	Elkhorn	Broadwater	Mont.	111 56	46 18
13	Tobacco Root	Madison	Mont.	111 55	45 26
14	Tobacco Root	Madison	Mont.	111 55	45 26
15	Bridger	Gallatin	Mont.	111 59	45 54
16	Wind River	Sublette	Wyo.	108 52	42 38
17	Wind River	Sublette	Wyo.	109 11	42 45
18	Wind River	Sublette	Wyo.	109 51	43 09
19	Absaroka	Teton	Wyo.	110 05	43 44
20	Absaroka	Park	Wyo.	109 33	44 56
22	Bitterroot	Ravalli	Mont.	114 13	46 42
23	Bitterroot	Ravalli	Mont.	114 13	46 42
24	Bitterroot	Ravalli	Mont.	114 20	46 15
25	Bitterroot	Ravalli	Mont.	114 17	45 33
26	Bitterroot	Lemhi	Idaho	114 18	45 28
27	Salmon River	Lemhi	Idaho	114 06	45 02
28	Salmon River	Valley	Idaho	114 28	44 36
29	Pioneer	Beaverhead	Mont.	113 55	45 20
30	Red Mt. Cont. Div.	Lewis&Clark	Mont.	112 14	46 28

Appendix 3. Estimated annual cone crops for *Pinus albicaulis*.

STAND	ESTIMATED CONE CROP/M^2							
	1976	1975	1974	1973	1972	1971	1970	1969
16	2.71	2.52	0.25	2.52	1.01	2.52	--	--
17	2.02	3.80	1.60	1.60	1.37	1.13	--	--
18	1.25	1.25	0.65	0.77	0.57	1.50	--	--
19	0.68	1.73	0.16	0.92	0.92	0.72	--	--
20	1.23	1.94	1.66	0.71	0.62	1.28	--	--
10	0.58	0.77	0.69	0.17	0.64	0.86	0.22	--
01	0.64	3.77	1.20	2.21	0.92	1.75	0.92	--
02	1.13	4.91	5.38	4.63	3.12	4.63	1.23	--
07	0.00	0.09	8.96	3.13	3.65	3.91	1.65	3.48
06	0.52	0.40	2.65	1.62	1.79	2.54	0.75	1.73
08	1.70	0.38	2.57	0.19	0.19	1.51	0.19	1.88
12	1.53	6.12	1.88	2.24	2.00	3.88	1.41	4.23
11	0.25	2.06	0.55	0.46	0.46	1.30	0.25	1.26
09	0.94	1.37	1.58	1.15	1.50	0.47	0.85	--
14	1.49	3.60	3.34	0.53	2.73	3.78	0.53	--
13	0.27	0.18	0.36	0.27	1.34	0.63	0.18	--
05	0.87	0.00	1.77	0.60	0.93	0.75	--	--
04	1.50	0.33	1.20	0.66	0.23	0.63	--	--
15	1.04	0.03	1.22	0.00	0.10	0.06	--	--
03	0.19	0.00	3.80	1.83	0.48	1.27	--	--
22	2.51	1.13	4.86	2.27	2.35	2.67	1.22	1.05
23	0.45	0.79	0.52	0.79	0.81	0.34	0.05	0.05
24	0.69	0.23	0.27	0.29	0.31	0.29	0.04	0.06
25	0.74	3.68	0.84	3.78	1.68	1.10	0.74	0.42
26	0.14	2.30	0.34	0.98	1.15	0.64	0.24	0.41
27	1.12	2.59	0.80	1.92	1.09	0.68	0.32	0.47
28	0.11	0.93	0.36	0.61	0.41	0.21	0.11	0.16
29	1.10	2.80	8.41	2.80	6.20	3.30	0.90	3.60

[redacted]