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Cone production in *Pinus albicaulis* Forests

Tad Weaver and F. Forcella

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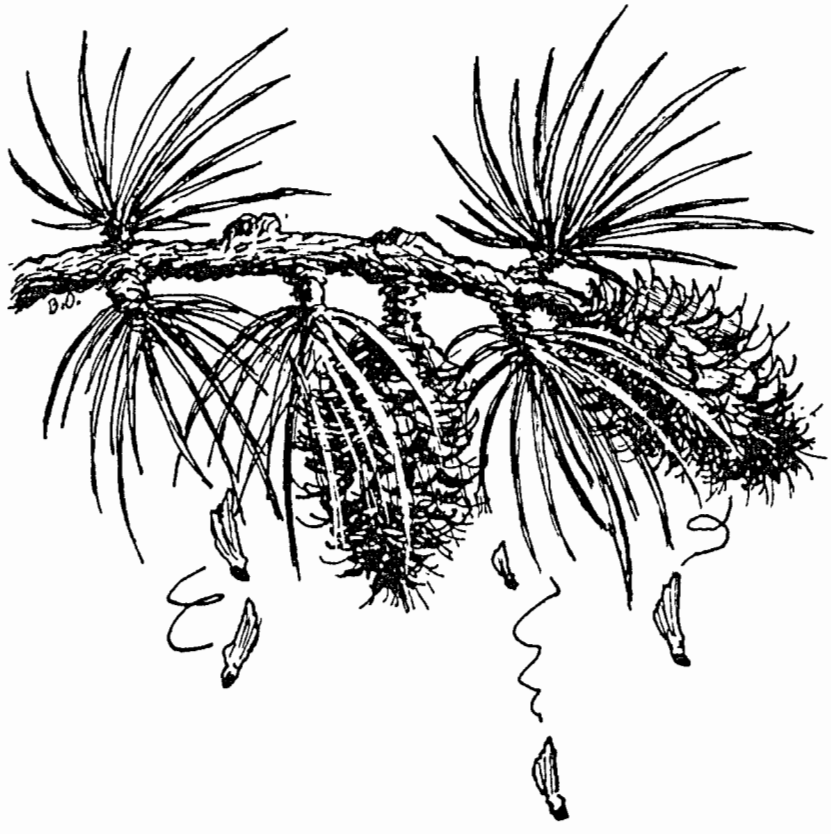
April 1986

Proceedings—Conifer Tree Seed in the Inland Mountain West Symposium

Missoula, Montana, August 5-6, 1985

CONE PRODUCTION IN PINUS ALBICAULIS FORESTS

T. Weaver and F. Forcella



FOREWORD

The symposium "Conifer Tree Seed in the Inland Mountain West" started, developed, and matured in much the same manner and time frame as many conifer cone crops. Like the biological stresses that often stimulate cone production, the stress of knowledge needs prompted the initiation of this symposium.

The first suggestion that a symposium be held to consolidate the available cone and seed knowledge came at a January 27, 1983, meeting of Forest Service Intermountain Station and Northern Region scientists discussing cone and seed production information needed to enhance natural and artificial regeneration in the Northern Rockies. Like the initiation of a cone bud, the idea for a symposium was nothing really new, it just came at the right time and fell into a fertile environment of silviculturists, geneticists, and entomologists.

A steering committee, chaired by Dr. Raymond C. Shearer of the Intermountain Research Station, was formed and proceeded with the planning. Committee members were: Dr. George Blake, School of Forestry, University of Montana; Mr. Jerald E. Dewey, Pest Management, Northern Region, Forest Service; Dr. A. K. Hellum, Department of Forest Science, University of Alberta; Dr. George E. Howe, Division of Timber Management, Northern Region, Forest Service; and Mr. Wayne Maahs, Forestry Division, Champion International Corporation. The School of Forestry and Center for Continuing Education of the University of Montana handled many of the logistical details for the symposium and the Intermountain Research Station edited and published the proceedings.

Numerous meetings, letters, announcements, coordination sessions with authors, and a host of other details preceded the very successful symposium, August 5-6, 1985. Included were 40 papers presented by silviculturists, geneticists, entomologists, physiologists, pathologists, nurserymen, and others. The objective of the symposium--to consolidate information and research conducted on conifer tree cones and seeds native to the Inland Mountain West of the United States and Canada--was met, and 164 attendees left with a much better idea of what is known about western conifers. This symposium culminated efforts of many people, and, like a cone that survives all the hazards and produces seed at the end of its development period, succeeded in producing a very viable proceedings.

Wyman C. Schmidt, Silviculture Project Leader
Intermountain Research Station
Forest Service, U.S. Department of Agriculture
Bozeman, MT

Proceedings—Conifer Tree Seed in the Inland Mountain West Symposium

Missoula, Montana, August 5-6, 1985

Compiler:

RAYMOND C. SHEARER, Research Forester, Intermountain Research Station, Missoula, Montana

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CONTENTS

Page

Keynote Address

Seed Conservation Problems: Natural and Unnatural
J. Derek Bewley and Andrew D. Powell 1

Section 1. Cone and Seed Biology 13

Review Paper:
Cone and Seed Biology
John N. Owens 14

Contributed Papers:
Idaho Western Redcedar (Thuja plicata Donn.) Conebearing Status in an Unusually Dry Year
William R. Gall and Allen S. Rowley 32
Effects of Cold Stratification and Seed Coat Sterilization Treatments on Pinyon (Pinus Edulis) Germination
Gerald J. Gottfried and L. J. Heidmann 38
Acetone is Unreliable as a Solvent for Introducing Growth Regulators Into Seeds of Southwestern Ponderosa Pine (Pinus Ponderosa var. Scopulorum)
L. J. Heidmann 44
Are You Getting Ponderosa Pine and Douglas-fir Cone Crops at High Elevations?
Glenn L. Jacobsen 47
Seed-Dispersal Characteristics of Conifers in the Inland Mountain West
Ward W. McCaughey, Wyman C. Schmidt, and Raymond C. Shearer 50
Cone Production on Douglas-fir and Western Larch in Montana
Raymond C. Shearer 63
Cone Production in Pinus Albicaulis Forests
T. Weaver and F. Forcella 68

Section 2. Cone Prediction, Collection, and Processing 77

Review Paper:
Cone Prediction, Collection, and Processing
D. G. W. Edwards 78

Contributed Papers:
Can We Attain British Columbia Seed Production Goals for Interior Spruce?
Paul J. Birzins 103
Cold Stratification for Lodgepole Pine Seed
A. K. Hellum and I. Dymock 107
Effect of Stratification Time and Seed Treatment on Germination of Western White Pine Seed
R. J. Hoff 112
Seed Dormancy in Three Pinus Species of the Inland Mountain West
Carole L. Leadem 117

Page

Net Retrieval Seed Collection
James L. McConnell and Jerry L. Edwards 125
Douglas-fir Seed Collection and Handling
Richard M. Schaefer III and Daniel L. Miller 129
Aerial Cone Harvesting in British Columbia
D. P. Wallinger 133
Reconditioning Stratified Seed at Pine Ridge Forest Nursery
Katherine A. Yakimchuk 140

Section 3. Seed Orchard and Seed Production Area Management 144

Review Paper:
Review of Seed Production Area and Seed Orchard Management in the Inland Mountain West
Jenji Konishi 145

Contributed Papers:
Production of Improved Western White Pine and Douglas-fir at Potlatch Corporation's Cherrylane Seed Orchard
Roger L. Blair 159
Potential and Actual Seed Yields from a Southern Pine Seed Orchard
David L. Bramlett 162
Effect of Nitrogen Fertilizer and Girdling on Cone and Seed Production of Western Larch
Russell T. Graham 166
Flowering of Pinaceae Family Conifers With Gibberellin $A_{4/7}$ Mixture: How to Accomplish it, Mechanisms and Integration with Early Progeny Testing
Richard P. Pharis and Stephen D. Ross 171
Potential for Container Seed Orchards
Stephen D. Ross, Andrea M. Eastham and Ralph C. Bower 180
Managing Black Spruce Seedling Seed Orchards for Cone and Seed Production
Ronald F. Smith 187
Variation in Cone and Seed Production from Natural Stands, Plantations, and Clonal-Banks of Lodgepole Pine
Cheng C. Ying and Keith Illingworth 191

Section 4. Effects of Biological Factors On Seed Production 200

Review Paper:
Influence of Vertebrates on Conifer Seed Production
Curtis H. Halvorson 201

Contributed Paper:
Squirrel Behavior Influences Quality of Cones and Seeds Collected from Squirrel Caches--Field Observations
Jeanne L. Pedro White and Monte D. White 223

Page

Review Paper:
Insects and Conifer Seed Production in the Inland Mountain West: A Review
Gordon E. Miller. 225

Contributed Papers:
Insects Destructive to Ponderosa Pine Cone Crops in Northern Arizona
Elizabeth A. Blake, Michael R. Wagner and Thomas W. Koerber. . . . 238
Western Spruce Budworm Impact on Douglas-fir Cone Production
Jerald E. Dewey 243
Protection of Blister Rust-Resistant Western White Pine Cones from Insect Damage with Permethrin and Fenvalerate
Michael I. Haverty and Patrick J. Shea 246
Insect Problems and Control Efforts Associated with Selected Douglas-fir Plus Trees
William F. Johns 251
Implantation and Injection of Systemics to Increase Seed Yield in Douglas-fir
Richard C. Reardon and Larry E. Stipe 252
Impact of Insects on Cone/Seed Production in Three Blister Rust-Resistant Western White Pine Seed Orchards
Patrick J. Shea 256

Review Paper:
Influence of Diseases on Seed Production
Jack R. Sutherland 260

Contributed Papers:
Diseases of Conifer Seedlings Caused by Seed-Borne Fusarium Species
R. L. James 267
Monoclonal Antibodies Recognizing the Seed-Borne Fungal Pathogen Sirococcus strobilinus
Leslie Ann Mitchell 272

Poster Paper Abstracts 279

Symposium Summary: Conifer Tree Seed in the Inland Mountain West
Stanley L. Krugman 282

Attendance Roster 283

CONE PRODUCTION IN PINUS ALBICAULIS FORESTS

T. Weaver and F. Forcella

ABSTRACT: Whitebark pine cone production was estimated for a 6 to 8 year period in each of 29 stands widespread in the northern Rocky Mountains. 1) One-time sampling was possible since the estimate was made by multiplying the number of branches per m^2 by an estimate of annual cone production made from counts of conelets, mature cones, or cone scars on successively older annual increments of those branches. 2) Average cone production ranged from 0.3 to 3.6 cones$\cdot m^{-2} \cdot yr^{-1}$ and from 22-270 seeds$\cdot m^{-2} \cdot year^{-1}$. 3) Regression analysis was used to relate the variance observed to time and place. a) Year-to-year variation in the cone yield of branches, trees, and stands in a region appears to be both internally and externally controlled. Internal control is suggested by the fact that good cone years were usually preceded by poor cone years. While external control is indicated by significant correlations between growth and weather conditions, control is not dominated by the effect of any one factor or any particular developmental stage. b) Although cone production of the average branch varied significantly within 30 percent of the trees and within 48 percent of the stands observed, it did not vary significantly among stands. c) Regressions relating stand cone production to easily measured stand characteristics such as canopy cover, fallen cones, and/or stand size explain no more than 50 percent of the variance among stands.

INTRODUCTION

Pinus albicaulis (whitebark pine) is a dominant or codominant tree in many high-altitude forests of western North America (Weaver and Dale 1974; Arno 1986). Its large, well-provisioned seeds are important not only for their reproductive function, but also as food for man, bears, squirrels, and nutcrackers (Blankenship 1905; Forcella and Weaver 1980; Kendall 1980b; Hutchins and Lanner 1982; Tombach 1983). Managers considering either of these functions might ask: What is average production? How does it vary between stands? How does it vary between years? And how might I estimate these variables in an unstudied stand?

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

In 1976 T. Weaver and F. Forcella were Professor of Botany and Graduate Research Associate, Biology Department, Montana State University, Bozeman. F. Forcella is now Research Agronomist, USDA Agricultural Research Service, Morris, MN.

This paper (1) demonstrates a method for estimating a stand's cone production over a 6 to 8 year period after a single sampling, (2) reports estimates made in 29 stands widespread in the northern Rocky Mountains, and (3) uses that data set both to determine the relationship of yield to easily measured stand characteristics and to determine the relationship of yield to regional weather conditions.

METHODS

Cone production.--Cone production in the 1969 through 1976 period was estimated for 29 P. albicaulis stands from the Montana-Idaho border [Bitterroot (5 stands) and Salmon River (2) Mountains], from southwest Montana [Little Belt (1), Big Belt (3), Castle (3), Elkhorn (2), Pioneer (1), Tobacco Root (2), Madison (3), and Bridger Mountains (1)] and from western Wyoming [Absaroka (3), and Wind River Mountains (3)]. More exact locations are given by Forcella (1977).

The measurements necessary for these estimates were made as follows:

1. Current, future, and past production were determined for 25 representative shoots, that is five shoots each from the tops of five representative trees.

2. The number of shoots per m^2 in the canopy was determined by counting the potential cone bearing leaders on each of the five trees and dividing by a canopy area calculated from the tree's greatest and least canopy diameters.

3. Tree cover in the study area was determined as a percent of 90 overhead points covered by the canopy; the points were examined through a vertical periscope held at meter intervals along three 30 meter lines placed parallel to the slope at three representative sites in each stand studied.

Though our method has the advantage of allowing one to sample production over a series of years simultaneously, the following problems should be recognized:

1. The trees were not sampled randomly because some trees could not be climbed.

2. Shoots could not be sampled randomly because some were in inaccessible parts of the crown.

3. Heavy bearing shoots may have been absent or undersampled due to animal predation. Trees raided by black bears (Ursus americanus), recognizable by claw marks and broken branches, were therefore not sampled. Less easily avoided were the effects of red squirrels (Tamiasciurus hudsonicus) who commonly cut leader shoots from the trees (Schmidt and Shearer 1971).

4. On the other hand, shoots bearing cones at the time of sampling are also apparent to man and are likely to be over sampled; this may compensate for underestimation due to predation.

5. Estimates of the coming cone crop will be high if significant numbers of immature cones abort (compare with Allen 1941, Finnis 1953, and Sarvas 1962); cone numbers predicted for 1977 were not significantly higher than the actual crop--as they would have been if abortion had been significant.

A second measure of cone production was made by counting cones which fell to the ground in three 6.67 x 30 M plots in each stand. Estimates of the 1973 cone crop were made in 14 stands in 1974, estimates of the 1974 cone crop were made in 28 stands in 1975, and numbers of old weathered cones were recorded in both years.

Relating production to environment.--A nested analysis of variance was used to evaluate the effects of place and time on cone production. The analysis detailed below determined the significance ($p<0.05$) of variation between 5 branches in a tree, 5 trees in a stand, 6 to 16 stands in a floristically defined subassociation and 29 stands in the entire Pinus albicaulis-Vaccinium scoparium association. Annual variation in production was simultaneously tested as an interaction in each nest of the analysis. The three floristic regions included: 1. the Wind River and Absaroka Mountains; 2. central and southwestern Montana; 3. the Bitterroot and Salmon River Mountains (compare with Forcella 1977).

The significant effects of time detected in the preceding analysis were tentatively attributed to weather. To clarify the relationship between cone yield and weather we regressed deviations of normalized cone yields against deviations of weather variables (monthly mean temperature and monthly total precipitation) from their means in each of the 46 months preceding abscission (compare with Eis 1976). Cone yields were normalized to eliminate the effect of large differences in average yield between stands. Regional average weather data were used (USDC 1966-1976, compare with Lowry 1966) because no data are available from Pinus albicaulis stands, because deviations in precipitation or temperature from normal at low altitude usually parallel those found at high altitude, and because regional averages should eliminate weather station peculiarities like frost pockets. Each regional weather datum summarizes the data from dozens of official weather stations.

Relating production to simple stand parameters.--Simple or multiple regressions of cone production (leader number x average leader yield, table 1) against canopy cover, tree basal area, fallen cone number, and stand size explained significant amounts of the observed variation. On the other hand, regressions of cone yield against stand age, stand area, stand elevation, stand slope-aspect, total productivity, total standing crop, and cover indicator plants either alone or in combination were never significant.

RESULTS AND DISCUSSION

Cone development.--Cone history is reviewed here as a basis for understanding our method, for relating seed production to climatic factors, and as partial explanation for within-stand tree distribution. The development of Pinus albicaulis cones occupies parts of three summers and, due to apical branch growth, evidence of progressively older cones is displayed at nodes increasingly removed from the branch tip.

1. Late in the first summer a bud develops at the branch apex.

2. Pistillate conelets emerge from these buds in the second summer about the time of snowmelt (early July); they are found in the first lateral branch whorl, are purple, are about 5 mm long, and are easily recognized. July is therefore the best month to analyze shoots to predict the two forthcoming cone crops (compare with Allen 1941). Staminate strobili mature in early July and pollination occurs at this time. By the end of the growing season (mid-September) the conelets are approximately 1.5 cm long by 0.9 cm in diameter.

3. Rapid growth begins again in July of the third summer and full size (6.3 x 4.7 cm) cones appear in the second branch whorl by mid-August. Cone maturation continues until mid-September or early October when abscission normally occurs. Undisturbed cones abscise and fall to the ground intact, but if Clark's nutcracker (Nucifraga columbiana) removes the cone scales before abscission, the cone axes may remain in lower whorls of the branch for up to 10 years (compare with Smechkin 1963). Perhaps abscission depends on a hormone produced in the cone scales shortly before abscission so that if the cones are destroyed prior to its synthesis abscission does not occur.

The cones exude and are coated with a viscous aromatic resin. The resin may reduce seed predation by squirrels (Smith 1970) and nutcrackers. It also bonds the cone scales together (Clements 1910) until the resin crystallizes or is consumed by fungi. When the cone falls from the tree, cone scales and the large wingless seeds fall away from the axis; small clusters of seedlings found on the forest floor may result either from in situ disarticulation or from animal caches (compare with Hutchins and Lanner 1982).

Table 1.--Cone crops, locations, and stand characteristics for 28 Pinus albicaulis stands

STD[1]	MTN[2]	STATE[1]	CLIM[4]	COVER[5]	SIZE[6]	AGE[7]	1976	1975	1974	1973	1972	1971	1970	1969	MEAN±SE[8]
16	WR	WY	WR	63	2	198	2.7	2.5	0.3	2.5	1.0	2.5	--	--	1.9±0.4
17	WR	WY	WR	63	1	161	2.0	2.8	1.6	1.6	1.4	1.1	--	--	1.0±0.4
18	WR	WY	WR	71	1	214	1.3	1.3	0.7	0.8	0.6	1.5	--	--	1.0±0.2
19	AB	WY	WR	63	1	131	0.7	1.7	0.2	0.9	0.9	0.7	--	--	0.9±0.2
20	AB	MT	SC	49	1	210	1.2	1.9	1.7	0.7	0.6	1.3	--	--	1.2±0.2
09	AB	MT	SC	54	2	307	0.9	1.4	1.6	1.2	1.5	0.5	0.9	--	1.1±0.2
07	BB	MT	CN	61	2	120	0.0	0.1	5.0	3.1	3.7	3.9	1.7	3.5	3.1±1.0
06	BB	MT	CN	51	3	364	0.5	0.4	2.7	1.6	1.8	2.5	0.8	1.7	1.5±0.3
08	BB	MT	CN	66	3	355	1.7	0.4	2.6	0.2	0.2	1.5	0.2	1.9	1.1±0.3
03	LB	MT	CN	66	3	132	0.2	0.0	3.8	1.8	0.5	1.3	--	--	1.3±0.6
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
04	CA	MT	CN	37	2	55	1.5	0.3	1.2	0.7	0.2	0.6	--	--	0.8±0.2
10	MD	MT	SW	52	1	205	0.6	0.8	0.7	0.2	0.6	0.9	0.2	--	0.6±0.1
01	MD	MT	SW	73	2	150	0.6	5.8	1.2	2.2	0.9	1.8	0.9	--	1.6±0.5
02	MD	MT	SW	97	2	240	1.1	4.9	5.4	4.6	3.1	4.6	1.2	--	3.6±0.7
12	EH	MT	SW	73	2	135	1.5	6.1	1.9	2.2	2.0	3.9	1.4	4.2	2.9±0.6
11	EH	MT	SW	40	3	53	0.3	2.1	0.6	0.5	0.5	1.3	0.3	1.3	0.9±0.2
14	TR	MT	SW	56	2	160	1.5	3.6	3.3	0.5	2.7	3.8	0.5	--	2.3±0.5
13	TR	MT	SW	47	2	643	0.3	0.2	0.4	0.3	1.3	0.6	0.2	--	0.5±0.1
15	BR	MT	SW	53	2	320	1.0	0.0	1.2	0.0	0.1	0.1	--	--	0.4±0.2
29	PI	MT	SW	69	3	182	1.1	2.8	8.4	2.8	6.2	3.3	0.9	3.6	3.6±0.9
22	BT	MT	WE	50	2	423	2.5	1.1	44.9	2.3	2.4	2.7	1.2	1.0	2.3±0.4
23	BT	MT	WE	18	2	29	0.5	0.8	0.5	0.8	0.8	0.3	0.1	0.1	0.5±0.1
24	BT	MT	WE	13	1	32	0.7	0.2	0.3	0.3	0.3	0.3	0.0	0.1	0.3±0.1
25	BT	MT	WE	22	2	115	0.7	3.7	0.8	3.8	1.7	1.1	0.7	0.4	1.6±0.5
26	BT	ID	NV	32	2	59	0.1	2.3	0.3	1.0	0.2	0.6	0.2	0.4	0.8±0.3
27	SR	ID	NV	30	2	90	1.1	2.6	0.8	1.9	1.1	0.7	0.3	0.5	1.1±0.3
28	SR	ID	NV	31	2	188	0.1	0.9	0.4	0.6	0.4	0.2	0.1	0.2	0.4±0.1

1 Stand number.
2 Mountain ranges are: Absaroka(AB), Big Belts(BB), Bitterroot(BT), Bridger(BR), Castle(CA), Elkhorn(EH), Little Belts(LB), Madison (MD), Pioneer(PI), Salmon River(SR), Tabacco River(TR), and Wind River(WR).
3 States are: Idaho(ID), Montana(MT), and Wyoming(WY).
4 Climate regions are: Central(CN), Northeastern Valley(NV) of Idaho, South Central(SC), Southwest(SW), Western(WE) Montana, and Wind River(WR) Wyoming.
5 Tree canopy cover (percent).
6 Stand size where 1=0 to 0.75 ha, 2=0.75 to 1.25 ha, and 3=1.25 ha +.
7 Age of dominant trees.
8 Cones per square meter.

Cone-and-seed-production.--Average stand cone production ranged from 0.3 to 3.6 cones$\cdot m^{-2} \cdot yr^{-1}$ and averaged 1.4 ± 0.2 cones$\cdot m^{-2} \cdot yr^{-1}$ (table 1). Among the 6 to 8 years studied, maximum production in different stands ranged from 2.1 to over 100 times minimum production; in the median stand maximum production was 6.5 times minimum production (table 1). The average coefficient of variation (standard deviation/mean) between years in the average stand was 0.7.

The average mature pistillate cone weighed 23 ± 7 grams (range 10 to 50 gm) with cones produced in good years tending to be larger than those produced in poor years. Average cone production ranged, then, from a minimum of 7 to an average of 32 and to a maximum of 83 gm$\cdot m^{-2} \cdot yr^{-1}$ on a ground area basis. The range observed across all years and stands was 0 to 193 gm$\cdot m^{-2} \cdot yr^{-1}$. Cone production was approximately 9 percent of total above- and belowground production in 14 stands in which total production was measured (Forcella and Weaver 1977).

The numbers of cones found on the ground were usually fewer than scars counted in tree tops. This relationship is demonstrated by the regression equation:

$$C = 0.305 + 1.314\ F$$

where C = the number of 1974 cone scars counted in the treetop, F = the number of fresh cones counted on the ground in 1975, and $r^2 = 0.51$. Smechkin (1963) compared similar methods in a Pinus sibirica forest with the same result (r^2=0.62).

Table 2.--Comparison of cone and seed crops of several Pinus forest types[1]

Forest Type	Average Cones·m^{-2}·yr^{-1}			Average Seeds·m^{-2}·yr^{-1}			Reference
	#	grams	%[3]	#	grams	#[4]	
Pinus contorta	4.7	28	--	268	0.6	2	Smith 1968, 1970
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. cortorta bolanderi	---	52	20	---	---	-	Westman and Whittaker 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	Forcella and Weaver 1977

[1] Masses of seeds and cones not provided by the author were taken from Schopmeyer (1974).

[2] Ranges in figures represent smallest and largest data provided.

[3] Percent total productivity except third and fourth forest types which are percent aboveground productivity only.

[4] Percent total cone mass.

We attribute the deficiency of cones found on the ground (about 25 percent) to Clark's nutcracker, squirrel, and bear activity.

Typical cones contain about 75 ± 28 seeds, each weighing 0.1 ± 0.02 gm dry. Seed live weights are about 0.17 gm (Schopmeyer 1974). Seed mass usually comprises 30 percent of cone mass and may comprise 50 percent in an especially good cone year; the proportion of cone mass devoted to seeds in other conifers is usually lower (Smith 1970 and table 2). Average seed production ranged, then, from a minimum of 2.3 to an average of 10.5 to a maximum of 27 gm·m^{-2}·yr^{-1}, i.e., from 23 to 105 to 270 seeds·m^{-2}·yr^{-1}. The range observed across all years and stands was 0-63 gm·m^{-2}·yr^{-2} and 0-630 seeds·m^{-2}·yr^{-1}. Seed production was about 3 percent of total arboreal production in 14 stands studied intensively (Forcella and Weaver 1977a). Of the approximately 75 scales on a typical cone, one third, mostly apical and basal scales, were infertile.

Comparison of Pinus albicaulis forests with other pine forests (table 2), leads to the following conclusions: Pinus albicaulis forests produce normal cone crops (32 gm·m^{-2}·yr^{-1} average). Because the cones are heavy, cone numbers are relatively small (1.4 cones·m^{-2}·yr^{-1} average). Since a large proportion of the cone is devoted to seed, seed production is relatively high (10 gm·m^{-2}·yr^{-1} average), yet because the seeds are large, seed numbers are normal (105 m^{-2}·yr^{-1} average). The net effect is to deposit normal numbers of abnormally well provisioned seeds.

Variation in cone production potential.--Total cone production is the product of mean shoot production (=cone production potential) multiplied by the number of fertile shoots per hectare. Yet, since the density of fertile shoots in a stand may be less than optimal, the yield of the average fertile shoot may be a better index of site production potential than is the total number of

cones actually produced in the stand. In the following discussion we therefore compare production potentials across vegetational units of increasing size (trees, stands, sub-association, and the entire association) by considering a sample of branches of fixed size and ignoring the actual number of shoots producing cones.

Cone crops varied significantly between branches in 29 percent of the trees studied, and between trees in 48 percent of the stands studied, but they did not vary significantly between stands in any region or between stands in all the different regions. One might conclude:

1. that cone production varies little between branches of a tree due to identical genetics and similar mesoenvironmental conditions,

2. that it varies more between trees in a stand due to greater dissimilarity in genetics and mesoenvironmental conditions, and

3. that it differs relatively little between stands in a region due to averaging of between-tree heterogeneity in forests with relatively constant genetic and mesoenvironmental conditions.

The fact that fertile branches have similar cone production potentials throughout a region or even throughout an association supports our expectation that the average cone production of a stand is determined primarily by the number of fertile shoots per hectare and their interaction with weather conditions.

Variability in time.--In the analysis of cone production potential just discussed, the between-year effect was tested as an interaction at each level. Branch production, tree production, and stand production varied significantly between years ($p=0.05$) in 60 percent, 78 percent, and 100 percent of the cases, respectively. When all stands in the three regions were considered simultaneously there were no significant differences between years.

Variability of production in time is apparently due, in part, to internal factors. Excellent cone years (with yields one standard deviation or more above mean yield) were preceded in 20 of 29 cases by poor cone years (with yields equal to or less than the mean). Since the probability of a poor seed year so defined is 50 percent, this is a significant deviation (<0.05) from our expectation. In other species poor fruit years are also followed by good fruit years, apparently because initiating fruits cannot compete with maturing fruit for available carbohydrates during initiation and development (Kozlowski 1971). The amplitude of natural cycles in fruiting might be increased by natural selection if poor seed years preceding excellent seed years resulted in better establishment of the tree through temporarily overprovisioning previously starved-out predator populations (compare with Janzen 1971, Forcella 1980); such selection could occur only if the seed predator used the subject as its principle source of food. Other variations may not have internal causes. For example, we see no physiological or evolutionary reason for the fact that 16 of 21 excellent cone crops were preceded 4 years earlier by a poor cone year ($p<0.05$).

Especially poor cone years (with yields more than one standard deviation below the mean) were not significantly correlated with yields in any previous year; we therefore think a poor cone year is more likely determined by weather rather than by internal factors.

We hypothesized that the demonstrated synchrony of variation in cone production within a stand and within a region is due to weather; and similarly, that the lack of synchrony between regions is due to differences in weather between regions. To clarify the relationship between cone yield and weather we regressed deviations of normalized cone yields against deviations of weather parameters (mean temperature and total precipitation) from their means in each of the 46 months preceding cone abscission as explained under methods (compare with Eis, 1976).

Cone production was correlated with preceding weather conditions, but in no simple way (table 3); six observations follow:

1. In well-sampled regions (represented by six to eight stands) correlations with temperature or rainfall significant at the 0.05 level may occur in half and correlations significant at the 0.001 level may occur in 20 percent of the 46 months preceding cone maturation. While significant correlations become progressively harder to detect as sample sizes decrease to two stands per climatic region, it might be possible to detect significant correlations in every month if sample sizes were increased sufficiently.

2. Though many correlations are highly significant, few explain much of the observed variation in cone yield. The average r^2 is 0.21 for precipitation and 0.20 for temperature and the r^2 of correlations significant at the 0.001 level are only 0.30 for precipitation and 0.35 for temperature. Assuming that variation in regional data parallels variation in higher altitude conditions, this suggests that each of the 46 months preceding cone abscission plays a small but important part in determining yield. If final yields of P. albicaulis are, in fact, determined by a summation of everyday conditions, unique events are notably less important to yields than they are for pinyon pine (Forcella 1981).

3. Numbers of significant correlations for both temperature and precipitation are similar in the prebud, bud, pollination, and cone maturation years.

4. Forty-five percent of the significant temperature correlations and 48 percent of the significant precipitation correlations occurred in winter months (November-April) when 'inactive'

Table 3.--Statistically significant relationships of cone yield to weather of the 46 months preceding cone drop in southwest Montana[1]. Correlation coefficients are presented with their signs; regressions significant at the 0.1 percent, 1 percent, and 5 percent level are indicated by a, b, and no letter respectively

Factor	Temperature				Precipitation			
Year[2]	preb	bud	juv	mat	preb	bud	juv	mat
JAN	-29				+40b		-51a	+34b
FEB		-32	+43a	+42b	-40b		-35b	+48a
MAR	+39b				-45a		+54a	
APR						+29	-31	
MAY		+45a	-30	-37b		-36b		
JUN			+50a	-26		+32	-49a	
JUL	-40b				-33			
AUG		+33			+46a	-40b		
SEP	-26							-56a
OCT			+41b		-32	+31	-31	+46a
NOV			+41b		-32	+31	-31	+46a
DEC		+32			-48a		+27	

[1] Normalized deviation of yield was regressed against deviation from average climatic data as explained in the text. Correlations for other regions were generally of similar size, sign and significance and generally showed similar seasonal distribution. They will be provided upon request.

[2] Years are those before bud formation (preb), of cone bud formation (bud), of juvenile pollinated cones (juv), and of cone maturation (mat).

trees might be assumed to be little affected. Correlations with winter precipitation could be due to its effect on summer soil water supply. The remaining significant temperature correlations were 20 percent in spring (May-June), 16 percent in summer (July-August) and 19 percent in fall (September-October). The remaining significant precipitation correlations were 15 percent in spring, 18 percent in summer, and 19 percent in fall.

5. Negative correlations are slightly more common than positive correlations between cone yields and summer (80 percent negative in July-August) and winter (57 percent negative in November-April) temperatures, as they are with spring (70 percent negative in May-June), fall (65 percent negative in September-October), and winter (62 percent negative in November-April) precipitation. We are not ready to conclude that high temperatures and heavy precipitation lower yields.

6. The fact that highly significant correlations between yield and a given developmental period may differ in sign between different areas is consistent with the observation that year-to-year variability in cone production disappears when one averages across regions.

Our results will frustrate anyone wishing to predict future cone crops from weather data. The highly significant, but weak, correlations observed suggest that a complex physiological model would be needed to make such predictions and that its final prediction wouldn't be available until shortly before the crop matured. Similar results could be had by sampling branches in a specific stand for numbers of mature or juvenile cones and, since stands in a region behave similarly, results from a representative stand might predict regional crops reasonably.

Variability associated with easily measured stand characteristics.--The considerable variability of average cone production among stands must be caused directly by site characteristics such as climate and soils and stand characteristics such

Table 4.--Regressions relating cone production[1] to easily measured stand characteristics[2]

Regression equations.	r^2
$C_a = 0.470 + 0.00032$ canopy cover^2	0.42
$C_a = 0.288 + 0.023$ basal area	0.28
$C_a = 0.812 + 0.439$ fallen cones	0.32
$C_a = 0.450 + 0.00023$ canopy cover^2 + 0.206 fallen cones	0.46
$C_a = 0.430 + 0.00032$ canopy cover^2 + 0.470 stand size	0.52
$C_g = 0.515 + 0.00039$ canopy cover^2 + 0.734 stand size	0.49
$C_p = 0.269 + 0.00011$ canopy cover^2 + 0.001 stand size	0.32

1 Cone production in the average year (C_a) is expressed as cones$\cdot m^{-2} \cdot yr^{-1}$. C_g and C_p represent cone production in good and poor years respectively.

2 Units were percent of ground area for canopy cover, m^2/ha for basal area, and new plus old cones/m^2 on the ground for fallen cones. Stand size was scaled with 1 = 0 = 0.75 ha, 2 = 0.75 to 1.25 ha, and 3 = more than 1.25 ha.

as age, density, and the genetic allocation of photosynthate to reproduction. Few of these variables were studied because their measurement was too costly, time consuming, or difficult. On the other hand, correlations of average cone production with easily measured stand characteristics were tested because any strong correlations discovered would be useful for managers who wish to predict production in particular stands.

Measures of stand cover and fallen cones should be correlated with cone production since they index numbers of potentially fruiting branches and their previous fruitfulness (table 4). Canopy cover alone explained 42 percent of observed variation in cone production. Basal area only explained 23 percent of the variance, probably because branch numbers were more closely related to tree cover or circumference than cross-sectional areas. Perhaps due to uneven consumption by animals, numbers of fallen cones explained only 32 percent of the observed variation. A regression combining canopy cover and numbers of fallen cones was our second best (r^2=0.46).

Our best simple predictor of cone production (table 4, r^2=0.52) involved stand size with canopy cover. Besides explaining observed variation best, this estimator has the advantage of being least expensive to apply--both canopy cover and stand size can be estimated from aerial photos in the non-field season. The 'small stand effect' is likely due to poorer fertilization in small stands than in large ones; Sarvas (1962) observed poor pollination in Pinus sylvestris when stands were smaller than 2 ha. The fact that yields of cones in good cone years (C_g=yields greater than median yields) seem to be more affected by stand size than yields in poor cone years (C_p=yields less than in median years) suggests that other factors (probably weather), override the pollination effect in poor cone years.

Other potential estimators of stand production studied were less useful. Regression of yield against stand age, stand area, stand elevation, stand slope-aspect, productivity, biomass, and the cover of indicator plants alone showed no significant correlations. Complex combinations of these factors in multiple regressions increased attributal variability (r^2) to 60 percent but since these regressions are biologically uninterpretable they are not reported.

SUMMARY AND CONCLUSIONS

Evidence of cone production--juvenile cones, mature cones, or cone scars--located at progressively older nodes of terminal branches can be used to estimate cone yields of a branch over a 6 to 8 year period from a single observation. The product of mean branch yields, so determined, and fruiting branch density (branches per m^2) provides a measure of stand cone yield through the same period.

Average reproductive production in the 29 stands observed ranged from 0.3 to 3.6 cones$\cdot m^{-2} \cdot yr^{-1}$ and 23 to 270 seeds$\cdot m^{-2} \cdot yr^{-1}$. The coefficient of variation (SD/mean) between years for cone production in the average stand was 0.7 cones$\cdot m^{-2} \cdot yr^{-1}$. While seed numbers are comparable to those observed in other pine forests their weights were greater. Cone production comprised about 9 percent of total arboreal production.

Cone yield potentials varied significantly between branches in 30 percent of the trees studied and between trees in 48 percent of the stands studied, but never between stands.

Cone yields varied significantly between years in branches, trees, and stands in a region. Some internal control is suggested by the fact that high-yield years usually followed low-yield years. External control is indicated by significant correlations between regional weather and cone production. These correlations suggest that temperature and precipitation conditions have significant, but not dominant, effects in prebud, bud, juvenile cone, and mature cone years and all months of the year. Unique events seem less significant, therefore, for Pinus albicaulis than for Pinus edulis (Forcella 1981).

Easily measured stand characteristics are never more than mediocre predictors of average cone production. Our best regressions were based on canopy cover, canopy cover with fallen cones, and canopy cover with stand size. They explained 42, 46, and 52 percent, respectively, of the observed variation. Fortunately, the best predictor is also least expensive to apply.

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