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Authors: Tad Weaver and J. Jacobs

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OCCURRENCE OF MULTIPLE STEMS IN WHITEBARK PINE

T. Weaver
J. Jacobs

ABSTRACT

Depending on the stand, Montana-Wyoming whitebark pines (Pinus albicaulis) *may have multiple stems in 8 to 79 percent of the trees. The clumps had one to 11 stems with stand medians between two and three. Multiple stems may arise from several seeds germinating together, from basal branching, or both. Median stem number and maximum stem number per clump decrease with stand age, probably due to both within-clump and between-clump competition. While declines are slight in open woodlands, clumps almost disappear in closed forests. The presence of clumps is correlated with stand density in other conifers as well.*

INTRODUCTION

While most trees tend to be single stemmed, a few (such as *Quercus*, *Populus*, *Salix*, and *Sequoia*) are often multiple stemmed (Elias 1980). Stem number in trees must be determined by two factors: (1) the tendency to form, at one point, stems that are genetically identical (from, for example, spontaneous basal branching or wound-induced branching), maternally related (poly-embryony or seeds cached from one tree), or less strongly related (seed cached from different trees) individuals and (2) the tendency of multiple stems to survive at that point.

Whitebark pine (*Pinus albicaulis*) has long been noted for its tendency to occur in clumps with stems fused, or not fused, at the base (Harlow and Harrar 1958; Sudworth 1908). Multiple-stem origin (factor 1) was originally attributed to branching (Sudworth 1908), then to branching and/or seed caching (Weaver and Dale 1974), and most recently almost exclusively to seed caching (Lanner 1980; Linhart and Tomback 1985). The importance of stem survival (factor 2) in the determination of the number of stems in a clump has received little attention. The objectives of this note are to demonstrate the multiple-stem phenomenon for the whitebark pine of subalpine woodlands, to examine evidence for the mode of multistem initiation, and to open discussion on the effect of survival of the stems in a clump.

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T. Weaver is Plant Ecologist and J. Jacobs is Forest Ecology Associate, Department of Biology, Montana State University, Bozeman, MT 59717.

METHODS

Clump sizes were observed in 19 stands located in 10 subranges of the Rocky Mountains between latitude 43.5° and 46.5° N. All stands were subtimberline woodlands with canopies dominated by whitebark pine and understories dominated by grouse whortleberry (*Vaccinium scoparium*); none of the stands was krummholz. In each stand, the number of stems was counted on each tree in a representative 500-m^2 (12.6-m [41.3-ft] radius) circular plot. The stand was aged by coring three representative dominant trees. Canopy cover was estimated by determining, with a periscope, the percentage of 33 points that was covered. The locations, climate, soils, and vegetation of the study areas, as well as the sampling methods, are described in greater detail by Weaver and Dale (1974).

The 52 seedlings observed for basal branching were planted one-seed-per-pot and grown under normal nursery conditions for 2 years. The seeds were collected just north of Yellowstone National Park in the Palmer Creek-Bear Creek drainage at an altitude of 2,677 m (8,700 ft).

THE PHENOMENON

Observations in 19 woodland stands—neither krummholz nor forest stands—in the Rocky Mountains between latitude 43.5° and 46.5° N. (table 1) support five descriptive statements about clumping in whitebark pine.

1. There were both single-stemmed and multiple-stemmed trees in every stand.
2. There were more multiple-stemmed than single-stemmed clumps in 37 percent of the stands.
3. Clumps with more than seven stems were rare in stands over 150 years old. The fact that the smaller stems in older clumps were often dead suggests that weaker associates were competitively excluded (Lanner 1988).
4. Over half of the clumps were multiple stemmed in stands with cover less than 48 percent and less than half the clumps were multiple stemmed in stands with cover greater than 60 percent. Competition associated with stand closure probably selected against stems in clumps, since competition from the time of establishment would give clumped stems a relatively small height and would allow them to be overtopped and outcompeted by trees outside the clump.
5. These forest trees had one to 11 stems with a median averaging 2.36. Clumps containing as many as 22 stems have been reported in open subalpine stands of the Sierra Nevada (Tomback 1989).

Table 1—Stem number in *Pinus albicaulis* clumps appearing in 19 Montana-Wyoming stands. The stands are arranged in order of arboreal cover

Tree cover	Basal area	No. clumps per plot	Stand age	Single stemmed	Percentage of trees by stem number class										
					1	2	3	4	5	6	7	8	9	10	11
Percent	*m²/ha*		*Yr*	*Percent*											
21	5.1	43	40	21	21	23	26	12	7	5	2	4			
27	10.8	67	133	45	45	34	10	6	3	0	1	0	1		
33	12.7	50	116	48	48	28	12	10	0	2					
45	23.5	37	190	43	43	45	3	3	3	0	3				
48	13.5	32	210	65	65	13	13	3	6						
48	17.2	50	140	48	48	30	8	8	2	4					
50	11.5	26	290	92	92	8									
51	21.0	23	420	35	35	48	13	0	4						
55	15.3	34	160	59	59	29	9	3							
57	12.7	33	140	30	30	27	16	18	3	0	3	0	0	0	3
63	20.2	46	400	61	61	37	2								
66	13.4	72	113	53	53	21	14	7	3	1	0	1			
66	13.4	61	170	90	90	3	2	2	3						
67	15.3	68	113	56	56	21	12	7	1	3					
75	17.3	53	210	53	53	26	11	6	2	2					
78	17.8	54	225	61	61	23	9	7							
84	13.1	58	99	53	53	28	3	5	7	0	2	0	2		
84	17.3	43	289	60	60	28	6	4	0	2					
85	23.5	30	283	63	63	14	13	3	7						

CLUMP INITIATION

Many multistemmed whitebark pine clumps undoubtedly arise from different seeds deposited at one spot, most likely by nutcrackers (Hutchins and Lanner 1982), but occasionally by squirrels and chipmunks or, conceivably but rarely, by a cone falling intact (Linhart and Tomback 1985). One can easily demonstrate this by pulling clumps and counting entirely separate stems. We suggest that mature trees arising through this mechanism may be recognized by the acute angles between the stems of trees competing with each other; this form is illustrated by Linhart and Tomback (1985).

We give two lines of evidence that some whitebark pine clumps arise by spontaneous basal branching and note that damage to apical meristems by insects, vertebrates, or climate might also stimulate basal branching. First, of seedling clumps pulled in the field, some consist of single trees with a single root system. Second, nursery seedlings, planted one-seed-at-a-time, often have multiple stems. For example, seedlings grown from one lot of seeds were branched at the base in over 84 percent of the cases and exhibited stem frequencies even higher than those seen in natural stands of the region (tables 1 and 2). The developmental tendency of whitebark pine to branch at the base may be related to its tendency to branch profusely and widely at higher nodes—a tendency that has led dendrologists to contrast the "lyrately branching" form of whitebark pine with the conical form of most other Rocky Mountain conifers (Harlow and Harrar 1958). We suggest that obtuse basal branching, as well as strong crown branching, indicates a morphologic tendency of individuals that normally grow in open stands to optimize energetically through extensive branching. Such branching is energetically efficient because it develops a large canopy with minimal competition among branches and a minimal investment in trunk biomass. We suggest that—although forces such as crushing snow might sometimes spread clumps of genetically distinct individuals obtusely—obtuse basal branching often, or usually, indicates a genetically uniform clump.

Genotypic analysis of multistemmed clumps should shed light on the relative contributions of basal branching and the germination of clumped seeds to multiple stemming in particular whitebark pine stands. Analyses made in two Alberta stands (Furnier and others 1987) and one Wyoming stand (Linhart and Tomback 1985) show: (1) that while 58, 70, and 83 percent, respectively, of the clumps examined had mixed origins, as many as 42, 30, and 17 percent may have arisen by branching alone, and (2) that, while most clumps are of mixed origin, 22, 19, and 46 percent, respectively, of the stems in the mixed clumps were genetically undistinguished from their neighbors and may well have arisen by branching. Genotypic analysis may have misclassified some distinct stems as branches; this is unlikely in studies based on 11 loci (Furnier and others 1987), and somewhat more likely in studies based on only four loci (Linhart and Tomback 1985).

Table 2—Branching of pine seedlings grown under greenhouse conditions

Species	Sample size	Percent of seedlings with "X" branches				
		1	2	3	4	5
Pinus albicaulis	52	15	15	58	6	6
Pinus contorta[1]	198	90	10	0	0	0

[1]In contrast to *Pinus albicaulis* branches, the branches of *Pinus contorta* were weak and not competitive with the main stem.

SURVIVAL OF STEMS IN CLUMPS

We observed that while multiple-stemmed trees are common in open woodlands just below timberline, they are rare in denser forests a few tens of meters lower. We attribute the difference not to sources of multistems, but to the survival of clumped stems. In a closed forest, trees in a clump should be at a disadvantage. Trees in a clump are very dense, and the clump can be expected to self-thin if other trees are nearby. One might even expect all trees in the clump to disappear, since their competition with each other will reduce the likelihood that any one will grow fast enough to stay in the canopy. On the other hand, if the stand is open—due to its occupation of a marginal habitat where "safe sites" for establishment are few or if the stand is thinned—we expect the multistem habit to be most energetically efficient.

Multistems are most efficient in open stands because (1) single stems have less circumference than multiple stems of equal cross-sectional area, (2) leaf area is proportional to circumference (Marshall and Waring 1986; Shinozaki and others 1964), and therefore (3) branched crowns require less photosynthate per unit of leaf area for support than single stems do. For example, simple geometry shows that two-, three-, four-, and five-stemmed trees have 140, 172, 200, and 222 percent of the circumference (our leaf area index) of a single-stemmed tree with the same cross-sectional area (our index of photosynthetic cost). One wonders whether the basal area differences underestimate differences in structural costs, since clumped trees growing in open stands are generally shorter than relatives growing in closed stands. This seems unlikely since the shorter trees of clumps will have longer, more costly, radial reaches in both shoot and root zones; such compensation has been demonstrated in juniper (Weaver and Lund 1982). While hormonal coordination might allow single-genotype clumps to outperform multiple-genotype clumps or conjoined stems in a clump to outperform single-stemmed trees, we have no evidence for either hypothesis. Nor do we have estimates of the possible impacts of clumping on group function—whether they might be positive (by transpiration reduction through mutual shelter or water supply increases due to snowdrift creation) or negative (by evaporation of rain or snow from a large canopy).

If competition significantly affects the degree of multistemming in open versus closed stands of whitebark pine, we might expect the same phenomenon in stands of other tree species. With or without "cache-planting," one sees that clumping is most common in open stands. In contrast to its forest form, thick-barked Douglas-fir (*Pseudotsuga menziesii*) is often clumped at lower timberline and along rocky ridges at higher altitudes, probably as a result of damage to apical meristems and survival of multiple stems or perhaps nutcracker caching (Lanner 1988). Typically single-stemmed lodgepole becomes multistemmed at lower timberline in areas such as meadow borders in northwestern Yellowstone National Park, due to survival of multiple stems arising after leader damage or germination of seeds from a cone that fell intact. While subalpine fir (*Abies lasiocarpa*) is strongly single stemmed in forests, its lower branches root and layer to form tight clumps in mountain meadows (Billings 1969) and krummholz sites (Marr 1977). The tendency of pines in open stands of warmer environments such as *Pinus edulis* (Vanderwall and Balda 1977), and *Pinus ponderosa* and *Pinus flexilis* of Montana, to branch low and profusely, but without multistemming, may be an adaptation to decrease exposure to groundfire and/or high soil-surface temperatures.

CONCLUSIONS

From the above we conclude that:

1. Multiple stems could arise from basal branching, from multiple establishment of seeds deposited near each other, or both.
2. Either basal branching or seed caching could yield more stems per clump than normally occur in mature whitebark pine stands.
3. Whether it arises through basal branching or seed caching, stem number is ultimately controlled by competition among members of a clump (and declines therefore with clump age) and competition between adjacent clumps (and declines therefore with canopy closure).
4. Branching seems to account for 31, 26, and 46 percent of total multiple stemming in three particular whitebark pine stands. We speculate that branching may dominate in woodlands where most clumps are obtusely branched and may be less important in woodlands where most clumps are acutely branched.

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

Q. (from Dave Mattson)—Nutcracker-dispersed trees that were not multistemmed might support the branching hypothesis, what about *Pinus sibirica* and *Pinus pumila*?

A.—*Pinus edulis* and *Pinus flexilis*, from the lower timberline, are nutcracker-dispersed trees that are mostly single stemmed. It is not clear to me either why companion seedlings fail to establish or why the tree fails to branch lower; perhaps fire or high surface heat select against multiple stems. Clumping seems more characteristic of cooler-moister woodlands and may be due, as in *Pinus albicaulis*, to a combination of caching and basal branching. While multiple stems have been reported in *Pinus sibirica and Pinus pumila*, I do not know whether and under what conditions it is important; at this symposium Tomback and Holtmeier both described clumping in closely related *Pinus cembra*. Lanner (1988) described clumping in wing-seeded conifers (*Pinus longaeva* and possibly *Pseudotsuga menziesii*) dispersed by nutcrackers.

Q. (from Cathy Stewart)—Are the single stems typical of closed-canopy forests due to lack of caches or to competitive thinning?

A.—I see both single-stem and multiple-stem reproduction in relatively dense stands. I would therefore attribute the lack of mature multiple-stem clumps to thinning induced by within-clump and between-clump competition.

Q. (from Ron Lanner)—If branching occurs at both the base and the crown of whitebark pine trees, why is it rare on the lower trunk?

A.—Our seedlings branched naturally and it is obvious that upper crowns branch naturally. I agree that branches on the lower trunk are rare, but have no solid explanation for their absence there; browsing or sand and snow blowing near the ground surface may contribute.