Whitebark Pine Community Processes, Environment and Human Influences: Revisiting Montana State University Work of 1971-2000

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ABSTRACT

I revisit 30 years of whitebark pine (WBP, *Pinus albicaulis*) reflecting work reported in >30 WBP papers. Using a sample of 47 stands from the northern Rocky Mountains, I document the remarkable openness of WBP stands. We show strong self-thinning and seedling failure, related to soils, not light, and ongoing production/decomposition though 600 years. WBP's remarkable multiple-stemmed trees arise from seed caches/polyembryony combined with lack of light competition. WBP's usual timberline range seems limited upward by growing season length, wind, growing season length, and soil condition and downward by competition, none much directly temperature related. Human impacts discussed include foraging, trampling/compaction, exotic species invasion, and white pine blister rust, which may be significantly ameliorated by introduction of genes from resistant European stone pine species.

INTRODUCTION

I revisit whitebark pine (WBP, Pinus albicaulis) studies made by my plant ecology lab during the 1971- 2000 period in the northern Rocky Mountains. Objectives are keying the availability of useful information, freshly integrating many observations, and speculating on/pondering unresolved problems. A fourth objective is to document, as requested by the Hi5 historical section, early work in the field. This is done in greater depth by Weaver (2022). This review emphasizes the plant ecology lab's ~34 papers and focuses on the work of my fine associates (D Dale, F Forcella, J Jacobs, J Keck, W McCaughey, J Lichthardt, D Gustafson) and of Wyman Schmidt (USDA Forest Service, Forestry Sciences Laboratory, Bozeman) who was so important to the organization and reporting of early WBP research.

I divide my review into three segments: 1) the WBP forest and its dynamics, 2) the response of WBP to its environment, and 3) human impacts on the WBP forest.

THE WBP FOREST AND ITS DYNAMICS

Forest Structure and Dynamics

A typical WBP forest is an open stand of multi-stemmed five-needled trees. Its structure is broadly described by comparing forty-seven stands ranging from 0-600 years (Weaver et al. 1990). Canopy cover increases rapidly from zero at initiation to saturation (~60%) at 100-200 years and then plateaus (table 1). Leaf area, indexed by the sum of circumferences of all component trees, rises more rapidly and levels off similarly. Simultaneously, canopy height increases steeply to 12 m at 200 years and levels off (Weaver and Dale 1974).

Stand density is initially ~1700 seedlings ha-1, peaks soon at ~4600 seedlings ha^{-1} and declines exponentially to 50 ha^{-1} at 400 years (table 1). The initial rise indicates continued seeding from external sources into forests too young to produce their own seed. The number of resultant small trees (0-10 cm diameter at breast height; dbh) declines from establishment to near 50 ha^{-1} at 400 years. The disappearance of these trees must be due either to death and decomposition in place or to graduation into the larger size class (10-90 cm dbh). The large trees also begin to thin after 200 years.

Basal area ($\sum\pi$ (dbh/2)^2, an index of standing crop) rises rapidly over the first 100-200 years, then growth apparently tapers (table 1 and Forcella and Weaver 1977) due to the sum of two processes: loss of dying trees and ongoing diameter growth of living trees. Despite the death or graduation of most small trees, the total basal area of small trees is maintained by ongoing diameter growth, which would be impossible without the plentiful light of the open forest. Similarly, the basal area of large trees increases constantly, despite the death of one-third of them, between 400-600 years. The pattern and magnitudes are very similar to those modeled by Keane et al. (1990). The change in basal area and standing crop over time (production) was measured much more elegantly (Forcella and Weaver 1977). This paper partitioned biomass/growth into leaf, branch, bole, root, and bark components—the latter two rarely measured—and shows that due to their long lives, WBP forests can be more massive than those of temperate forests at lower altitudes or in other areas.

The large number of disappearing trees—1450 ha^{-1} small ones between years 100-400 and 450 ha-1 large ones between years 200-400—calls our attention to the fate of the missing trees, a rare subject in forestry. The understory of WBP forests is trash-free and thus, must harbor a potent decomposing agent. Because regular ground fires are not reported, we speculate that fungal decomposition is rapid under long-lying moist-warm (0^{o}C) snow packs. The depth of snow packs in lower altitude WBP forests may be near 2 m, i.e. as indicated by the height to which lichens are excluded from tree trunks (Eversman et al. 1990), possibly by the relatively warm, moist conditions in the snow packs.

Current reproductive effort was estimated by counting cones in the canopy. To compare production across a series of preceding years, we analyzed branch samples by recording cone production of sample branches at progressively earlier times. This was done by recording, for each branch, numbers of juvenile cones, current cones, and scars left by previous cones at annual nodes from the preceding 5-11 years. Average cone crops were near 1.5 m^{-2} for stands older than 100 years (Weaver and Forcella 1986). High cone yields tended to follow low yields, i.e. the trees exhibited masting behavior. Ecologically, masting partially controls seed-consuming mammal populations, such as sedentary red squirrels (*Tamiasciurus hudsonicus*) and chipmunks (*Tamias* spp.), but has less effect on mobile seed predators, such as Clark's nutcrackers (*Nucifraga columbiana*). We could not identify weather conditions that correlated well with yields, perhaps because too few weather stations were located within WBP stands for meaningful results. Yields were inconsistent region-wide, thus usually providing cross-stand dispersal opportunities.

The understory of the WBP/whortleberry association, is dominated by a low shrub (whortleberry, *Vaccinium scoparium*) and may contain 5-10 species of low-density herbs, including glacier lily (*Erythronium grandiflorum*), elk sedge (*Carex geyeri*) and arnica (*Arnica* spp.) (Weaver and Dale 1974, Forcella 1978). The crustose lichen *Parmeliopsis* occupies the bases of many trees and, above 2 m, are fruticose lichens (*Letharia*, *Usnea*, and *Bryoria*), leafy lichens (*Melenelia*), and crustose lichens (*Parmeliopsis* and *Lecanora*) (Eversman et al. 1990). The macrofungal (mushroom) richness may be near 60 species (Keck 2001).

Table 1. Whitebark pine forest dimensions. Values from Weaver, Forcella and Dale (1990).

	CANOPY		DENSITY (trees/ha)			BASAL AREA (m^2/ha)		
Stand age (years)	Cover%	Σ.Circa[a]	Seedling	0-10 cm dbh	>10 cm dbh	0-10 cm dbh	>10 cm dbh	Total
0	0	0	0	0	0	0	0	0
100	40	70	1000	1500	1000	24	14	38
200	57	75	1000	200	1300	25	32	57
–								
400	60	75	50	50	850	18	40	58

[a] Leaves and branches are connected directly to roots by elements in the sapwood, thus sapwood on the circumference correlates well with leaf area. Sapwood is expressed as the sum of circumferences, m/ha.

Table 2. Comparison of environments of major Rocky Mountain environmental zone habitat types (HT). Relatively high values are shaded.

	Climate[b]		Water holding capacity[c]					Nutrients[d]			
HT[a]	T	AP	WHC	depth	Clay	Sand	Org C	N	Ca	K	Mg
	°C	cm	cm	dm	%	%	T/ha	T/ha	T/ha	T/ha	T/ha
Alpine	8	106	3.8	5	90	10	124	10	3	0.3	0.5
Abla/Pial	10	82	4.4	22	96	4	35	3	2	0.8	1
Psme	12	58	10.3	13	82	18	45	4	15	2	5
Feid	13	38	10.1	5	73	27	130	11	27	1.9	6
Bogr	16	35	11.7	6	70	30	82	9	33	2.7	7

[a] HTs: Alpine, conifer forests (moist *Abies lasiocarpa*, ABLA and drier *Pseudotsuga menziesii*, PSME), grasslands (moist *Festuca idahoensis*, FEID and dry *Bouteloua gracilis*, BOGR)

[b] Climate: growing season temperature, T (Weaver 1980), annual precipitation, AP (Weaver 1980).

[c] Water holding capacity (WHC): A&B horizons, and the determinants, soil depth, clay, sand, and organic carbon.

[d] Nutrients: metric tons per hectare.

Multiple Stems and the Stand Life Cycle

WBP forest is characterized by its apparently multi-stemmed trees, as well as by the openness of the canopy discussed above. Two forces are involved. First, multi-stems are actually separate individuals arising from seeds planted in groups (1-3 most commonly but as many as 14) by seed-caching Clark's nutcracker (Hutchins 1990). Regardless of the number of seeds in a cache, clump sizes may be increased by the occurrence of multiple seedlings/stems arising from single seeds. Single seeds commonly produce multiple seedlings (one to >5) but most commonly three (Weaver and Jacobs 1990). Second, and equally important, the openness of the forest eliminates the competition that prevents self-thinning following close establishment of trees arising from caches or multiple embryos. As a confirming aside, I note that other tree species, e.g. Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), also may exhibit multiple stems in open stands that lack within-canopy competition.

As a result of both the rarity of seedling establishment and the planting of trees by nutcrackers, I propose, in four statements, that WBP forests are 'climax/self-sustaining' in a somewhat unusual sense, i.e. perhaps only when associated with Clark's nutcracker. First, observation of an altitudinal transect (Weaver 1990b) shows a clean high forest with no invasion by subalpine fir; i.e. it seems to be a climax species. This is in contrast to seral lodgepole pine forests below it, which are regularly replaced by subalpine fir (cf. Pfister et al. 1977). Second, the forest dynamics section above shows that the forest evolves in an orderly way through 600 years without replacement by other tree species. Third, while WBP produces abundant seeds (Weaver and Forcella 1986), its capacity to maintain/reproduce itself, to sustain itself, seems slight. That is, while seedlings appear in young stands (<300 years), they apparently do not survive for long. Both seedlings and small trees are essentially absent in older stands. The absence is likely due, in both cases, to subterranean competition with established trees. Fourth, while the stand may survive for >600 years, the sites must eventually be reset in two steps. Step 1 is by catastrophe, most likely fire—as indicated by plentiful charcoal in the soils of most or all WBP/whortleberry forests. Step 2 is by delivery of short-lived seeds from afar, i.e. they are not from 'in-house' seed banks. That delivery is surely from nearby productive stands by Clark's nutcracker.

ENVIRONMENT AND WBP

WBP often forms a timberline community. Its environment has been characterized with in-stand measurements in Montana (Weaver and Dale 1974) and across its north- south range (Weaver 1990a) to guide studies of its function, compared with vegetation zones above and below to explain its altitudinal distribution (Weaver 1977, 1979, 1980, 1994a), and compared with the environments of the five closely related stone pine species to demonstrate the similarity of the environmental requirements of all the stone pines (Weaver 1994a). Given easy access to this information via DOI and Scholar works references provided in the literature cited section, I focus instead on in situ community function, altitudinal distribution, and the within-stand competition leading to the low canopy cover normal to WBP stands. In comparing environment and exotic plant changes along the altitudinal gradient, I often substitute for WBP, qualities of a slightly lower altitude forest type, subalpine fir (*Abies lasiocarpa*). In the 'human influences' section, I consider whether the nearly identical climates of the five stone pines (Weaver 1994a) might allow the establishment of these species in the Rockies.

In Situ Function

WBP performs 'normally' in its normal habitat type (HT). We expect diameter growth of WBP to occur between May and September (bark slip), probably with a maximum (spring wood) in early summer when water, nutrients and temperatures are most favorable and tapering (summer wood), perhaps after cessation of branch growth, as water availability dwindles. Buds break in June, shoots grow in June-July and cones mature in September (Schmidt and Lotan 1980). I consider specific effects of environmental factors below, one at a time: temperature, water, nutrients, and competition.

WBP seedlings germinate and grow in the 10-40°C range, photosynthesis may be significant between 5-35°C (Jacobs and Weaver 1990) and these temperature ranges may suggest the physiological abilities of mature material. For example, photosynthesis probably occurs outside the diameter growth season, i.e. at least in April and in October whenever average maximum temperatures rise to 5-10°C and even intermittently during the winter. In general, temperatures measured in-stand correlate directly with temperatures experienced (e.g. air, soil and plant temperatures), thus temperature measurements correlate well with processes affected and so provide a solid basis for modeling.

In the northern Rocky Mountain summer, the subalpine fir/WBP HTs experience drought, at least in the 0-25 cm root zone. For instance, Weaver (1977) reported summer time water stress of >1 MPa in 1971 and >0.2 MPa in 1972. Drought was significantly greater in the Douglas fir zone below. In winter, soils under deep snow do not freeze. Thus, soil water is constantly replenished by snow melting from the snowpack above and strongly so as the pack begins to deteriorate in spring, perhaps as early as March (Weaver 1994a). Modelers should consider that in contrast to temperature data, in high mountain environments precipitation data are less dependable and may even be misleading. This is because much of apparently large water deposits (table 2) may be blown/sublimed off-site, intercepted and evaporated from trees or soils, run off, or percolate downward below the reach of roots—due to the low water holding capacity of the soils (table 2). Rare in-stand seasonal measures of soil water (e.g. Weaver 1977, Sirucek 1996) are needed, at least for confirmation of models.

Nutrient availability also varies with season (Weaver and Forcella 1979)—nutrients likely being released by decomposition from organic matter under the winter snowpack and being recaptured by spring-summer growth. Such nitrogen and phosphorus dynamics are demonstrated under experimental snowpacks in mountain meadows environmentally like those often adjacent to WBP stands (Weaver 1974, Weaver and Collins 1977, Yano et al. 2015).

If WBP were gardened, i.e. if competition were removed, it would likely be more successful in warmer and richer sites downslope. The escape of lodgepole pine in Argentina-Chile and Monterey pine (*Pinus radiata*) in Hawaii demonstrate such release. We discuss examples of such WBP release below.

Altitudinal Distribution

On an altitudinal transect, WBP is usually absent from dry grasslands of the plains (*Bouteloua gracilis*) and foothills (*Fesuca idahoensis*) and low forests (Douglas fir) above. It may appear in the subalpine fir zone, gains dominance upward toward timberline, and disappears in the alpine (Arno and Weaver 1990). The subalpine fir/alpine segment of this transect is beautifully demonstrated at the Big Sky Ski Resort near Bozeman, Montana (Weaver 1990b). Thus, WBP is a timberline species declining both upward and downward.

Temperature seems to have little direct effect on WBP's distribution, because average growing season temperature is near 10°C, which is within the seedling growth/photosynthesis range, minimum temperatures occur in the hardened period in winter, average July maxima are near seedling optima, and even absolute maximum temperatures allow photosynthesis and root growth (Jacobs and Weaver 1990, Weaver 1994a).

I suspect WBP is relatively drought intolerant, and so imagine that it may be inhibited upward by westerly winds in summer delivering dry air from lower altitudes or sand/ice scouring particles that reduce its tolerance by removing its needles' water-tight cuticles (Weaver 2001). In contrast to its exclusion from moist subalpine ridges by drought, at dry lower timberline (e.g. west slope of Montana's Crazy Mountains) one can see substantial WBP forest heavy with *Letharia vulpina* (fruticose lichen). I speculate that it occupies here a humid microenvironment formed by drainage of moist air from above and pooling behind glacial moraines. Counter-intuitively, its atmospheric demands seem to be bracketed by dry air in the moist climate above and moist air in the dry climate below.

Growing season length may also limit its distribution upward. The WBP community's productivity was related to the productivities of other communities on the Rocky Mountain altitudinal gradient by regressing their yields against various presumptive predictors. The best predictor by far ($r^2 = 0.85$) was growing season length, defined as months with average air temperatures >0°C and no drought (Weaver 1994a). Thus, along the altitudinal gradient, production is low in high altitude sites (e.g. alpine and WBP) due to the short, low-temperature regulated season. Production is also low in grasslands due to the short, dry-soil regulated season, and greatest near the forest boundary where neither temperature nor water conditions are so extreme.

I attribute the diminishment of WBP downslope to competition with other conifers usually assumed to be favored by higher temperatures but which may be favored as much or more by soils that store/supply more water and nutrients (table 2). This hypothesis is supported by the fact that WBP can establish at these sites when its competitors are removed. That is, WBP appears on lower sites where fire or logging have removed competing conifers , especially so when understories established before the disturbance resist the success of small randomly distributed windblown conifer seed more than well provisioned WBP seeds planted in relatively plush open spots by Clark's nutcracker.

Still lower, grasslands and shrublands, perhaps especially fescue (*Festuca idahoensis*) grasslands, may be colonized by other conifers as well as WBP. Colonization may occur, especially if destructive fire is excluded or soil disturbance, e.g., rodent burrowing, cattle grazing, reduce competition. While small- seeded conifers may randomly broadcast their seeds more widely, the large well provisioned seeds of WBP work well with Clark's nutcracker in delivering them to secure sites and planting them at depth where their reserves support root penetration to relatively moist, rich, and less competitive soil layers. Despite the successful entry of such seedlings, they rarely find resources to become more than scraggly clutter in grazing lands.

Soils, Competition and Canopy Cover

As emphasized above, WBP forest structure is exceptionally open, orchardlike. The stand's openness must be due to competition among the trees for a resource other than light, which is surely not limiting in such open stands. This resource limitation cannot be absolute because basal area continues to increase through time but must, nevertheless, act constantly across years. Water supply is a candidate critical variable, being renewed each winter but being exhausted in late summer of each year. Nutrient supply (e.g., N, Ca, etc.; table 2) behaves similarly, being drawn down/exhausted by spring growth (twig extension and spring wood) and rejuvenated by decomposition under snow. The nutrient dynamic was examined across major HTs by Weaver and Forcella (1979).

Either or both limitations are related to soil properties. First, the low water holding capacity of the soil (table 2) provides little absolute buffer against summer drought—characteristic of the northern Rocky Mountains—and less buffering than in the downslope forests with greater canopy cover. Second, the large excess of precipitation over water holding capacity may lead to confusion regarding the position of WBP on the water gradient, as much of the precipitation goes unused. Third, the large excess of water results in leaching, which explains the relatively low concentrations of calcium, potassium, magnesium, and probably nitrogen in WBP soils, deficiencies that differentiate WBP from lower forests.

HUMAN IMPACTS

Pine nuts were a major foodstuff for Paleo-Indians and still are important to competing chipmunks, squirrels, Clark's nutcracker, and bears (*Ursus* spp.). Seed production values often are 20-250 m^{-2} or 2-25 gm^{-2} (Weaver and Forcella 1986). Production is variable and, though masting is significant, it is not regional. Masting favors highly mobile seed-consuming animals like nutcrackers over more sedentary mammals (Weaver and Forcella 1986). While nutcrackers harvest seeds from the treetops, squirrels often drop whole cones and cache them for winter use by themselves and bears, which again leads to less stand regeneration than dispersal by birds. The influence of animals on WBP establishment from seed was elegantly observed by Hutchins (1990) and tested experimentally (McCaughey and Weaver 1990a&b).

Other foodstuffs include whortleberries, which can be numerous, ranging 7-372 berries m^{-2}, the numbers not related to canopy cover (Weaver et al. 1990). Of the herbs present, glacier lily likely is the most nutritious while others (e.g. *Carex geyeri*) provide forage for cattle and wildlife (Weaver and Dale 1974, Forcella 1978, Forcella and Weaver 1979). Macro-fungal diversity may be similar to that in subalpine fir (~60 species and 0-163 kg ha-1) and Douglas fir forests (~61 species and 0- 216 kg ha^{-1}, Keck 2001).

Hiking trails in WBP forests cover a small area, damages mostly brittle shrubs and forbs, and introduce exotic species that remain at the trailside (Dale and Weaver 1974). Trampling damages or eliminates whortleberry, soils are strongly compacted, and both recover very slowly (Weaver and Dale 1978, Weaver et al. 1979). Trampling impacts at these sites increased from hikers to horses; motorcycles were most damaging of all going uphill and least damaging going downhill (Weaver and Dale 1978). The study sites from which these conclusions were drawn could be resampled, with little effort, for a unique 50-year reanalysis.

If burned, WBP forests are likely to return if seeds are locally available and nutcrackers deliver and plant them. The same might occur if sites were lightly logged. If logged, exotic species surely will increase, relatively scarce nutrient elements (table 2) will be exported, and compaction will occur. Nutrients are most concentrated in needles, twigs and bark. Thus, the amount of exported nutrients declines from harvest of whole trees, through boles, to least with peeled boles, as is done in some Italian forests (Weaver and Forcella 1977).

Invasion of exotic species in WBP and fifteen other environmental zones was compared by recording their presence in four disturbance zones of each (table 3, Weaver et al. 1990, 1995, 2001) In the WBP zone, 14 species with measurable cover (table 3, shaded) were found on constantly disturbed road-shoulders, six were found on road-cuts (once disturbed and undergoing primary succession), four were found on cleared right-of-way, where they competed with residual understory vegetation, i.e. secondary succession, and none appeared in undisturbed forest, where invaders compete with both over and understory vegetation of the 'near climax' vegetation originally present. Similar trends occurred where the responding variable was total exotic species present (15, 12, 12, 0 species) or exotic species with >30% constancy (13, 11, 6, 0 species, table 3). The principal exotic species were domestic grasses (*Bromus inermis*, *Poa pratensis*, and *Phleum pratense*), dandelion (*Taraxacum officinale*), and legumes (*Trifolium hybridum*, *T. repens*, *Melilotus officinale*, and *Medicago lupulina*).

With respect to exotic species, the generality and application of the WBP conclusions can be compared with observations in four other vegetation zones (table 3). The total number of exotic species increases from alpine (6) and WBP (15) to forests and grasslands below (18-21). We suggest that the colder environments above are probably too rigorous for exotics normally arriving from warmer sites or that WBP sites may be too remote for propagule delivery. In all zones, the number of exotic species declines with decreased disturbance and increased native competition, although the decline weakens downslope. Note that data from cleared rights-of-way are lacking in alpine and grassland sites in table 3 because no trees were

Table 3. Exotic species presence/numbers by habitat type (HT) and disturbance regime.

		All exotic species[e]				Number of exotic species[c] Constancy >30%[e]				Species with measurable cover[f]			
HT[a]	reps	Sh[b]	Cut	Clear	UnD	Sh[b]	Cut	Clear	UnD	Sh[b]	Cut	Clear	UnD
Alpine	11	6	4		4	2	1		0	1	0		0
WBP	10	15	12	12	0	13	11	6	0	14	6	4	0
Psme	10	20	17	12	9	11	9	5	5	10	7	4	3
Agsp	8	18	18		15	9	11		8	8	4		4
Bogr	7	21	21		19	12	12		9	7	5		1

[a]Environmental zones (HTS) are Alpine, forest (WBP/*Abies lasiocarpa* and Psme/*Pseudotsuga menziesii*) grassland (moist, *Agropyron spicatum* Agsp and dry, *Bouteloua gracilis* Bogr)

[b]Disturbance regimes are road shoulder (Sh), road cut (Cut, 1°), cleared (Clear, 2°) and undisturbed (UnD)

[c]Exotic species number is reported with three measures.

[d]number of exotic species even if only in one replication

[e]number of exotic species in >30% of the stands

[f]number of exotic species with measurable cover

cleared from these zones. These observations can be applied to broader two-dimensional landscapes of forest and rangeland. If the establishment of exotic species is proportional to the amount of competition/disturbance, then establishment of exotic species on disturbed sites near and far from roads should be equal, i.e. exotic species establishment in logged areas (far distance) might be similar to that of cleared rights-of-way (near distance). This assumption may over-estimate the invasion of remote sites because delivery of propagules is less there than along trails or roads.

Introduction of the white pine blister rust from Europe has been, by far, man's most damaging act for WBP. I suggested in 1998 that WBP's extreme susceptibility might be greatly reduced by introducing genes from closely related and highly resistant European stone pines. Their resistance may well be transferred by simple hybridization, i.e. collect European pollen (*Pinus cembra* or *P. sibirica*) and transfer it to mature WBP in wild or arboretum settings. Success is probable because closely related pines usually hybridize easily. Thus, I expect the F1 to be polygenically resistant and, as the F1s backcross in the wild, some F2 will be even more resistant (naturally selected) and some less resistant (naturally eliminated). Potential difficulties include: 1) Species may be genetically incompatible despite the common tendency of closely related pines to hybridize, 2) Despite similar latitudes, phenological (day-length) differences may inhibit natural crossing and backcrossing. If so, the first crosses must be artificial but the failure will fade as backcrossing dilutes any Eurasian daylength control, 3) F1 and F2 progeny might not tolerate the WBP environment. This is unlikely since half their genes are native and half come from trees drawn from similar environments (Weaver 1994b), 4) Genes introduced with the resistant European material explode to create a weedy invader. This also is unlikely since the F1 are immediately half WBP and in each succeeding generation, the European genes will become further diluted. The probability of concentration of European genes is diminishingly small, first, because pollen from surrounding native WBP is much more available than pollen from the F1 and F2 hybrid trees and, second, selection for European genes will be low because European phenotypes are doubtless less well adapted to Rocky Mountain than Swiss environments, 5) Immediate introduction might have allowed natural crossing and free spread of the resistance genes in the wild (as suggested by parenthetic 'in the wild' above). While cautious controlled breeding, might be favored by some, this approach would be more expensive in dollars and time. Currently, lab/garden crossing may be necessary anyway, because natural populations of WBP are already so sparse.

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