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Washoe and Ponderosa Pines on Promontory Hill near Merritt, B.C., Canada.

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Abstract

Morphological and ecological characteristics of a population on Promontory Hill, earlier identified as Washoe pine, have been compared to ponderosa pines native to the drier Interior of British Columbia. The results demonstrate that the ranges of variability of all investigated traits of Washoe pine are all within the respective ranges exhibited by ponderosa pine (*Pinus ponderosa* var. *ponderosa*, North Plateau race).

Key words: Flora of North America, Pinaceae, *Pinus*, *Pinus ponderosa*, *Pinus washoensis*, taxonomy, morphology, ecology.

Zusammenfassung

Morphologische und ökologische Merkmale einer früher als Washoe Kiefer identifizierten Population auf dem Promontory Hill wurden mit den entsprechenden Charakteristika der im trockeneren Inland Britsch Kolumbiens heimischen Ponderosa Kiefer verglichen. Die Ergebnisse zeigen, daß die Variationsbreite aller bei der Washoe Kiefer untersuchten Merkmale vom Variationsumfang der entsprechenden Merkmale der *Pinus ponderosa* var. *ponderosa*, North Plateau Rasse, voll abgedeckt wird.

Introduction

Pinus ponderosa DOUGLAS ex C.LAWSON (var. *ponderosa*, or more specifically the North Plateau race of the forestry literature) dominates the lowest, driest fringe bordering the steppe, of the Montane Forest in the drier Interior of southern British Columbia, Canada (BRAYSHAW 1970). My acquaintance with ponderosa pine of this general area is also documented in BRAYSHAW (1955, 1965).

Part of what was formerly considered to represent one continuous population of ponderosa pine, near the summit of Promontory Hill (50°12' N, 120°58' W, altitude 1732 m s.m.), 15 km northwest of Merritt, B.C., has subsequently been identified as Washoe pine (HALLER 1965), *Pinus washoensis* H.MASON & STOCKW. (1945). To verify the validity of this identification, the present study was carried out in 1985. Time, however, seemed not ripe then for the acceptance of the results, as publication was denied. Only a brief note sub '*Pinus ponderosa*' in 'Trees and Shrubs of British Columbia' (BRAYSHAW 1996: 64, 65) so far testifies to this investigation. Correspondence (see also LAURIA, this volume: 655 - 671) that ensued following the publication of this book again opened an opportunity to present a summary of my former observations on the Washoe pine stand on Promontory Hill, and of its comparison with British Columbia populations of *P. ponderosa* var. *ponderosa* (North Plateau race) with which it is in contact, and to which it appears to be most closely related (CRITCHFIELD 1984).

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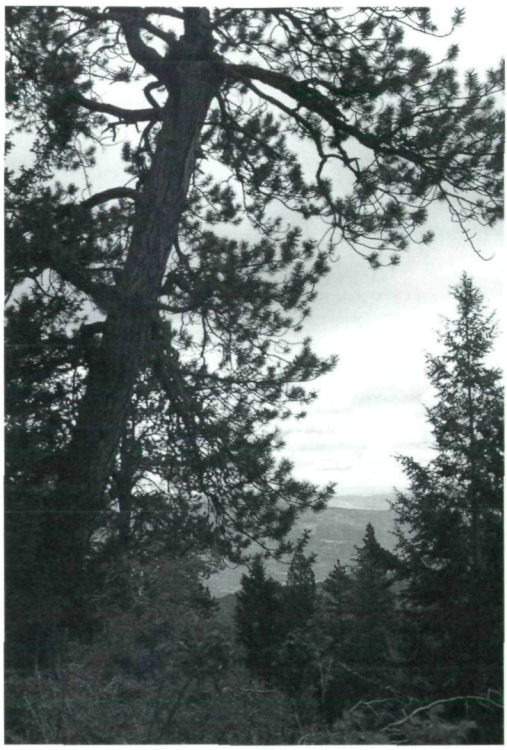

Fig. 1: Adult Washoe pine tree on Promontory Hill. Young Douglas-fir trees on right. Photographed in 1985. Collections T.C. Brayshaw 85-62 [V 143530] and 85-168 [V 143531].

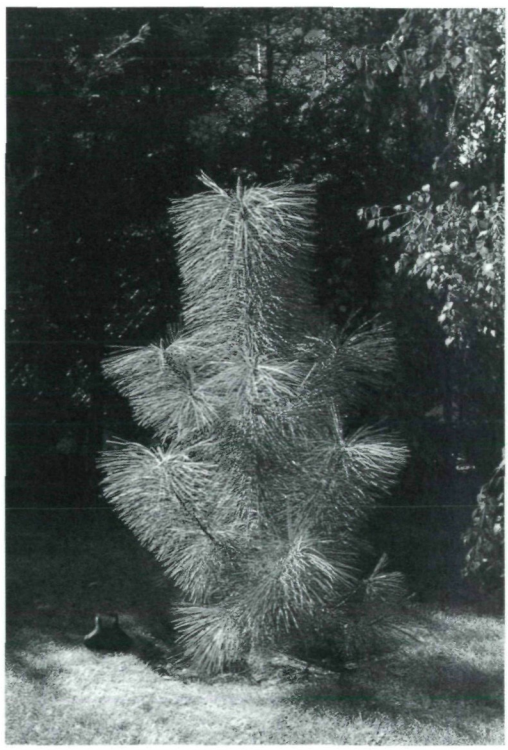

Fig. 2: Seedling Washoe pine, offspring of the tree in fig. 1. Photographed in 1991 in the grounds of the Royal British Columbia Museum, Victoria. Voucher specimen T.C. Brayshaw 90-297 [V 148458].

The Data

The Washoe pine stand on Promontory Hill (fig. 1) occupies the upper slopes on the south side of the hill, facing southwest to southeast and is continuous with, and intergrades with, stands of typical ponderosa pine, which occupy the lower slopes and adjacent valley bottom. The terrain on the upper slopes of that hill is broken and rocky. There is some young Douglas-fir (*Pseudotsuga menziesii*), and some young pines up to altitudes around 1450 m. Pine Grass (*Calamagrostis rubescens*) dominates the herbaceous ground-cover, as is normal in the dry forests at that altitude (BRAYSHAW 1970).

Cone and seed production, though abundant in ponderosa pine at lower altitudes, was very sparse in the Washoe pine stand, leading to disappointingly few fully measurable samples of this pine. Above an altitude of about 1460 m no cones were to be found on the trees or on the ground, and no young pine reproduction was seen. The few seed-producing trees were at or near 1400 m altitude.

Elsewhere in that region, ponderosa pine forms rather open, often park-like stands up to an altitude of around 1200 m. Above that level it may invade burned Douglas-fir forests

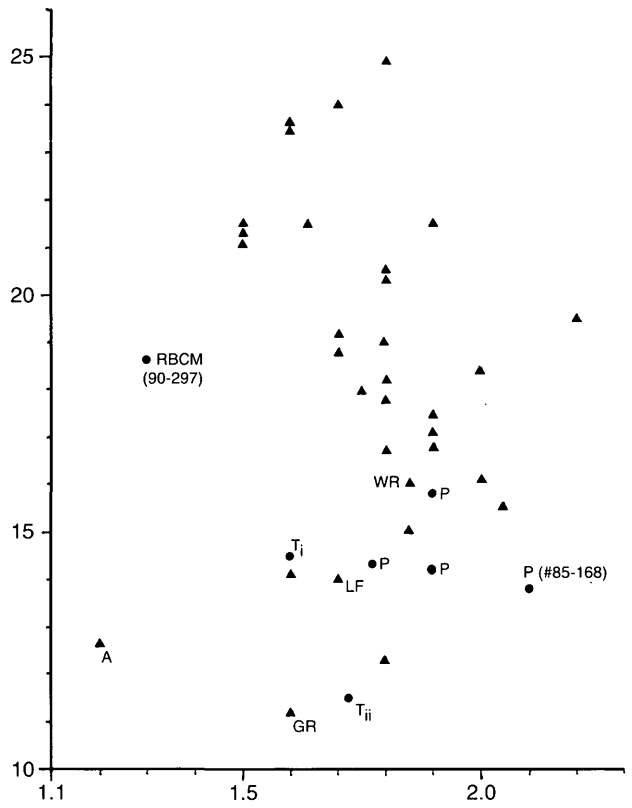

Fig. 3: Leaf dimensions of Washoe (dots) and ponderosa pines (triangles): vertical axis = length in cm, horizontal axis: width in mm. For abbreviations see table 1, for identification of specimens see text.

and become a seral dominant, but will eventually yield to Douglas-fir, which is the climax dominant of the Montane Forest at higher, moister and cooler levels. Ponderosa pine requires full sunlight for effective growth after its first year, and does not regenerate in the deepening shade produced by the more luxuriently growing Douglas-fir.

In August and October, 1985, I collected herbarium specimens of Washoe pines on Promontory Hill (in October also seeds, some of which were sown to grow seedlings). Their collection numbers are: T.C. Brayshaw 85-61 [V 143769], 85-62 [V 143530], 85-67 [V 143768] 85-124 [V 139395], 85-167 [V 143772], 85-168 [V 143531], and 85-169 [V 143771]. Specimen nos. 85-61 and 85-167 are from the same tree, as are specimens 85-62 and 85-168. These collections, as well as a larger collection of ponderosa pines from across British Columbia, are filed in the herbarium of the Royal British Columbia Museum, Victoria, B.C. [V], where a complete list of specimens examined is available. Sources of Washoe and ponderosa pines compared in this study are listed in table 1.

Leaf characters: The leaf dimensions of the Washoe pines lie within the range of dimensions for ponderosa pine, but are on average shorter, stouter and stiffer than the ponderosa pine average (fig. 3, table 2).

Tab. 1: Identification of sources of significant samples, and their abbreviations in fig. 3 to 8.

Ponderosa pine		
a) Points along northern edge of range:		
A	Argenta	50°10' N, 117°55' W
GR	Gang Ranch	51°30' N, 122°18' W
LF	Little Fort	51°27' N, 120°12' W
WR	White River	50°21' N, 115°34' W
b) Point on western edge of range, in Cascade Range:		
S	Skagit River	49°01' N, 121°04' W

Washoe pine	
MR	A cone collected from type locality (Mt. Rose, Nevada) by R. Hunt.
P	Trees sampled on Promontory Hill, B.C.
Ti	Type specimen, sheet 1.
Tii	Type specimen, sheet 2.
RBCM	Young tree planted at [V], from seed from a tree on Promontory Hill.

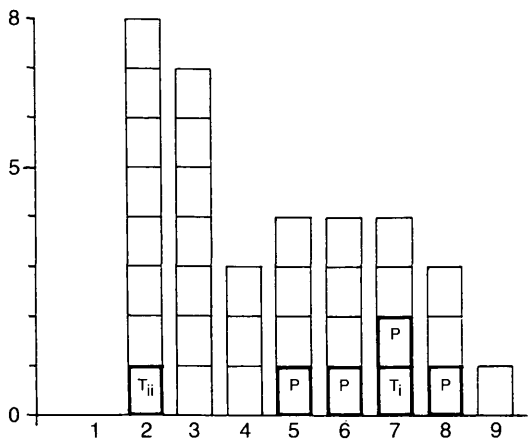

Fig. 4: Leaf characters of Washoe and ponderosa pines: horizontal axis = number of resin canals present in cross-sections of a leaf, vertical axis = number of trees. For abbreviations see table 1. 'Boxes' with thick borders represent *Pinus washoensis* trees (ordinal position within a vertical column is not significant).

My little experience of growing seedlings of both species in Victoria, at sea level, shows that leaf growth here starts in mid to late March, and elongation continues for about four months, ending about mid to late July. Under sea level conditions the *Pinus washoensis* leaves grow longer, and are more slender and flexible (figs 2, 3) than those of their parents at high altitudes, and are indistinguishable from those from seedlings of typical *P. ponderosa* grown from seed collected at low altitudes. The seedling in fig. 2 (collection no 90-297 [V 148458]) is the offspring of the tree shown in fig. 1, which is represented by specimen 85-168 [V 143531]. Growing pine leaves would not get four months for elongation at the upper altitudes on Promontory Hill, where the ground may be frozen until late April or early May, leaving perhaps two months for leaf elongation before the process is again stopped. This abbreviation of the growing season probably accounts for the shorter leaves (fig. 1), and for the shorter-than-average cones of Washoe pine compared to ponderosa pine. It is significant that similarly short-leaved ponderosa pine trees are found at the northern limit of the range of that species (fig. 3), where the trees would be subject to similar local climatic constraints to those at the higher altitudes on Promontory Hill.

The numbers of resin canals in the leaves vary widely in these two pines. My little project in counting them indicates that the range in canal number in Washoe pine does not exceed the range in typical ponderosa pine (fig. 4), and shows no excentric trend within the ponderosa pine range.

Cone characters: The cones of Washoe pine are described by MASON & STOCKWELL (1945) as 5-8 cm long, with 160-190 scales. Thus they are shorter, but with more scales than normal in ponderosa pine.

Tab. 2: Assignment of morphological index scores.

		Pinus washoensis		*Pinus ponderosa*	
		Character value	Score (0)	Character value	Score (1 or 2)
Leaf	length (cm)	10 - 15	0	over 15	1
	no. resin canals	7 - 10	0	2 - 6	1
Cone	length (cm)	5 - 8	0	over 8	1
	no. of scales	160 - 190	0	under 160	1
Seed*	ratio: wing length/ body length	1.5 - 2.0	0	over 2.0	2
Total score:			0		6

* No seeds = score 1.

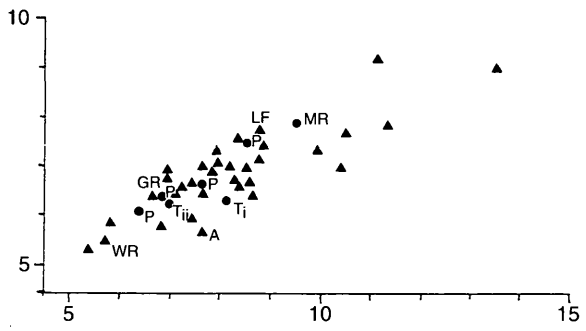

Fig. 5: Cone dimensions (mature, open cones) of Washoe (dots) and ponderosa pines (triangles): horizontal axis = length in cm; vertical axis = width in cm. For abbreviations see table 1.

The size variation seems to be true locally on Promontory Hill, where the cones do appear to be smaller with increasing altitude. However, comparison with ponderosa pine cones from across British Columbia indicates that the size range of Washoe pine cones, while shorter than the average for ponderosa pine cones, is still within the overall ponderosa pine cone size range (fig. 5). As in leaf dimensions, the Washoe pine trend in cone dimensions parallels that of ponderosa pine at the latter's northern limit.

The number of cone scales in Washoe pine varies widely, but falls within the overall range of numbers in ponderosa pine, deviating from the average less than do the ponderosa pine cones from the northern limit of that species (fig. 6). All the cones from Promontory Hill had fewer than 150 scales.

As with the North Plateau race of ponderosa pine in this region, most seed-producing cones are dark purple at submaturity, but a few, probably not more than 1 % of them, are green.

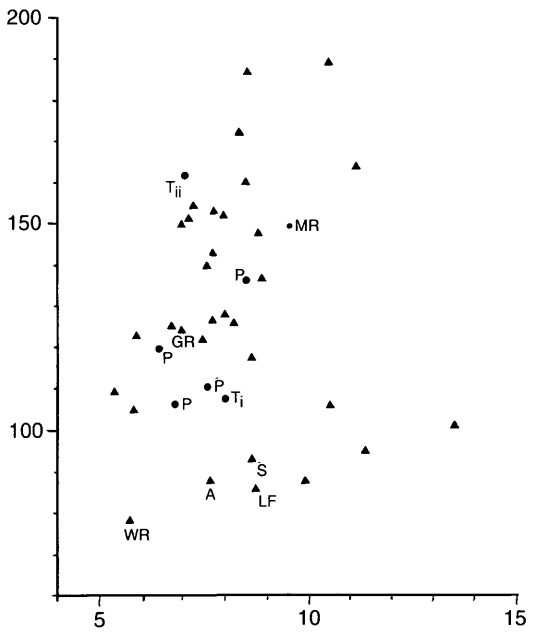

Fig. 6: Cone characters of Washoe (dots) and ponderosa pines (triangles): horizontal axis = cone length in cm, vertical axis = number of scales per cone. For abbreviations see table 1.

Seed characters: The ratio of wing length / body length of the seeds averaged less in Washoe pine than in ponderosa pine, but the ranges in this ratio overlap broadly. This character is not completely independent of others, since it is related to the size of the cone and the position of the seed in the cone. In October 1985 only three Washoe pine trees on Promontory Hill had produced seeds. Wing length / body length ratio of these samples is graphed in fig. 7, and suggests that it is, on average, smaller in Washoe pine than in ponderosa pine, as could be expected.

Morphological index: Fig. 8 summarizes the character comparisons. The values for the diagnostic characters used to make up this index are set out in table 2, and are based on

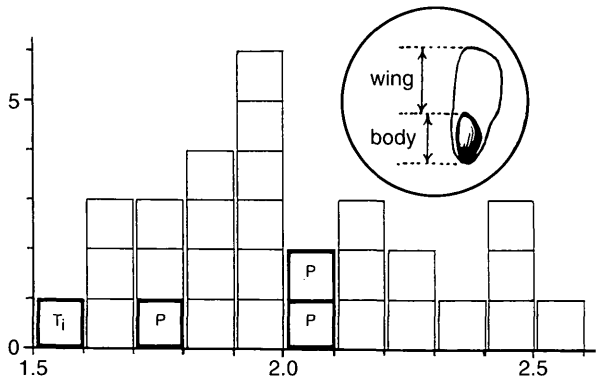

Fig. 7: Seed characters of ponderosa (normal 'boxes') and Washoe pines ('boxes' with thick borders): horizontal axis = categories of ratios of seed wing length / seed body length, vertical axis = number of trees.

the description of *Pinus washoensis* by MASON & STOCKWELL (1945). In this scheme, 'ideal' *P. washoensis* should score '0' or '1', while 'ideal' *P. ponderosa* should score '6'. The index scores received by the trees of the two populations sampled for this study should be expected to cluster in discrete areas of the graph (fig. 8), but instead they are mixed together in what appears to be a single population, though the few specimens of Washoe pine show a slight tendency toward low scores.

Conclusions

The results presented here demonstrate that all the differences by which ponderosa and Washoe pines have been distinguished, are differences of degree of expression, not of kind, and are of a nature that could conceivably be modified by environmental factors. Even HALLER (1965), who identified the stand on Promontory Hill, questioned the status of Washoe pine as a species distinct from ponderosa pine.

CRITCHFIELD (1984) postulated that Washoe pine originated by natural selection, beginning in interglacial or preglacial time, producing a race genetically adapted to the harsh, high altitude environment that it occupies today. However, as LAURIA (this volume: 655 - 671) demonstrates, the taxonomic and genetic arguments, on which the specific recognition of Washoe pine has been based in the past, are invalid or questionable. The results of this study indicate that any differences that may exist between Washoe and the type variety of ponderosa pine (presumably corresponding to the North Plateau race) are phenetic responses of *Pinus ponderosa* to environment.

The complete failure of pine reproduction on the uppermost slopes of Promontory Hill, where I found only adult trees with no cones or seeds, indicates that this population of pines is not an established species occupying an environment to which it is genetically adapted. It is an immigrant population, originating from seeds of the North Plateau race of ponderosa pine, carried up by wind from lower altitudes, and existing here temporarily, beyond the limits of its natural environment. If there is no replenishment by wind-blown seeds, this high-altitude stand will last only through the lifetime of the existing tree generation. The appearance of young Douglas-fir trees among the mature pines reinforces the impression of a seral community.

I envision an occasion, a century or more ago, when, during one or a few warm years, a fire destroyed the entire Douglas-fir forest that dominated the upper slopes of Promontory Hill above about 1200 m. From a heavy seed crop of ponderosa pines of the lower slopes

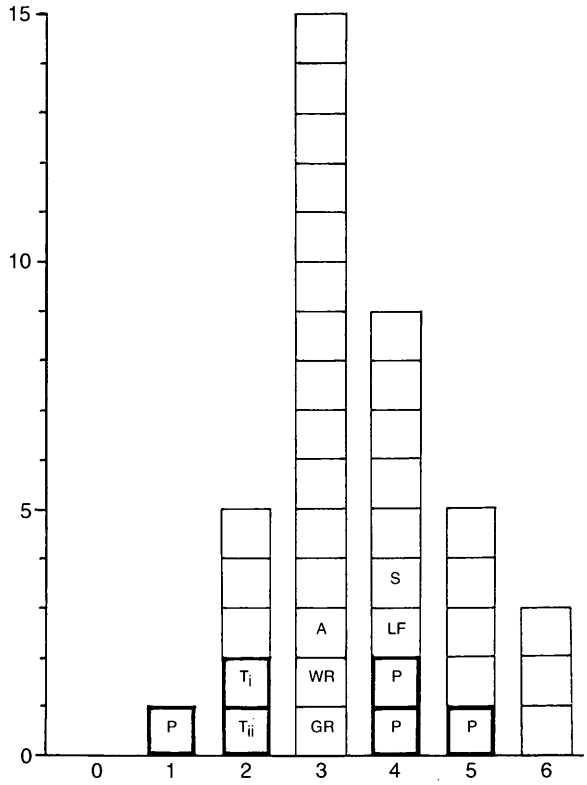

Fig. 8: Morphological index: horizontal axis = score, vertical axis = number of samples. 'Ideal' *Pinus washoensis* would score '0' and 'ideal' *P. ponderosa* '6' (see text and table 2). For abbreviations see table 1. Washoe pine trees are represented by boxes with thick borders.

and the valley below, a strong southwesterly wind carried seeds far up the slopes, to deposit them on the bared ground. In the absence of Douglas-fir competition the seedling pines were able to become established and grow into the present stand. However, they would perforce respond to the returning, unusually harsh conditions, such as low temperatures and short growing seasons, at altitudes above their species' accustomed range, with somewhat stunted growth and inhibited reproduction.

On Promontory Hill we are seeing a stage in natural forest succession. Many young Douglas-fir trees are now again growing up among the older pines. In the absence of fires or other disturbances, this stand may eventually become an example of the *Pseudotsuga - Arctostaphylos - Calamagrostis* association (BRAYSHAW 1970). This situation may not completely exclude pines. At borderline altitudes (around 1200 to 1450 m) the broken, rocky ground may prevent Douglas-fir from forming a completely closed and shady canopy. Openings may persist in which ponderosa pine can get established in favorable years into small, subdominant groups, forming overall a forest mosaic.

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