Allopatric hybridization and introgression between *Juniperus maritima* R. P. Adams and *J. scopulorum* Sarg. II. Additional Evidence from nuclear and cpDNA genes in Montana, Wyoming, Idaho and Utah

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ABSTRACT

A previous study using data from nrDNA (ITS), maldehy, and petN-psbM (cpDNA) confirmed that allopatric hybridization is occurring at Wallowa, OR, eastern WA, and southeastern BC into western Montana. nrDNA was found to be of less use in detecting hybrids than a single copy nuclear gene (SCN), maldehy. This might to be due to concerted evolution in nrDNA or relictual effects from ancient speciation. The uniform presence of either *J. maritima* cpDNA in western BC and WA or *J. scopulorum* cpDNA in eastern BC, WA, OR, and MT suggests allopatric introgression by air-borne pollen. *Juniperus* trees in the study area can be divided into roughly four zones: 1. typical *J. maritima*: Puget Sound, Vancouver Island, islands in the Strait of Georgia, and western BC; 2. intermediate trees: eastern WA, Wallowa, OR, southeastern BC, and western MT; 3. trees introgressed from *J. maritima* into *J. scopulorum*: Montana and northeastern Wyoming; 4. mostly typical *J. scopulorum*: south eastern ID, Utah and southward in the Rocky Mtns. Published on-line **www.phytologia.org** *Phytologia 97(3): 187-199 (July 1, 2015).* ISSN 030319430.

KEY WORDS: *Juniperus maritima, J. scopulorum, nrDNA, maldehy, petN-psbM,* leaf terpenoids, hybridization, introgression, Pleistocene refugia, recolonization, Wisconsin glaciation.

Recently, I published an extensive analysis of reputed allopatric hybridization and introgression between *Juniperus maritima* and *J. scopulorum* (Adams, 2015). The overall trend was the presence of *J. maritima* in the northwestern US and British Columbia (BC) with intermediate trees (hybrids and back-crosses) in eastern WA and OR, eastern BC and Kalispell, MT (Fig. 1.). The cp marker (petN-psbM) gave the clearest delineation between the taxa. All the intermediate trees had *J. scopulorum* cpDNA (via pollen), with only two intermediate trees having *J. maritima* cp DNA (Wallowa, WO, Fig. 1). *Juniperus maritima* nrDNA (ITS) was found in all trees, except for two putative hybrids at Williams Lake, BC (WL, Fig. 1) and two hybrids at Fairmont Hot Springs, BC (FH, Fig. 2). Maldehy appeared to be a more sensitive indicator of hybrids than nrDNA, in that several trees contained heterozygous maldehy from *J. maritima and J. scopulorum* (Fig. 1).

However, I was surprised to find no typical *J. scopulorum* (by all three DNA markers) in Wallowa, eastern Washington, or Kalispell, MT. Five reference *J. scopulorum* trees from Utah and New Mexico were pure *J. scopulorum* (by the three DNA markers) (Fig. 1). Left unanswered was the extent of introgression eastward into *J. scopulorum* in Montana, Wyoming, Idaho and Utah. The purpose of the present paper is to extend the analyses of the previous work (Adams, 2015) to include additional *J. scopulorum* trees from Montana, Wyoming, Idaho and Utah to further analyze the eastern extent of introgression.

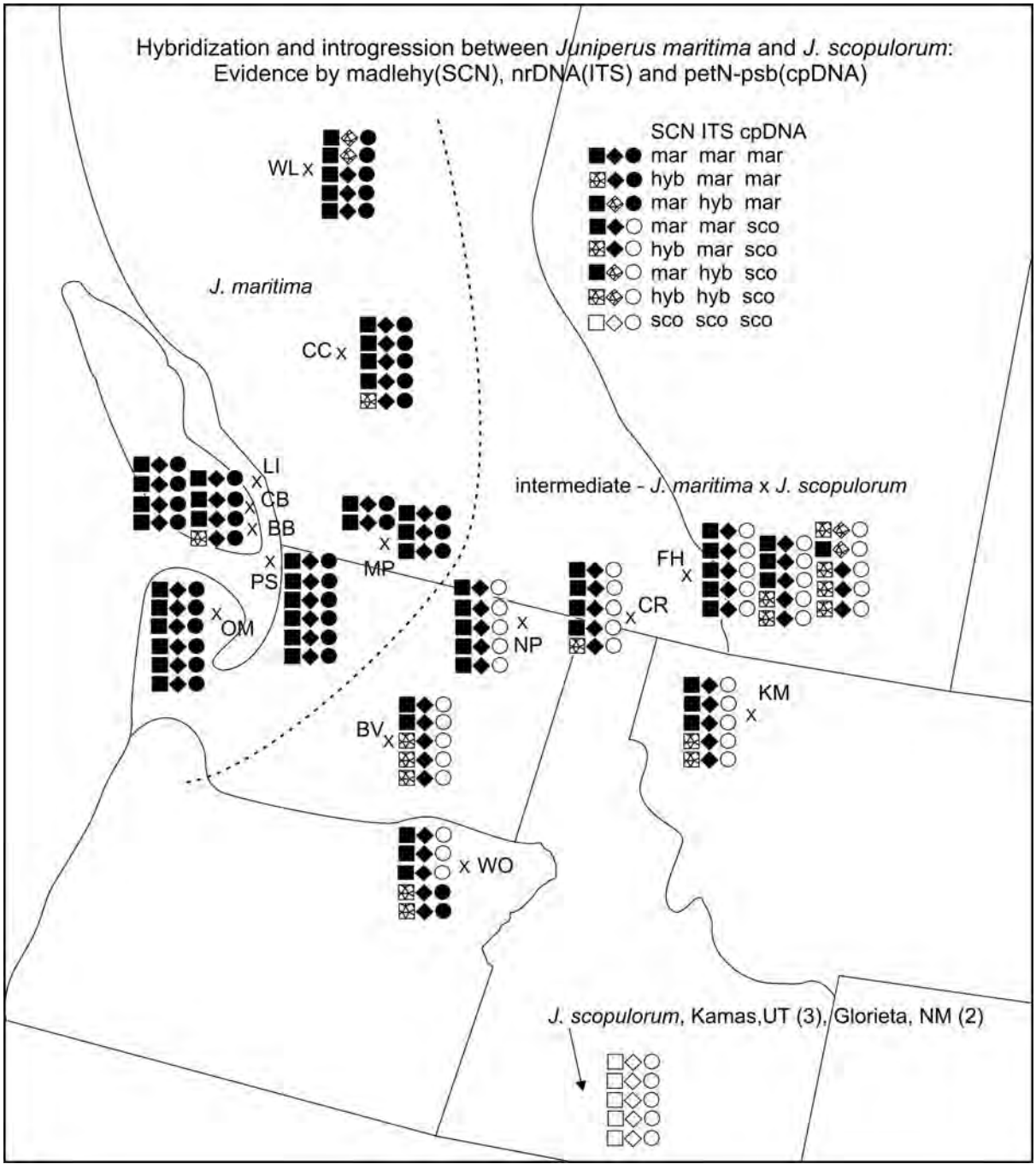


Figure 1. Combined classification of trees based on maldehy, nrDNA, and cpDNA sequence data. From Adams, 2015.

MATERIALS AND METHODS

Plant material: (species, population acronym, location, vouchers):

J. maritima: BB, Brentwood Bay, Vancouver Island, BC, *Adams 11056-11058;* CB, Cowichan Bay, Vancouver Island, BC, *Adams 11061-11063*; LI, Lesqueti Island, BC, *Adams 11064-11066*; Vancouver Island, BC; PS, San Juan Island, WA, *Adams 11067, 11068*; Whidbey Island, WA, *Adams*

11075; Fidalgo Island State Park, WA, *Adams 11076*; Skagit Island, WA, *Adams 11077-1178* (*11077* is the national big tree for *J. scopulorum*, but should be the *J. maritima*, national big tree); WL, Williams Lake, BC, *Adams 13436-13440*; Cache Creek, BC, *Adams 13431-13435*; MP, Manning Park, BC, *Adams 13426-13430*; Olympic Natl. Forest, WA, *Adams 11999-12004*.

J. scopulorum: Reference, Kamas, UT, *Adams 10895-10899,13887-13891*, and Glorieta Pass, NM, *Adams 10933-10935*.

Putative *J. maritima x J. scopulorum*: CR, Creston, BC, *Adams 14026-14030*; FH, Fairmont Hot Springs, BC, *Adams 13421-13425, 14001-14010*; *Adams 14001-14010*; Northport, WA, *Adams 14031-14035*; BV, Beverley, WA, *Adams 14036-14040*; WO, Wallowa Mtns., OR, *Adams 11935-11939*; KM, Kalispell, MT, *Adams 12995-12999*;

Additional *J. scopulorum* from the northern Rocky Mtns.: Soda Springs, ID, *Adams 7063-7066*, Moorcroft, WY, *Adams 10876-10878*; Big Sky, MT, *Adams 10882-10884*; Butte, MT, *Adams 10885-10889*. Voucher specimens are deposited in the Herbarium, Baylor University (BAYLU).

One gram (fresh weight) of the foliage was placed in 20 g of activated silica gel and transported to the lab, thence stored at -20^{o} C until the DNA was extracted. DNA was extracted from juniper leaves by use of a Qiagen mini-plant kit (Qiagen, Valencia, CA) as per manufacturer's instructions.

Amplifications were performed in 30 µl reactions using 6 ng of genomic DNA, 1.5 units Epi-Centre Fail-Safe Taq polymerase, 15 µl 2x buffer E (petN-psbM), D (maldehy) or K (nrDNA) (final concentration: 50 mM KCl, 50 mM Tris-HCl (pH 8.3), 200 µM each dNTP, plus Epi-Centre proprietary enhancers with 1.5 - 3.5 mM $MgCl_2$ according to the buffer used), 1.8 µM each primer. See Adams, Bartel and Price (2009) for the ITS and petN-psbM primers utilized. See Adams (2015) for maldehy primers and PCR conditions.

The PCR reaction was subjected to purification by agarose gel electrophoresis. In each case, the band was excised and purified using a Qiagen QIAquick gel extraction kit (Qiagen, Valencia, CA). The gel purified DNA band with the appropriate sequencing primer was sent to McLab Inc. (San Francisco) for sequencing. Sequences for both strands were edited and a consensus sequence was produced using Chromas, version 2.31 (Technelysium Pty Ltd.). Minimum spanning networks were using PCO3d and MINSPAN software (Adams et al., 2009; Adams, 1975; Gower, 1966, 1971; Veldman, 1967).

RESULTS AND DISCUSSION

DNA sequencing gave: nrDNA (1270bp), with 5 substitution differences between the reference populations of *J. maritima* (BB) and *J. scopulorum* (KU, GN); petN-psbM (828bp), 8 nucleotide differences plus a 7 bp indel; maldehy (522bp, *maritima*; 529 bp, *scopulorum*), 2 differences plus a 7 bp indel. Each of these sequences displayed fidelity in the reference populations except for two trees in the Kamas, UT population (Table 1). Based on these distinct differences, an effort was made to classify each plant as to species or hybrid for maldehy and nrDNA. Of course, it may be that some positions will be heterozygous by chance, from relictual speciation or from ancestral hybridization.

Table 1 shows the classification of 101 individuals for each of these three gene regions. All of the samples from the Puget Sound - Strait of Georgia - Olympic Mtns, plus Manning Park were uniformly classified as *J. maritima*, except for *11063*, Cowichan Bay, Vancouver Island, for which maldehy was heterogenic for both substitutions, and, thus, classified as a hybrid. nrDNA was slightly more conserved in detecting hybrids, with 10 hybrids and 2 back-crosses, compared to maldehy that found 16 hybrids (Table 1). In only one case (13421, Fairmont Hot Springs, BC) did nrDNA and maldehy classify the same tree as a hybrid. However, another case (10889, Butte, MT) had *J. maritima* maldehy and intermediate (or backcrossed) nr DNA (Table 1). The conserved nature of the multi-copy nrDNA (up to

millions of copies per cell) might be due to concerted evolution (Liao, 1999). The latter author argues that because rRNAs are structural molecules, multiple gene copies are necessary to supply the demand for ribosomal subunits in the cell. Since these sub-units function only when assembled into a large complex, homogeneity of rRNAs is critical for regular, functional ribosome assembly and translation to function normally. Liao (1999) concludes that "a possible biological function of concerted evolution is to maintain homogeneous gene copies in a family so that homogeneous transcripts can be produced." However, concerted evolution is thought to be a slow process over numerous generations. Hybrids would seem likely to be heterozygous for both parents nrDNA.

The distribution of cpDNA (petN-psbM) shows a clear trend (Fig. 2) with *J. maritima* petN confined to the western BC, Vancouver Island - Puget Sound, WA, and Olympic Mtns., WA, with the exception of two trees in the Wallowa Mtns., OR (WO). Likewise, *J. scopulorum* petN is confined to southeastern BC, eastern WA, Kalispell, MT (KM) and 3 trees in the Wallowa Mtns., OR (Fig. 3). The pattern is suggestive of *J. scopulorum* pollen flow carrying petN towards the northwest. Four nrDNA hybrids were found in the Williams Lake (WL) and Fairmont Hot Springs (FH) populations (Fig. 3) and another four plus two backcrosses in the intermediate (MT, WY) zone (Fig. 3). Mostly typical *J. scopulorum* nrDNA occurred from Idaho southward (Fig. 3).

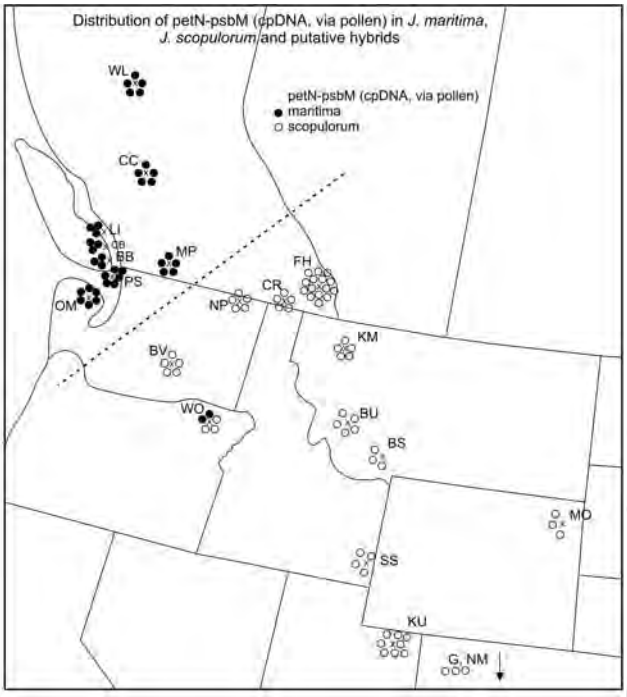


Figure 2. Classification by cpDNA (via pollen). Note the sharp break in western BC in petN.

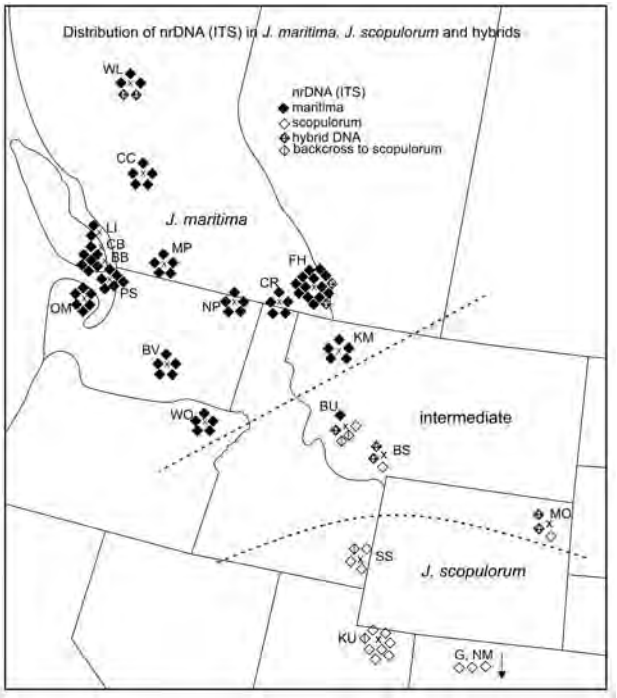


Figure 3. Classification by nrDNA. Note the zone of intermediate nrDNA in Montana and Wyoming.

The distribution of maldehy types gives an interesting comparison to nrDNA and petN (Fig. 4). Homogenic *J. scopulorum* maldehy trees were confined to southern Montana and southward in the Rocky Mtns. However, homogenic *J. maritima* maldehy individuals were widespread across the study area (Fig. 4). One hybrid was found in the CC (Cache Creek) population, whereas all the other hybrid maldehy plants were in eastern BC, Beverly, WA (BV), Wallowa Mtns., OR (WO) and Kalispell, MT (KM). Kalispell (KM) and Wallowa (WO) appear to be at the northwestern boundary of typical *J. scopulorum*. The area of intermediates (Fig. 4) is similar, but not identical, to that of the nrDNA intermediates (Fig. 3).

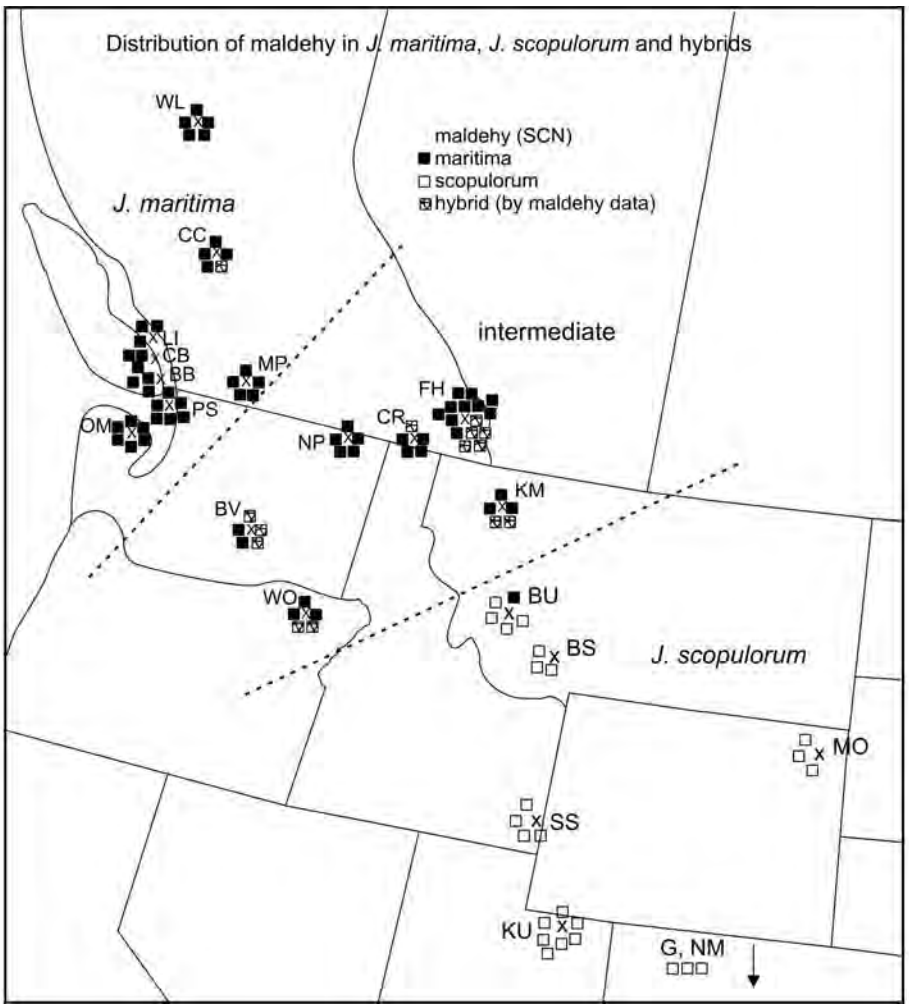


Figure 4. Distribution of *J. maritima, J. scopulorum* and intermediates as per the classification by their maldehy sequences.

Figure 5 shows combined mapping using all three gene classifications. The study area can be divided into roughly four zones:
1. typical *J. maritima*: Puget Sound, Vancouver Island, islands in the Strait of Georgia, and western BC;
2. intermediate trees: eastern WA, Wallowa, OR, se BC, and western MT;
3. trees introgressed from *J. maritima* into *J. scopulorum*: Montana and ne Wyoming;
4. mostly typical *J. scopulorum*: se ID, Utah and south in the Rocky Mtns.

The second zone contains two individuals (in the BB and CC populations) that were intermediate in maldehy, along with two individuals at Williams Lake (WL) that were intermediate in nrDNA (Fig. 4). No individuals that are pure in all three genes are present east of the dashed line (central BC and WA). Wallowa (WO) is the only eastern location in which individuals (2) contained *J. maritima* cpDNA (petN). Fairmont Hot Springs (FH) had the most hybrid individuals, as well as the only individual that was classified as an hybrid in both maldehy and nrDNA (Fig. 5).

nrDNA (ITS) differs by 5 bp between *J. maritima* and *J. scopulorum*. In the third zone several individuals had 2 or 3 nucleotides that were homozygous as *J. scopulorum*, and 3 or 2 that were heterozygous (*J. scopulorum* + *J. maritima*). This seems suggestive of a backcross or F_2 individual. It may be that some heterozygous trees are the result of previous hybridization, a relict from speciation, or the nrDNA may reflect concerted evolution in homogenizing individuals. Southeastern Idaho, Utah and New Mexico contain mostly pure *J. scopulorum*.

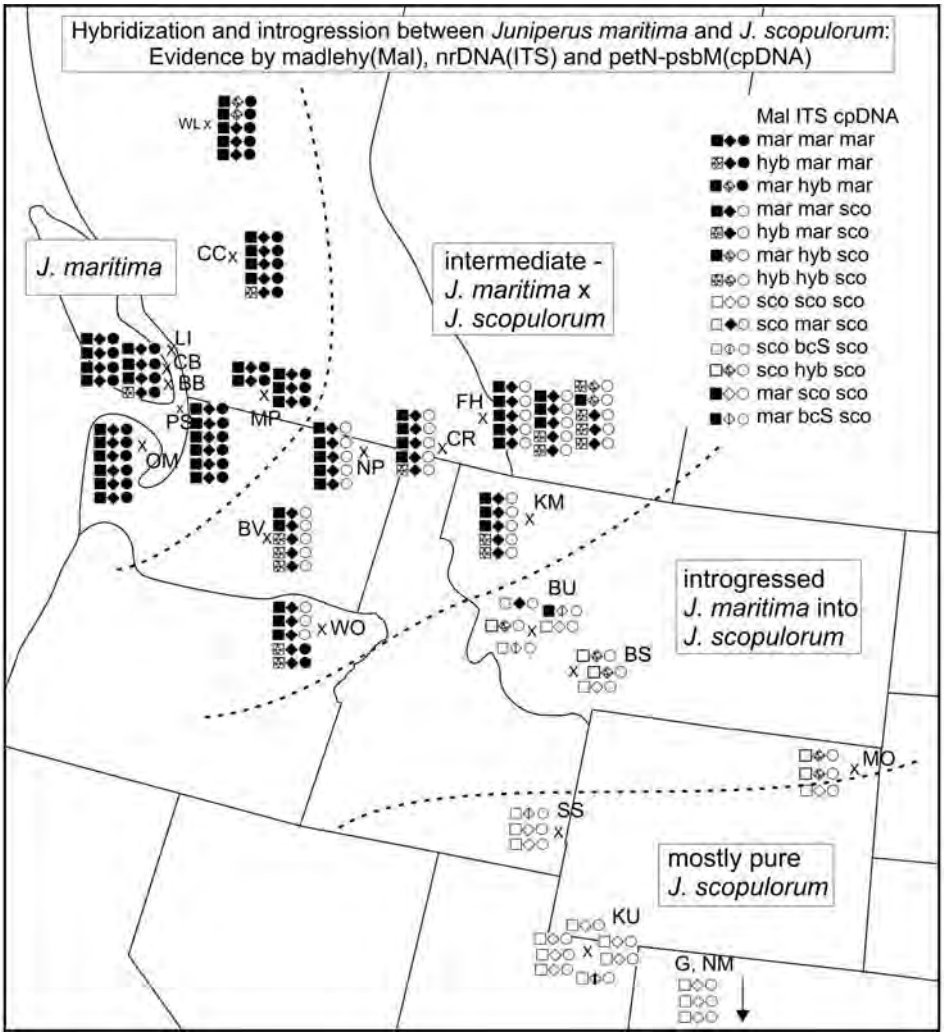


Figure5. Combined classification based on maldehy, nrDNA, and cpDNA sequences.

Inheritance of nrDNA

Chaing et al. (2001) found that in the artificial hybrids between *Begonia aptera* (pollen) and *B. formosana* (maternal), nrDNA was predominantly that of the maternal parent, *B. formosana* (diamonds, Fig. 6). This might explain the incongruence between the patterns for cpDNA (Fig. 2) and nrDNA (Fig. 3) in *Juniperus*, if maternal dominance is a factor in the inheritance of nrDNA.

Volkov, et al. (1999) reported that one of the parental nrDNAs was eliminated in the allopolyploid genome of cultivated tobacco. Fukuoka et al. (1994) found that the nrDNA in γ-ray irradiated tetraploid rice was homogenized in a short time.

Aguilar et al. (1999) made artificial hybrids between *Armeria villosa* ssp. *longiaristata* and *A. colorata*, then examined the inheritance of nrDNA in F_1 and F_2 generations. They found the expected additive pattern in polymorphisms for five of the six variable sites in F_1 plants. However, in the F_2 generation, there was a bias towards one parent (*A. colorata*). Backcrosses showed homogenization of five of the polymorphic sites to the recurrent parent.

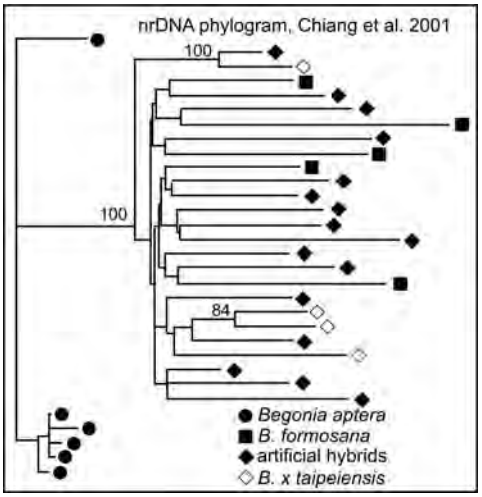


Figure 6. Phylogram based on nrDNA for *Begonia* and hybrids (adapted from Chiang, et al. 2001). Notice the grouping of the hybrids (triangles, nrDNA) with the maternal parent, *B. formosana* (shaded squares), rather than with the pollen (paternal) parent *(B. aptera*, shaded circles).

Okuyama et al. (2005) examined introgression in *Mitella* using nrDNA ITS and ETS, and cpDNA and found that cpDNA revealed the most introgression, ITS regions showed a moderate amount of introgression and the ETS region gave no evidence of introgression. They concluded that non-uniform concerted evolution between the ETS region and ITS regions may explain these different patterns of introgression.

Comparison with variation in leaf essential oils

Re-analysis of the terpene data, by removing CM (found to be *J. blancoi*, introgressed by *J. scopulorum*, Adams, 2011b, Adams, 2014) and adding *J. maritima* (MA, Vancouver Island, BC) shows MB oil (Manning Park, BC) similar to *J. maritima* oil (MA, Fig. 2). There appears to be a cline from MA (*J. maritima*) to Manning Park, to the DB, WO, KM, WB, TB group (Fig. 7).

Note also the differentiation of the Montana populations (BM, Butte, MT; BR, Bridger, MT; MM, Missouri River, n MT) from the uniform oils in the central Rocky Mtns. (Fig. 7). This is in close agreement with the zones based on all three gene regions (Fig. 5.)

However, it should be noted that although it seems intuitive that hybrids would have intermediate amounts of terpenes, Adams and Tsumura (2012) found that in *Cryptomeria japonica* hybrids, cis-thujopsene, widdrol and cedrol were inherited in Mendelian fashion with a second (dominant/recessive) gene involved. Several of the F_1 hybrids had oils very similar to the Haava parent's oil.

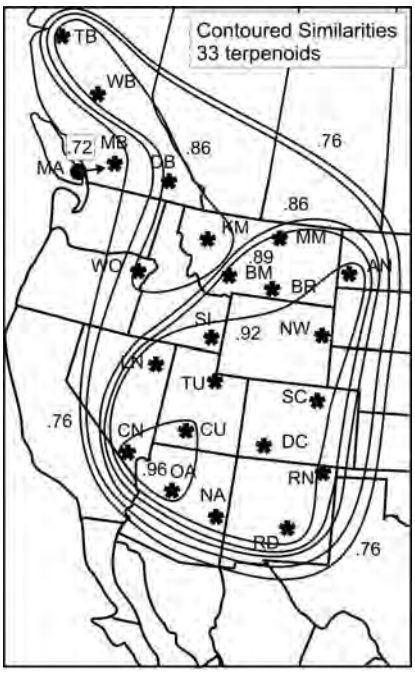


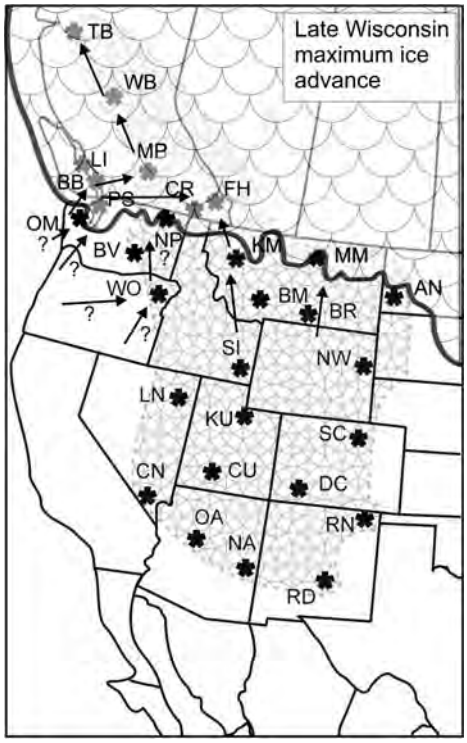
Fig. 7. Contour mapping of leaf oils. From Adams, 2011a.

In a study of the inheritance of the leaf terpenoids of *Pseudotsuga menziesii* var. *menziesii* x var. *glauca*, Adams and Stoehr (2013) found that cross *menziesii* 226 x *glauca* 267 produced 4 hybrids with oils very similar to the *glauca* parent and 6 F_1 hybrids with intermediate oils. In a second cross, of the 10 major terpenoids, 8 showed dominance values like one of the parents (Adams and Stoehr, 2013). Nine of

the terpenes were transgressive to both parents. So, it may not be unexpected that the contour mapping of terpenes (Fig. 7) show the oils of the putative hybrids to be more like one of the parents (*J. scopulorum*, Fig. 7).

Pleistocene Patterns

The late Wisconsin maximum ice advance is shown in figure 8 (based on Flint, 1971 and Crandell, 1971). All of the Canadian *J. maritima* and hybrid populations were glaciated. In addition, the Kalispell, MT (KM), Missouri River, MT (MM) and Amidon, ND (AN) populations were probably exterminated. Other populations (BM, BR and NW) were likely displaced by boreal forests and tundra (Flint, 1971; Porter, 1971). *Juniperus scopulorum* is a lower montane species. With the widespread lowering of vegetation zones, it likely moved to lower, drier habitats throughout most of the central Rocky Mountains. Adams (1983) reviewed the literature on packrat middens and pollen profiles. Wells (1970) and Martin and Harwell (1957) suggested that life zones descended 300 to 1100 m throughout the southwest and Great Basin from 13,500 to 10,000 ybp. The current separation of *J. scopulorum* and *J. virginiana* appears to have been bridged with the eastward expansion of *J. scopulorum* and the western expansion of *J. virginiana*. Trees of *J. scopulorum* are currently growing in ravines in northeastern New Mexico and western Oklahoma panhandle, while *J. virginiana* has now migrated westward into the Canadian River canyons in the Texas panhandle. The population of *J. scopulorum/virginiana* in Palo Duro Canyon resembles both species and is likely a relictual stand of hybrid origin (Adams, 1983).



With the retreat of the Wisconsin glacial ice, and the subsequent altithermal period 9000 to 5000 ybp (Wells, 1970), *Juniperus* expanded into the drying, higher elevation habitats that it occupies today. Figure 8 shows the proposed post-Pleistocene re-colonization of the northern portion of the ranges of *J. maritima* and *J. scopulorum*. The *J. maritima* BC populations could have been recolonized by seed from a Wallowa Mtns., OR refugium (WA, Fig. 8) and thence northward to the present day northern-most population at Telkwa, BC (TB). At Telkwa, *J. scopulorum* is found on dry, southeast facing slopes (ca. 45º - 60º). It seems likely that *J. maritima*, that grows along the seashore in western BC and Puget Sound, WA was re-colonized from a refugium south of the Olympic Mtns. or western WA/ Oregon.

Of course, the Wallowa population was likely displaced lower, and perhaps a bit to the south during the Wisconsin. The Amidon, ND (AN) population is similar to populations in the central Rocky Mountains and seems likely to have been derived by seed from the nearest *J. scopulorum* population (perhaps near Newcastle, WY, NW) or any of the scarp-land *J. scopulorum* populations to the south.

Figure 8. Putative re-colonization routes *J. maritima* and *J. scopulorum* following the Wisconsin (ice boundary based on Flint, 1971;Crandell, 1971).

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Table 1. Classification of 101 *Juniperus* individuals based on maldehy (SCN), nrDNA and petN-psbM (cpDNA). * newly reported in this paper. Sample numbers are Adams collection numbers.

Samples (trees)	maldehy	nrDNA	petN/psbM
10895 scopulorum, Kamas, UT	scop	scop	scop
10895 scopulorum, Kamas, UT	scop	scop	scop
10896 scopulorum, Kamas, UT	scop	scop	scop
10897 scopulorum, Kamas, UT	scop	scop	scop
10896 scopulorum, Kamas, UT	scop	scop	scop
10897 scopulorum, Kamas, UT	scop	scop	scop
13887 scopulorum, Kamas, UT*	scop	scop	scop
13888 scopulorum, Kamas, UT*	scop	**bc to scop**	scop
13889 scopulorum, Kamas, UT*	scop	scop	scop
13890 scopulorum, Kamas, UT*	scop	scop	scop
13891 scopulorum, Kamas, UT*	**marit**	scop	scop
10933 scopulorum, Glorietta, NM	scop	scop	scop
10934 scopulorum, Glorietta, NM	scop	scop	scop
10935 scopulorum, Glorietta, NM*	scop	scop	scop
7063 scopulorum, Soda Springs, ID*	scop	**bc to scop**	scop
7064 scopulorum, Soda Springs, ID*	scop	scop	scop
7065 scopulorum, Soda Springs, ID *	scop	scop	scop
7066 scopulorum, Soda Springs, ID*	scop	scop	scop
10876 scopulorum, Moorcroft, WY*	scop	scop	scop
10877 scopulorum, Moorcroft, WY*	scop	**hybrid**	scop
10878 scopulorum, Moorcroft, WY*	scop	**hybrid**	scop
10882 scopulorum, Big Sky MT*	scop	**hybrid**	scop
10883 scopulorum, Big Sky MT*	scop	**hybrid**	scop
10884 scopulorum, Big Sky MT*	scop	scop	scop
10885 scopulorum, Butte, MT*	scop	**hybrid**	scop
10886 scopulorum, Butte, MT*	scop	**marit**	scop
10887 scopulorum, Butte, MT*	scop	**bc to scop**	scop
10888 scopulorum, Butte, MT*	scop	scop	scop
10889 scopulorum, Butte, MT*	**marit**	**bc to scop**	scop
11056 maritima, Brentwood Bay, VI	marit	marit	marit
11057 maritima, Brentwood Bay, VI	marit	marit	marit
11058 maritima, Brentwood Bay, VI	marit	marit	marit
11061 maritima, Cowichan Bay, VI	marit	marit	marit
11062 maritima, Cowichan Bay, VI	marit	marit	marit
11063 maritima, Cowichan Bay, VI	**hybrid**	marit	marit
11999 maritima, Olympic Mtns., WA 912m,	marit	marit	marit
12000 maritima, Olympic Mtns., WA 912m,	marit	marit	marit
12001 maritima, Olympic Mtns., WA 912m,	marit	marit	marit
12002 maritima, Olympic Mtns., WA 1671m,	marit	marit	marit
12003 maritima, Olympic Mtns., WA 1671m,	marit	marit	marit
12004 maritima, Olympic Mtns., WA 1671m,	marit	marit	marit
11064 maritima, Yellow Point Lodge, VI	marit	marit	marit
11065 maritima, Lesqueti Island, BC	marit	marit	marit
11066 maritima, Lesqueti Island, BC	marit	marit	marit
11067 maritima, Friday Harbor, San Juan,WA	marit	marit	marit
11068 maritima, English Camp, San Juan, WA	marit	marit	marit

Table 1. Classification of 101 *Juniperus* individuals (contd.)

11075 maritima, sand dune, Whidbey Isl., WA	marit	marit	marit
11076 maritima, Fidalgo Isl. St. Pk, WA	marit	marit	marit
11077 maritima, Skagit Isl. WA, ca 360 yr old	marit	marit	marit
11078 maritima, Skagit Isl., WA	marit	marit	marit
13426 maritima, Manning Park, BC	marit	marit	marit
13427 maritima, Manning Park, BC	marit	marit	marit
13428 maritima, Manning Park, BC	marit	marit	marit
13429 maritima, Manning Park, BC	marit	marit	marit
13430 maritima, Manning Park, BC	marit	marit	marit
13431 Cache Ck, BC	marit	marit	marit
13432 Cache Ck, BC	marit	marit	marit
13433 Cache Ck, BC	**hybrid**	marit	marit
13434 Cache Ck, BC	marit	marit	marit
13435 Cache Ck, BC	marit	marit	marit
13436 Williams Lake, BC	marit	**hybrid**	marit
13437 Williams Lake, BC	marit	marit	marit
13438 Williams Lake, BC	marit	**hybrid**	marit
13439 Williams Lake, BC	marit	marit	marit
13440 Williams Lake, BC	marit	marit	marit
13421 Fairmont Hot Sprs, BC	**hybrid**	**hybrid**	**scop**
13422 Fairmont Hot Sprs, BC	marit	marit	scop
13423 Fairmont Hot Sprs, BC	marit	marit	scop
13424 Fairmont Hot Sprs, BC	marit	marit	scop
13425 Fairmont Hot Sprs, BC	marit	marit	scop
14001 Fairmont Hot Sprs, BC	marit	**hybrid**	scop
14002 Fairmont Hot Sprs, BC	marit	marit	scop
14003 Fairmont Hot Sprs, BC	marit	marit	scop
14004 Fairmont Hot Sprs, BC	**hybrid**	marit	scop
14005 Fairmont Hot Sprs, BC	marit	marit	scop
14006 Fairmont Hot Sprs, BC	**hybrid**	marit	scop
14007 Fairmont Hot Sprs, BC	**hybrid**	marit	scop
14008 Fairmont Hot Sprs, BC	**hybrid**	marit	scop
14009 Fairmont Hot Sprs, BC	**hybrid**	marit	scop
14010 Fairmont Hot Sprs, BC	marit	marit	scop
14026 Creston, BC	marit	marit	scop
14027 Creston, BC	marit	marit	scop
14028 Creston, BC	**hybrid**	marit	scop
14029 Creston, BC	marit	marit	scop
14030 Creston, BC	marit	marit	scop
14031 Northport, WA	marit	marit	scop
14032 Northport, WA	marit	marit	scop
14033 Northport, WA	marit	marit	scop
14034 Northport, WA	marit	marit	scop
14035 Northport, WA	marit	marit	scop
14036 Beverly, WA	**hybrid**	marit	scop
14037 Beverly, WA	marit	marit	scop
14038 Beverly, WA	marit	marit	scop
14039 Beverly, WA	**hybrid**	marit	scop
14040 Beverly, WA	**hybrid**	marit	scop
12995 Kalispell, MT	marit	marit	scop

Table 1. Classification of 101 *Juniperus* individuals (contd.)

12996 Kalispell, MT	marit	marit	scop
12997 Kalispell, MT	**hybrid**	marit	scop
12998 Kalispell, MT	**hybrid**	marit	scop
12999 Kalispell, MT	marit	marit	scop
11935 Wallowa Mtns, OR	**hybrid**	marit	scop
11936 Wallowa Mtns, OR	**hybrid**	marit	scop
11937 Wallowa Mtns, OR	marit	marit	scop
11938 Wallowa Mtns, OR	marit	marit	scop
11939 Wallowa Mtns, OR	marit	marit	scop