INFRASPECIFIC TERPENOID VARIATION IN *JUNIPERUS SCOPULORUM*: EVIDENCE FOR PLEISTOCENE REFUGIA AND RECOLONIZATION IN WESTERN NORTH AMERICA

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Abstract

Populations of *Juniperus scopulorum* were sampled throughout its range and the steam volatile terpenoids removed for chemosystematic study. Canonical variate analysis revealed three major trends: isolation of the Puget Sound–Vancouver Island populations for a considerable time; differentiation of populations from northern Mexico dating to pre-Pleistocene (?); and a possible Pleistocene refugium in eastern Oregon for the (re)colonization of the glaciated British Columbian populations of *J. scopulorum*. Pleistocene glaciopluvial periods are reviewed as to their effects on vegetation and past distributions of *J. scopulorum*. Hybridization and introgression of *J. scopulorum* with *J. horizontalis* and *J. virginiana* is examined in light of both the present and past distributions of these taxa. Interspecific relationships are also examined between *J. scopulorum, J. blancoi, J. horizontalis,* and *J. virginiana*.

Introduction

Juniperus scopulorum Sarg. is a widely distributed conifer in western North America (Fig. 1). It is a member of the section *Sabina* (Zanoni and Adams, 1979) with fleshy female cones and scale-like leaves. It is also a member of the entire (non-serrated) leaf margined group (Adams et al., 1981) which, on the North American mainland, consists of *J. blancoi* Mart., *J. horizontalis* Moench, *J. scopulorum* Sarg., *J. silicicola* (Small) Bailey and *J. virginiana* L. These five taxa are very similar in both their morphology and terpenoids (Adams et al., 1981). In fact, *J. scopulorum* has been treated as a variety of *J. virginiana* and is so recognized in at least one recent flora (Weber, 1972) but not in most floras (Zanoni, 1978). Another index to the closeness of *J. scopulorum* and *J. virginiana* has been the degree of hybridization and gene exchange reported between these taxa. Studies using morphological data (Fassett, 1944b; Schurtz, 1971; Van Haverbeke, 1968) suggested that the two taxa intergrade across the Missouri River valley in the northern Great Plains. Additional studies using terpenoid data (Comer, Adams and Van Haverbeke, 1983; Flake, Urbatsch and Turner, 1978; von Rudloff, 1975) have confirmed such intergradation and support hybridization as the source of this variation. These reports agree with the suggestion of Hall (1952) that the northwestern portion of *J. virginiana* might be introgressed by *J. scopulorum* (Platte River Race of Hall, 1952). However, none of the aforementioned studies has specifically dealt with the validity of the "Platte River Race" of *J. virginiana* and that must await additional studies. A second area of possible hybridization between *J. scopulorum* and *J. virginiana* might be in the Texas Panhandle where populations of the two species persist as relict stands. Both species undoubtedly co-mingled during the Pleistocene (Maze, 1968) and as recently as 10,000 bp (Adams, 1977; Hafsten, 1961) when the southern Great Plains was dominated by a spruce-pine woodland.

The prostrate juniper, *J. horizontalis,* differs little from *J. virginiana* or *J. scopulorum* except for habit (Fassett, 1944a) and in several terpenoids (Adams et al., 1981; von Rudloff, 1975). Hybridization of *J. horizontalis* with *J. scopulorum* and with *J. virginiana* is appar-
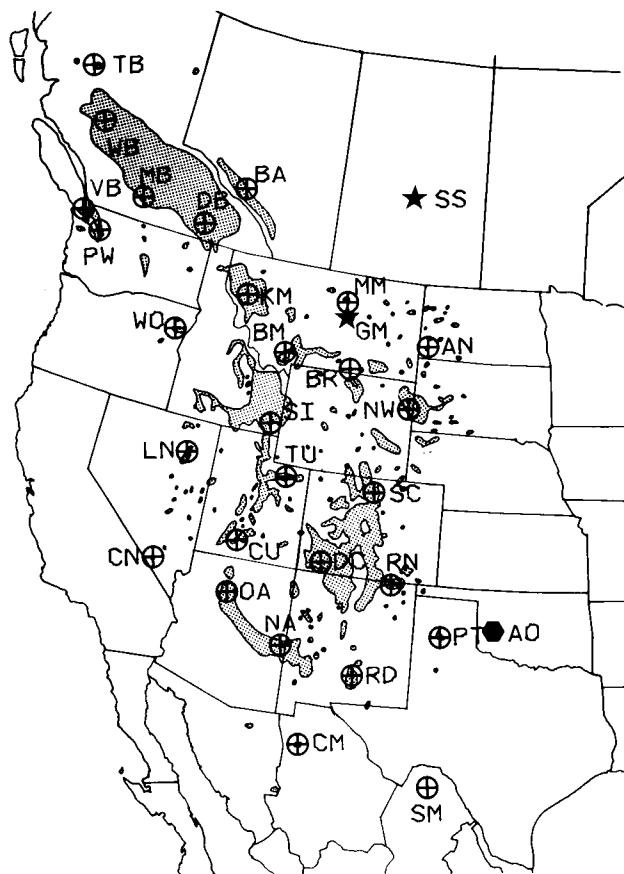
Fig. 1. The distribution of *Juniperus scopulorum* showing populations sampled and acronyms. Also shown are populations of *J. horizontalis* (SS, GM) and *J. virginiana* (AO) sampled.

ently common (Fassett, 1945a, b; Schurtz, 1971; von Rudloff, 1975). Areas of hybridization between *J. horizontalis* and *J. scopulorum* most frequently mentioned (Fassett, 1945a; von Rudloff, 1974) are western North Dakota; south of Bridger, Montana; and near Banff, Alberta. Fassett (1945c) treated putative hybrids of *J. horizontalis* × *J. scopulorum* as a variety (*J. scopulorum* var. *patens* Fassett) while putative hybrids (Fassett, 1945c) between *J. horizontalis* and *J. virginiana* were treated as *J. virginiana* var. *ambigens* Fassett. These names have not been generally followed by taxonomists, however.

Hybridization involving *J. horizontalis, J. scopulorum* and *J. virginiana* is becoming increasingly well documented, in sharp contrast to the previously reported hybridization and introgression between the rather dissimilar species, *J. ashei* and *J. virginiana*. Reports of the latter by Hall (1952) were not substantiated using terpenoids (Flake, von Rudloff and Turner, 1969, 1973) nor using both morphology and terpenoids (Adams and Turner, 1970; Adams, 1975, 1977).

Hybridizations involving *J. scopulorum* with *J. deppeana* and with *J. osteosperma* have been suggested (Hall, 1966) but no additional studies have been conducted.

Morphological variation in *J. scopulorum* is perhaps greater than in any other juniper species in North America except *J. deppeana* (Zanoni and Adams, 1976). Much of the variation is in habit, foliage color and the degree of branch flaccidness. Columnar growth

forms have been recognized as a variety (*J. scopulorum* var. *columnaris* Fassett) but these have been shown to be environmentally induced (Adams, 1982).

The purposes of this study were to examine the terpenoids of natural populations of *J. scopulorum* from throughout its range (Fig. 1), relate intraspecific variation to Pleistocene (or older) distributions, examine the genetic interactions (if any) with present (or past) taxa and to compare *J. scopulorum* with *J. blancoi*, *J. horizontalis* and *J. virginiana*.

Materials and Methods

Fresh foliage was taken from the populations indicated in Fig. 1. Fifteen trees were sampled at each location except for populations PW (8) and VB (13). Additional samples were often taken of individuals that appeared to be hybrids or morphologically unusual. When *J. scopulorum* was sympatric with another juniper species, five or more samples of the other species were also collected. The foliage was kept frozen in a mobile field trailer with a walk-in freezer. Voucher specimens and materials for steam distillation were subsequently removed. Vouchers are on deposit at the Science Research Center.

The volatile terpenoids were removed by steam distillation and analyzed by capillary gas/liquid chromatography (see Adams, 1975, for details). Peak identification was based on mass spectral-computer search reported for these taxa (Adams et al., 1981). Principal coordinate analysis (PCO) used an F (from ANOVA) weighted Gower metric (Gower, 1971) for the examination of possible hybridizations, and PCO follows Gower (1966) and Blackrith and Reyment (1971). Canonical variate analysis (CVA), used for analysis of geographic variation, was based on Blackrith and Reyment (1971), Cooley and Lohnes (1971) and Pimentel (1979). Due to program space limitations, analyses using CVA were limited to 30 characters and in those cases, the 30 terpenoids having the largest F ratios in ANOVA between the a priori groups used. Contour mapping of canonical variates, principal coordinates and differential similarities follow my previous formulation (Adams, 1970, 1977). Differential systematics of the canonical variate axes is an extension of the concepts previously formulated (Adams, 1970; Womble, 1951).

Results and Discussion

The first six eigenroots from CVA accounted for 90.37% of the variance among groups. The first 8 eigenroots were each highly significant by Bartlett's test of sphericity (Blackrith and Reyment, 1971) but biological meaning is often lost long before statistical non-significance occurs as has been noted by Blackrith and Reyment (1971). Table 1 presents the correlation between the terpenoid characters and the first 6 canonical axes. Note the highest correlation on the first axis is with α-eudesmol and β-eudesmol, which are present in much larger concentrations in the coastal populations. Most of the correlations are moderate indicating that the trends (axes) are the result of the total interaction of many characters (similar to shape in morphology) in determining the trends. The principal trend among populations is the divergence of the Puget Sound (PW)–Vancouver Island (VB) populations and to a lesser extent Manning Pass (MB) from the rest of *J. scopulorum* (Fig. 2). This trend accounted for 50.14% of the variance among populations.

The second canonical axis (16.6% of the among population variance) shows the divergence of the Mexico and Texas Panhandle populations (Fig. 3). Notice that the first two trends involve chiefly populations on the periphery of the range.

The third canonical axis accounted for 8.1% of the variation and shows (Fig. 4) the divergence of the Texas Panhandle population and an interesting co-differentiation of British Columbian populations, centered at the Manning Pass population.

The fourth axis displays a northwest to southwest differentiation from the central portion (Fig. 5) and accounted for 7.3% of the variation among populations. The differentiation of the Serrianas del Burro (SM) population in northern Coahuila, Mexico, is emphasized along with a marked pattern of differentiation from Soda Springs, Idaho (SI), northwestward into

Table 1. Canonical correlation between variables and canonical axes based on 27 *J. scopulorum* populations. Compounds in parentheses are tentatively identified.

Variable	Canonical axis					
	1	2	3	4	5	6
% yield	0.07	0.39	−0.46	0.53	−0.02	0.11
tricyclene	0.16	0.25	−0.19	−0.14	0.47	−0.05
α-pinene/α-thujene	0.38	−0.38	0.29	0.43	−0.13	−0.01
sabinene	0.49	−0.33	0.40	0.27	0.16	0.08
myrcene	0.26	0.04	0.45	0.40	0.31	−0.34
α-terpinene	0.22	−0.24	0.58	0.52	0.10	0.14
γ-terpinene	0.22	−0.09	0.60	0.39	0.03	0.04
ρ-cymene	0.25	−0.12	0.10	0.46	−0.10	−0.18
terpinolene	0.28	−0.29	0.58	0.43	0.05	0.07
2-nonanone	0.03	0.56	0.12	0.11	0.56	0.06
(isomer of β-terpineol)	0.33	−0.24	0.21	0.10	0.29	−0.08
linalool	0.06	0.22	0.20	0.03	0.19	−0.12
isosafrole	0.26	−0.30	0.03	−0.46	0.16	0.42
4-terpineol	0.21	−0.08	0.51	0.47	0.09	0.08
(estragole)	−0.32	0.38	−0.54	0.22	−0.30	−0.15
unknown	0.38	−0.31	−0.19	−0.11	−0.05	0.14
unknown	−0.23	0.42	−0.07	−0.09	−0.52	−0.10
(carene hydrate)	0.03	0.47	−0.01	0.13	0.39	0.02
unknown	0.07	0.14	−0.62	−0.10	−0.05	0.21
safrole	−0.15	0.60	−0.25	−0.06	−0.57	0.01
unknown	0.05	0.31	0.22	−0.35	−0.50	0.02
methyl eugenol	−0.53	0.35	−0.36	0.08	−0.02	0.01
elemicin	−0.52	0.08	−0.09	−0.07	−0.05	0.08
elemol	0.33	−0.16	−0.36	−0.10	−0.03	−0.33
γ-eudesmol	0.27	−0.13	−0.12	0.13	−0.04	−0.28
α-eudesmol	−0.66	0.02	−0.07	−0.08	0.01	−0.23
β-eudesmol	−0.67	0.02	−0.02	0.11	−0.02	0.17
acetate II	0.14	−0.19	−0.08	−0.42	−0.06	0.37
unknown	0.14	0.16	−0.67	0.11	−0.10	0.19
manool	0.04	0.77	0.33	−0.12	−0.17	0.04

British Columbia. The Manning Pass population (MB) shows close ties to the Puget Sound populations (PW, VB) in contrast to the previous trend (Fig. 4). Some minor variation is apparent throughout the central portion of the range.

The fifth axis (Fig. 6, 5.7%) primarily emphasizes the differences between the Serranias del Burro (SM), Texas Panhandle (PT) and northern Chihuahua, Mexico (CM), populations. Some divergence is also seen in the northwestern populations.

The sixth axis accounted for only 2.6% of the variation among populations and shows mostly local differentiation (Fig. 7) with the exception of the northeastern populations, which show a regional pattern.

In order to visualize the overall trend, the composite differential was taken (Womble, 1951; Adams, 1970) for the six canonical axes with each trend (axis) weighted by the percent of variation accounted for. Since the differential emphasizes the amount of change from one population to another, populations that are not separated by contour lines have few differences. This analysis indicates (Fig. 8) that the central portion of the range of *J. scopulorum* is relatively uniform (Colorado, Utah, Nevada, Arizona, New Mexico) and that has been the case in the individual trends previously shown (Figs. 2–7). The greatest differentiation is shown between the Puget Sound populations (PW, VB) and interior
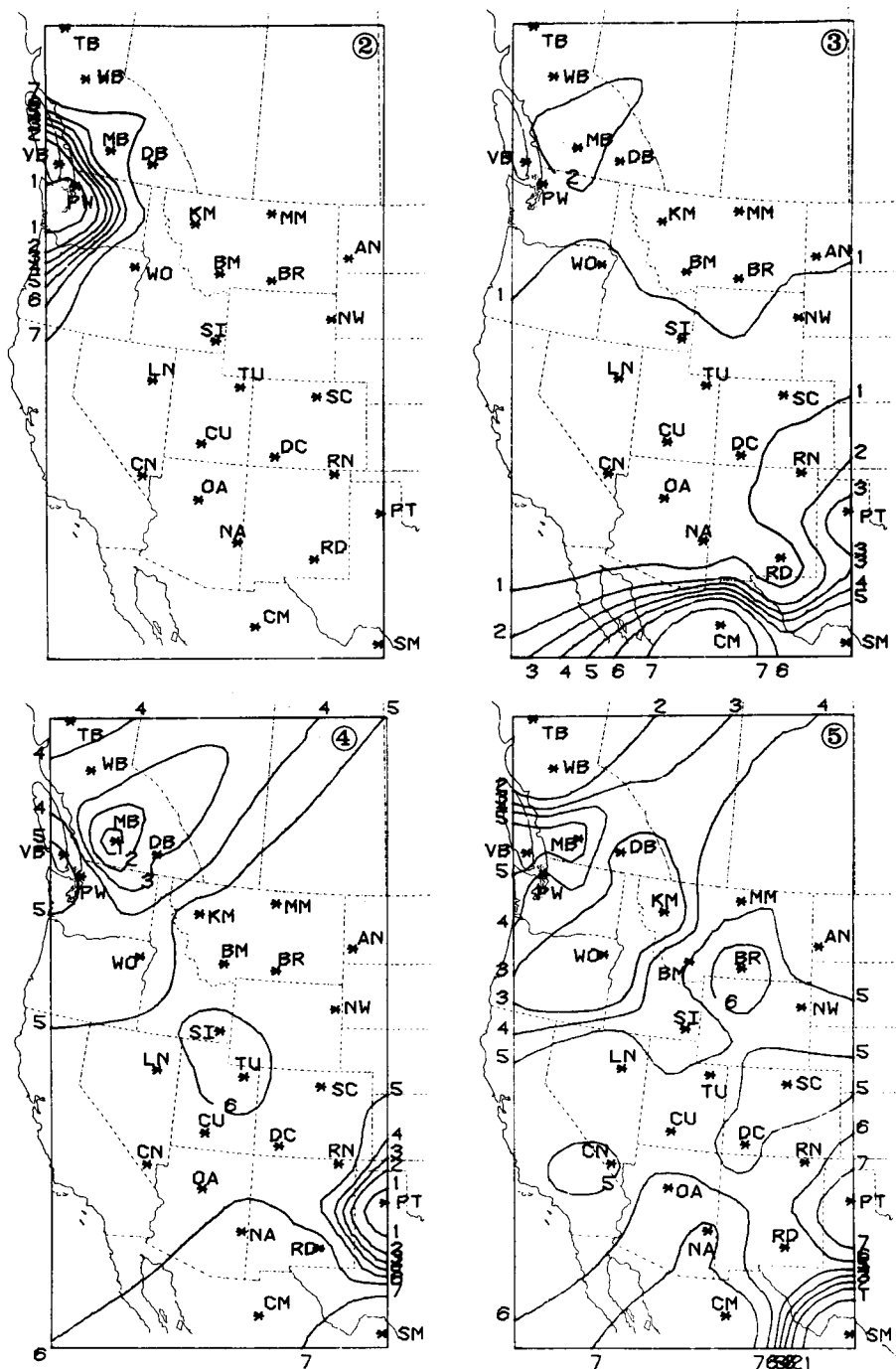
Figs. 2–5. 2: Contour map of the first canonical variate axis from CVA of 17 populations of *J. scopulorum* accounting for 50.2% of the variation among populations. Notice the sharp differentiation of the Puget Sound populations (PW, VB) and to a lesser extent MB. *3:* Contour of the second canonical axis (16.6%) which shows the divergence of the northern Mexico (CM, SM) populations and the Texas Panhandle (PT) population. Some co-differentiation of the northern-northwestern populations is also
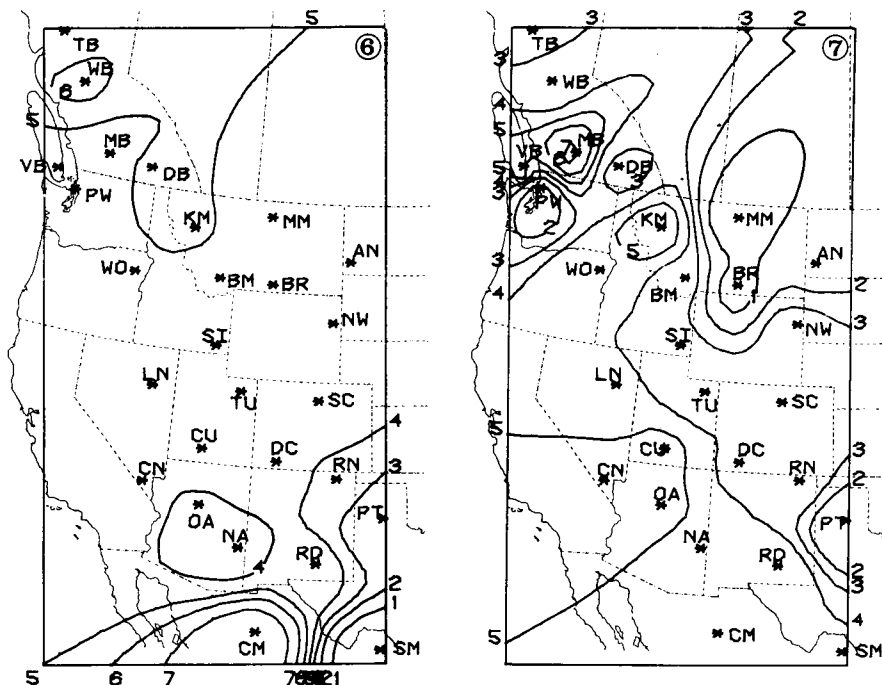
Figs. 6, 7. 6: The contour map of the fifth axis (5.7%) shows divergence between the Chihuahua, Mexico (CM) population and the Sierranas del Burro (SM) and the Texas Panhandle (PT) populations as well as differentiation of the northwestern populations. *7:* The sixth canonical axis accounted for only 2.6% of the variation among populations and shows divergence of the northeastern populations, differentiation between the Manning Park (MB) and Puget Sound populations. Other minor patterns are seen throughout the range.

populations. Each of the three southeastern populations (PT, SM, CM) shows differentiation from each other and from the greater portion of the central range of *J. scopulorum*. A corridor of similar populations is shown from northeastern Oregon (WO) to western Montana into British Columbia.

Pleistocene Patterns

In order to grasp better the impact of the glacial advances on populations of *Juniperus,* the late Wisconsin maximum ice advance is shown (Fig. 9) based on Flint (1971) and Crandell (1971). Not only were the Canadian regions occupied by such populations glaciated, but the areas near the present populations in northwestern Montana (KM), along the Missouri River (MM, GM) and southwestern North Dakota (AN) were too cold for the persistence of *J. scopulorum.* Other populations (WO, BM, BR, NW) were likely displaced by boreal forests and tundra (Flint, 1971; Porter, 1971). Since *J. scopulorum* is a

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evident. *4:* Axis three (8.0%) shows additional differentiation of the Texas Panhandle (PT) population and a pattern of differentiation of the Canadian populations from the main range and also from the Puget Sound populations. *5:* The fourth axis (7.3%) shows the divergence of the Sierranas del Burro (SM) population and a strong divergence running from Oregon up through British Columbia (WO to KM, DB, WB, and TB). Minor variation is seen throughout the central portion of the range.
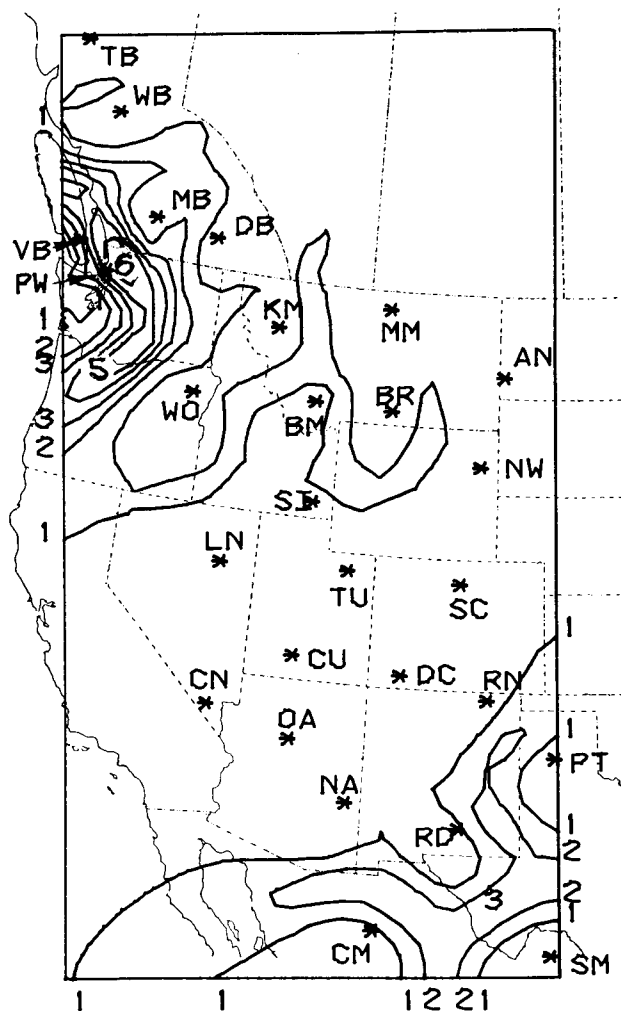
Fig. 8. The composite differential of the first six canonical axes, each weighted by the percent variance accounted for. Notice the major area of differentiation is with the Puget Sound populations. Populations separated by contour lines show differences in some of the canonical axes. Populations not separated by contour lines are very similar (few differences). There is a general pattern of differentiation of the southeastern populations (CM, SM, PT) from the central portion of *J. scopulorum* and from each other. Also shown is a corridor of similar populations running from WO to KM, DB, WB, and TB.

lower montane species, the widespread depression of vegetation zones may have merely moved it to lower, drier habitats rather than initiating large geographic migrations throughout most of the southern Rocky Mountains. The descent of junipers into previously desert environments is well documented in the packrat middens and pollen profiles of the southwestern United States (Martin and Mehringer, 1965; Van Devender, 1977, 1979, 1980; Van Devender and Riskind, 1979; Van Devender, Freeman and Worthington, 1978; Van Devender and Spaulding, 1979; Van Devender, Spaulding and Phillips, 1979; Van Devender and Wiseman, 1977; Wells, 1966, 1970, 1979; Wells and Berger, 1967; Wendorf and Hester, 1975). These studies show a general pattern of the depression of vegetation zones
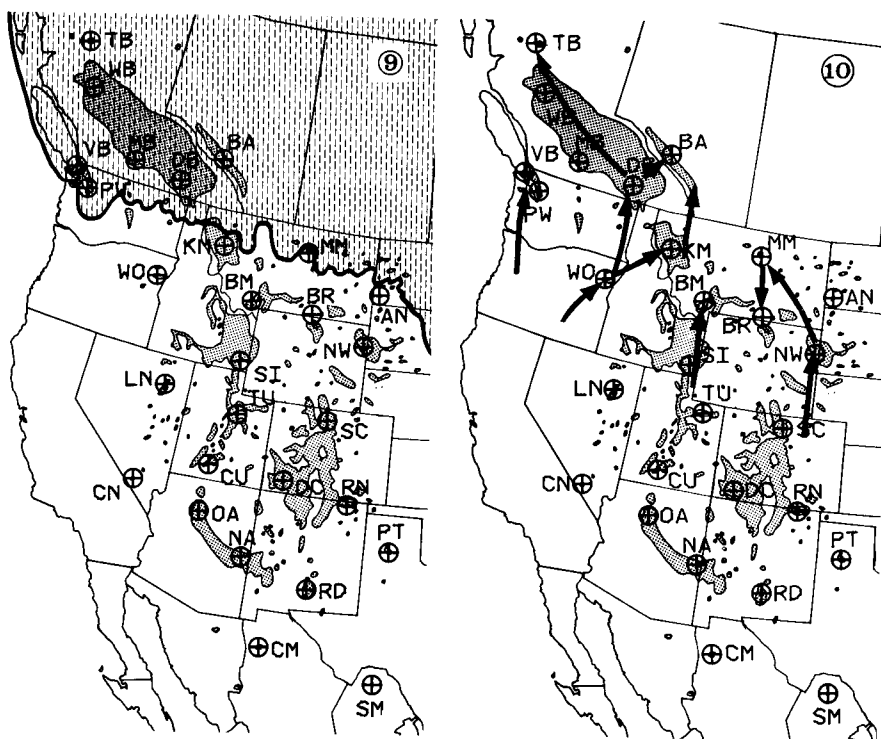
Figs. 9, 10. *9:* The late Wisconsin maximum ice advance is shown in relation to populations of *J. scopulorum* sampled and the present distribution (based on Flint, 1971 and Crandell, 1971). High mountain glaciers are not shown. Note that the Canadian populations were lost at this time. See text for discussion. *10:* Hypothetical migration pathways for the (re)colonization of the northern portion of the range of *J. scopulorum* during the altithermal period (9000 to 5000 years bp) based on terpenoid similarities.

from 300 to 1100 meters throughout the southwest and Great Basin from 13,500 to 10,000 bp. Although several of the southwestern junipers may have formed essentially continuous populations at that time (*J. erythrocarpa, J. monosperma, J. pinchotii*), the conditions would still prohibit *J. scopulorum* from forming any continuum from central Arizona into the mountains of northern Mexico (ex. linking NA and CM) or linking *J. scopulorum* populations from the Guadalupe mountains of Southern New Mexico (RD) to populations of the Serranias del Burro (SM) in northern Coahuila (Wells, 1966). The influence of the glacial advances on the climate of northern Mexico are still not known. Meyer (1973) found no evidence of climatic fluctuations near Cuatro Ciengas (central Coahuila) during the Wisconsin. However, the study site is currently a swampy area that may have persisted all through the Pleistocene and thus the pollen profile may not be representative of the region.

In the central portion of the range of *J. scopulorum* (Colorado, Utah, Wyoming), the few studies available suggest a downward displacement of Juniper woodland about 600 meters (Weber, 1971). If extrapolation of the work of Wendorf and Hester (1975) from the Llano Estacado (Texas Panhandle) to the eastern plains of Colorado is valid, then it would appear that *J. scopulorum* probably moved far out on the plains in advance of the spruce-pine woodlands. This eastern expansion of *J. scopulorum* easily overlapped with the western expansion of *J. virginiana*. The current separation of *J. scopulorum* and *J. virginiana* appears to parallel that of *Quercus gambelii* and *Q. macrocarpa* (Maze, 1968)

and *Pinus monticola* and *P. strobus* (Andreson, 1966). The eastern and western forest elements of the Great Plains appear to have been separated during the Pliocene until the Pleistocene glaciations (Andresen, 1966; Maze, 1968). Relict stands of *J. virginiana* are found in the Texas Panhandle and western Kansas (Little, 1971). *Juniperus scopulorum* is likewise found in relict stands in the scarp woodlands of the Great Plains (Wells, 1965) as well as the dry Laramie Basin in Wyoming (Wells, 1970).

The northern Great Plains (North and South Dakota in the U.S. and Saskatchewan and Alberta in Canada) apparently supported spruce after the last glacial retreat (13,000–10,000 bp), followed by a drier period (8000–7000 bp) and then a cooler/moister period (5500–2000 bp), according to Ritchie (1976). This drier period was undoubtedly important in the spread of *J. scopulorum* (and *J. horizontalis*) into North and South Dakota and Montana (Thompson and Kuijt, 1976). Data from the eastern northern Great Plains (Wright, 1970) also suggests a warmer/drier period from 10,000 to 6000 bp (antithermal period).

Reports from the northwestern United States indicate a similar pattern of cold/moist conditions (12,000 to 9000 bp) after the pluvial advance(s) then warming and drying conditions from 6700 to 4000 bp (Mack et al., 1978; Mack, Rutter and Valastro, 1978). Mehringer, Arno and Peterson (1977) reported that the ice had dissipated by 12,000 bp at Lost Trail Pass (Montana), and the area experienced a warm period from 7000 to 5000 bp. Baker (1970) found evidence of an altithermal at Yellowstone, Wyoming, from 10,160 to 5000 bp.

In the Puget Sound area, Crandell (1958, 1971) reported glacial advances from the Puget lobe of the Cordilleran glacier with the latest (Vashon) retreating from lowlands south of Seattle, Washington about 14,000 bp. According to Heusser (1971) the Willamette Valley to the south appeared to have a quite different pollen profile than the area north of Seattle. He suggested further that the Willamette Valley was much drier/warmer during the middle and last post-glacial than the Puget Sound lowlands. On Whidbey Island (near where population PW is located, Fig. 9), Porter (1971) found three glacial drifts dated at 46,700, 34,900 and 27,200 bp. The ice retreated from that area about 13,000 bp (Porter, 1971).

In summary, populations PW, VB, MB, WB, TB, DB, BA, KM, MM and AN (Fig. 9) were almost certainly exterminated during the Wisconsin and probably several times previously if reinvasion occurred following older Pleistocene glaciations. The other populations sampled were both elevationally and geographically displaced in the central portion of the range and principally elevationally displaced in the southern regions (Texas, New Mexico, Arizona and adjacent Mexico). An important factor in the spread of most junipers is a period of drought (or overgrazing) which opens habitat for invasion. This drier/warmer period appears to have occurred about 9000 to 5000 bp depending on the area. The relict population near Telkwa, B.C. (TB) occurs on a dry southeast facing slope (ca. 45° to 60° slope) and appears to have persisted there since the altithermal period. Other disjunct populations in Canada probably have a similar history. Disjunct populations in the central portion of the range are more likely to be relicts from pluval expansion into previously arid sites. Disjunctions to the far south (northern Mexico) are found in canyons along running streams, usually growing in the stream or where the roots can have a reliable water source. These populations show considerable differentiation and may have been isolated since before the Pliocene (Martin and Harrell, 1957).

Post-glacial Migration

The colonization by *J. scopulorum* of glaciated areas and other open habitats in the northern portion of the range probably occurred only 9000 to 5000 years ago. A map showing hypothetical migratory routes (Fig. 10) is based on the composite trend (Fig. 8). Of course, the southern populations were retreating in the southern portion of the range. The Puget Sound populations occur on very unusual sites that are not typical of those for

the rest of *J. scopulorum*. *Juniperus scopulorum* is generally a montane species that occurs on dry south facing slopes and on rocky bluffs from about central Colorado-Utah northward and usually in canyons at the southernmost locations. The Puget Sound populations occur near sea level, often next to the ocean spray in quite mesic conditions. Both physiologically and chemically, these populations are very different from the inland populations of *J. scopulorum*. The Puget Sound populations appear to have been separated for a long period, probably dating to before the Pliocene. The remainder of the northwestern populations are more similar to inland populations of *J. scopulorum*. Divergence most likely dates to the Pleistocene and a refugium may have been present in southeastern Oregon (Fig. 10). With the glacial retreat (Wisconsin), migration may have proceeded north to British Columbia and northeast to western Montana (Fig. 10). The Alberta population may have arisen from northward migration around the eastern side of the Rockies or northeastward from British Columbia. Migration proceeded northward in British Columbia perhaps even farther than Telkwa (TB) and retreated after the altithermal leaving a few relict populations. It should be noted that while the distribution map shows a vast area in British Columbia covered by *J. scopulorum,* this is not really an accurate representation for the populations are usually quite scattered in the area.

The area of southwestern Montana appears to have been colonized by plants from the south (Idaho, Utah) (cf. Figs. 8, 10). The northeastern portion of the range (North and South Dakota, northeastern Wyoming and eastern Montana) were probably colonized from southeastern Wyoming or northern Colorado. The rather strange clustering of the Montana populations has been previously noted by Flake, Urbatsch and Turner (1978). For example, their populations X and Z were shown to be somewhat different from populations in eastern Wyoming (I, J, K). This is the same pattern shown in Fig. 8 for that region. Population Z is from the same region as KM (Kalispell, Montana), X is from near BR (Bridger, Montana) and J is near NW (Newcastle, Wyoming). In addition, they showed that a population (Y) from near Butte, Montana (near the present BM site) was more similar to typical *J. scopulorum* than populations to the northwest (Z or KM) or to the east (X or BR). Although they suggested that these divergent populations might be due to hybridization with *J. horizontalis,* it now appears that population KM (Z) is part of the northwestern divergence pattern (Fig. 8) and population BR (X) is part of a northeastern divergence rather than products of hybridization. The differences between BR and NW (Fig. 8) coupled with the lack of differences between BR and MM favor a thesis that the BR population was founded by plants from the vicinity of the MM population.

Hybridization

The most obvious hybridization is between *J. scopulorum* and *J. horizontalis*. Individuals that appeared to be morphologically intermediate were collected at Banff, Alberta (BA), south of Bridger, Montana (BR), near the Missouri River (MM) and near Amidon, North Dakota (AN). Five plants of what appeared to be morphologically typical *J. horizontalis* were collected at Grass Range, Montana (GM, Fig. 1). None of the aforementioned was included in population samples used in the CVA analyses. At the Banff sites (east and west of Banff), the growth forms were so atypical of *J. scopulorum* that no trees from that population were included in the previous CVA. The east Banff population contained individuals that formed spreading shrubs from about 30 cm to 100 cm tall. However, several of these spreading shrubs had one or more upright stems 180 to 300 cm tall. Various kinds of analyses were tried, including CVA, principal component analysis (PCA), Wells' hybrid distances (Wells, 1980), and principal coordinate analysis using statistically derived character weights. Adams (1982) using artificial crosses of sunfish (*Lepomis*) and putative hybridization in *Juniperus,* has shown that the F (from ANOVA) weighted PCO and hybrid distances appear to be the most powerful multivariate methods for the detection of hybrid-
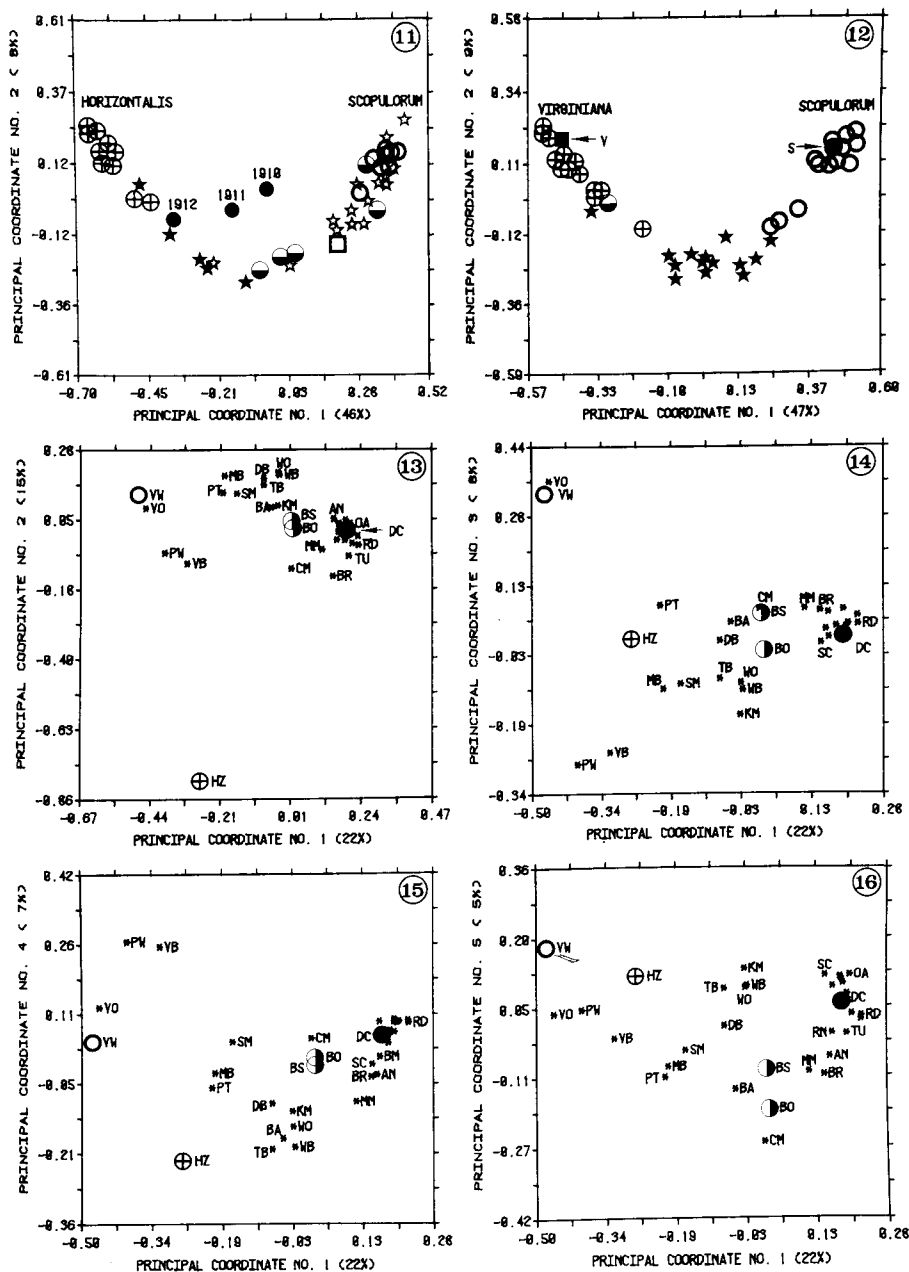
Figs. 11–16. 11: Principal coordinate analysis of *J. horizontalis–J. scopulorum* using F-1 weights (from ANOVA of *J. horizontalis* and *J. scopulorum*). Crossed circles are *J. horizontalis* from Saskatchewan. Open circles are *J. scopulorum* from Durango, Colorado (DC). Open stars are individuals from Banff, Alberta (BA), open square is an individual from population MM. Solid stars are putative *J. horizontalis* plants from Grass Range, Montana (GM). Half open circles are individauls from the Bridger, Montana (BR) population and solid circles are individuals from the Amidon, North Dakota (AN) site. *12:* Principal coordinate analysis of *J. virginiana–J. scopulorum* populations. S points to the average *J. scopulorum* from Durango, Colorado (DC) and V points to the average for *J. virginiana* from Washington, D.C. Open circles are for *J. scopulorum* from Raton, New Mexico (RN). Crossed

ization. Principal coordinate analysis was somewhat favored over the hybrid distance diagram of Wells due to the potential of PCO to easily handle a third or fourth taxon and allow the possibility of applying some statistical tests to the eigenroots obtained.

Principal coordinate analysis of *J. scopulorum* DC. (Durango, Colorado), *J. horizontalis* (SS, Saskatoon, Saskatchewan), and individuals from BA, BR, MM, GM and AN shows (Fig. 11) a number of intermediate individuals. Studies involving computer simulation of hybridization (Kistler, 1976) have shown that backcrossed individuals would be plotted about midway between hybrids and the recurrent parent in PCO. Two of the Banff plants are intermediate, some appear to be backcrosses, and others cluster with *J. scopulorum*. The plant from the MM site was the most shrubby plant found (240 cm tall × 300 cm wide) and its PCO position (open square, Fig. 11) does suggest that it might be backcrossed. The five extra plants collected at the Bridger population (BR) ranged in habit from slightly wider than tall to about three times as wide as tall. Three of these are strongly intermediate (Fig. 11), one is quite similar to typical *J. scopulorum* and the fifth (150 cm tall × 450 cm wide) might be backcrossed. The three individuals from Amidon, North Dakota, are interesting in that plant 1910 was judged to be a hybrid in the field (90 cm tall × 300 cm wide) and appears to be (Fig. 11). Plant 1911 had foliage in tight balls, with three stems arising from near the ground and curving upward then flattened at the top. It appears to be intermediate in its chemistry (although transgressive in many compounds). Its growth form was likely affected by the gaseous fumes at the burning coal vein (Adams, 1982), however, these fumes have been shown to have little effect on the terpenoids and the other morphological characters (Adams, 1982). Individual 1912 was sampled as typical of *J. horizontalis* (AN area), but it appears to be somewhat intermediate to *J. scopulorum* suggesting a possible backcross. Although the growth habit appears to be generally a reliable indicator of hybridization between *J. scopulorum* and *J. horizontalis*, this 8 cm high plant gave no indication of departure from *J. horizontalis*. This is shown even more graphically in the plants from the GM population (stars, Fig. 11), which show a trend from intermediates to more typical of *J. horizontalis* from Saskatchewan. Even the *J. horizontalis* from Saskatchewan (SS, Fig. 1), had two individuals that appear to tend toward *J. scopulorum*. These subtle changes were not found in *J. scopulorum* (except in the Banff population), inferring that although hybridization is occurring between *J. scopulorum* and *J. horizontalis*, there appears to be little if any gene flow (introgression) from *J. horizontalis* into *J. scopulorum*. In contrast, almost all of the *J. horizontalis* sampled which were sympatric with *J. scopulorum* appear to be introgressed. Additional studies should be made throughout the range

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open circles are for *J. virginiana* from Altus, Oklahoma (AO). Solid stars are for individuals from Palo Duro Canyon, Texas (PT) and the half solid circle is a *J. virginiana* individual from the northeastern Texas Panhandle. *13:* Plot of axis 1 and 2 from PCO using F-1 weights from ANOVA of *J. virginiana* from Washington, D.C. (open circle), *J. blancoi* from El Salto, and El Oro, Mexico (half solid circles), *J. horizontalis* from Saskatoon, Saskatchewan (crossed circle) and *J. scopulorum* from Durango, Colorado (solid circle). VO is *J. virginiana* from Altus, Oklahoma. All other acronyms are as previously defined. The first axis separated the *J. virginiana* from *J. scopulorum* and the Puget Sound populations (PW, VB) are shown to be similar to *J. virginiana*. Also note the separation of the Pacific northwest populations. The second axis separates *J. horizontalis*. There is little or no indication of intergradation of any of the populations towards *J. horizontalis*. *14:* Axis 1 is as in Fig. 13. Axis 3 (8% of the variation) emphasizes some differences between the *J. virginiana* populations (VW, VO) and the Puget Sound populations (PW, VB). *15:* This pattern again puts the *J. virginiana* and Puget Sound populations in relative close proximity, although axis 4 discriminates chiefly on the differences between the Puget Sound populations and *J. horizontalis*. The Oregon and British Columbia populations again show distinct clustering. *16:* The plot of the first axis and the fifth axis (5% of the variance) shows clearly the split between the *J. scopulorum* from the central portion of its range and the divergence of the northwestern populations.

of *J. horizontalis* to determine if this intergradation might be due to regional differentiation rather than introgression.

Hybridization between *J. scopulorum* and *J. virginiana* in the northern Great Plains has been documented by several researchers (see introduction) and was therefore not studied. An area not previously well studied is the southern Great Plains where relict stands of *J. virginiana* and *J. scopulorum* are found in the Texas Panhandle (PT, Fig. 1). The population sampled in Palo Duro Canyon (PT) is especially interesting as it is situated midway between the major ranges of the two taxa and the trees at that site are giant compared to either *J. scopulorum* from the Rocky Mountains or *J. virginiana* from western Oklahoma. This population is in a deep canyon with running water on the John Currie Ranch and has trees with trunks up to 60 cm dbh and 20 m tall. The area was once logged (John Currie, Jr., personal communication) and trees up to 25 m tall and 120 cm dbh were cut from there. These sizes are comparable with the semi-fossil remains of presumed *J. scopulorum* in the Laramie Basin, Wyoming (Wells, 1970), which had a trunk diameter of 1.3 m.

A transect of populations from *J. virginiana* (Washington, D.C.), Altus, Oklahoma (AO), Palo Duro Canyon, Texas (PT), Raton, New Mexico (RN), to typical *J. scopulorum* at Durango, Colorado (DC), gives an opportunity to examine the intergradation, although these taxa are not currently sympatric at any point along the transect. The Washington, D.C., site was chosen for *J. virginiana* because it occurs in what is believed to be the ancestral region for that taxon (Flake, von Rudloff and Turner, 1969, 1973; Flake and Turner, 1973). The Durango, Colorado, location (DC) for *J. scopulorum* was chosen because it is in the center of a very uniform portion of *J. scopulorum* that is most typical of that taxon. The western Oklahoma (AO) plants of *J. virginiana* show some differentiation (Fig. 12) from the Washington, D.C., population as expected from previous reports (Flake, von Rudloff and Turner, 1969, 1973). This differentiation is in the direction of *J. scopulorum* and is similar to results from the northern Plains (Van Haverbeke, 1968; Flake, Urbatsch and Turner, 1978; Comer, Adams and Van Haverbeke, 1983). The lone sample of *J. virginiana* from 90 miles (150 km) northeast of PT (near Canadian, TX) clusters (half circle, Fig. 12) with the western Oklahoma plants, but with stronger affinities to *J. scopulorum*. Plants from Palo Duro Canyon (PT) are almost exactly intermediate between the two taxa in their volatile oils with the exception of one individual which is more like the *J. virginiana* plants from western Oklahoma (Fig. 12, stars). Individuals from the Raton, New Mexico (RN), population mostly cluster closely with *J. scopulorum* from Durango, Colorado (DC), except for three individuals that show some affinities to *J. virginiana*.

In summary, it appears that *J. scopulorum* and *J. virginiana* essentially intergrade across the Great Plains as a series of relict populations. This pattern could be the result of at least three phenomena (Flake, Urbatsch and Turner, 1978; Van Haverbeke, 1968): relicts of an ancestral gene pool centered on the Great Plains with speciation east and west; allopatric introgression (perhaps relictual); or migratory tailings from the ancestral migration of *J. scopulorum*-like populations to form eastern United States populations of *J. virginiana*. The first possibility can be eliminated by the absence of suitable, stable habitats in the Great Plains dating from at least the Cretaceous to the present. The third hypothesis assumes that *J. scopulorum* is primitive to *J. virginiana* and that the evolution of the smooth leaf margined junipers in the western hemisphere proceeded from *J. scopulorum* eastward from more recent highly unstable habitats to a more ancient land mass (Appalachia) spawning *J. virginiana* and subsequently the entire diversity of smooth leaf margined junipers of the Caribbean (*J. bermudiana* L., *J. lucayana* Britt., *J. ekmanii* Florin, *J. gracilior* Pilger, *J. silicicola* (Small) Bailey and *J. urbaniana* Pilger & Ekman). My current research on the Caribbean junipers indicates that they are all closely related to *J. virginiana*. It seems improbable that this diversity could have been created from invading migratory populations since the Pleistocene. Of course, the migration could be postulated from *J. virginiana* westward, and that appears more plausible. However, in view of the parallel pattern obtained

in the northern Great Plains and now shown in the southern Great Plains and the likelihood that major shifts occurred in the populations and vegetation during the Pleistocene, the "migratory-tailing" hypothesis seems less likely than allopatric (or relictual sympatric) introgression.

Hybridization between *J. scopulorum* and *J. osteosperma* seemed most likely in the Thistle, Utah (TU), population where the two species are interspersed on a south facing slope. Examination of the volatile oils showed the taxa were completely separate and not hybridizing. No hybrids were found with any other sympatric species at other sites.

Comparison with Other Entire Leaf Margined Junipers

A recent comparison (Adams et al., 1981) of *J. scopulorum* (DC), *J. scopulorum* (near DB), *J. blancoi* (BS), *J. horizontalis* (SS) and *J. virginiana* (Washington, D.C.) indicated that *J. blancoi* was most similar to *J. scopulorum* from Colorado and to the plants of *J. virginiana* near Canadian, Texas. *Juniperus scopulorum* from British Columbia (near DB) showed interesting affinities to *J. virginiana* from Washington, D.C., by the mutual presence of several aromatic compounds from the phenylpropanoid pathway. In order to judge the direction of differentiation within *J. scopulorum*, ANOVA was performed using four groups: *J. virginiana* (Washington, D.C.), *J. horizontalis* (SS), *J. blancoi* (El Salto and El Salvador, Mexico) and *J. scopulorum* (DC). The resulting F ratios were then used as character weights to compute similarities (Adams, 1975b) and PCO. The first axis (22% of the variation among OTUs) performed an ordination from *J. virginiana* to *J. scopulorum* (Fig. 13) and second axis (15%) ordinated on similarity to *J. horizontalis* (Fig. 13). None of the *J. scopulorum* populations shows an overall trend toward *J. horizontalis*. However, that is not the case with respect to *J. virginiana*. All of the Pacific Northwest-Canadian populations are plotted rather intermediate between *J. scopulorum* (DC) and *J. virginiana* from Washington, D.C. (VW, Fig. 13). Note, however, that the Texas Panhandle population (PT) and Serrianas del Burro (SM) are also shown in a co-divergent direction with the northwest populations. Placement of the Puget Sound populations (PW, VB) is close to *J. virginiana* but well resolved from both *J. virginiana* and the rest of *J. scopulorum*. *Juniperus virginiana* from western Oklahoma (VO of Fig. 13) is shown very close to *J. virginiana* from Washington, D.C. (VW), in this ordination (recall that the ordination was designed with four a priori species groupings in contrast to Fig. 12), both populations of *J. blancoi* cluster with *J. scopulorum*.

The third axis removed 8% of the variation among OTUs and shows separation between *J. virginiana* and the Puget Sound populations (PW, VB) with all the *J. scopulorum, J. blancoi,* and *J. horizontalis* populations mapping intermediate on axis 3. Some affinity of the Manning Pass (MB) population is shown by its placement toward the Puget Sound populations. The fourth axis (7%) shows (Fig. 15) some additional unique variation in the Puget Sound populations, however, they are again allied most closely with *J. virginiana*. The fifth axis (5%) split the *J. virginiana* populations (Fig. 16) and emphasizes some of the *J. scopulorum* attributes of the western Oklahoma *J. virginiana* (VO) population. Notice again the clear separation of the northwestern, Texas Panhandle (PT), and Serranias del Burro (SM) from the central populations of *J. scopulorum*. Divergence of the northern Chihuahuan *J. scopulorum* (CM) population is also obvious (Fig. 16). It was not until the sixth axis (5%) was extracted that the *J. blancoi* population separated out from *J. scopulorum* (not shown). Clearly *J. blancoi* is very closely related to *J. scopulorum* (from its central range) and might well be considered conspecific.

Both the degree and direction of the divergence of the Puget Sound populations raises some interesting questions. Should these populations be considered conspecific with *J. virginiana*? Do they reflect a previous period of an even wider range for *J. virginiana*?

Another important aspect shown in Figs. 13–16 is the close similarity of the Serranias del Burro (SM) population to the Texas Panhandle population (PT). The Serranias del

Burro area is believed to serve as a refugium for disjunct eastern species as well as disjunct Rocky Mountain species apparently dating to the Pleistocene (Adams, 1977) for some species (*J. ashei*) but probably to before the Pliocene for eastern deciduous species (Martin and Harrell, 1957). Whether the SM population is intermediate to *J. virginiana* from central Texas must await further study, but it does appear to be intermediate to *J. virginiana* from western Oklahoma and Washington, D.C.

In summary, *J. scopulorum* is quite variable on the northwest, northeast, southeast and southern portions of its range, but is very uniform throughout the central portion of its range. The divergence of the Puget Sound population is comparable to the differences between *J. scopulorum* and *J. virginiana* and in the direction of *J. virginiana*. Although the divergence of the PT and SM populations could be explained by allopatric or relictual hybridization and introgression, the affinity of the Puget Sound populations to *J. virginiana* suggests that those populations (PW, VB) may be relictual from a pre-Pleistocene or perhaps a pre-Pliocene period when *J. virginiana*-type populations had a wider range. Morphological studies are currently being carried out and, together with the chemical data presented here, might resolve many of the problems posed here.

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