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Intra- and Interspecific Variation of *Juniperus virginiana* and *J. scopulorum* Seedlings Based on Volatile Oil Composition

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Key Word Index – *Juniperus virginiana*; *J. scopulorum*; Cupressaceae; Coniferae; hybridization; seedlings; intraspecific variation; interspecific variation; Great Plains.

Abstract – Comparisons of volatile oil constituents were made among samples of juvenile foliage collected from 78 *Juniperus virginiana* and 28 *J. scopulorum* seedling sources growing in a "common garden" environment. A canonical variate analysis, a principal coordinates analysis and hybrid distance diagrams of 30 chemical characters indicate both taxa are good species and that they exhibit clinal patterns in the Great Plains. In addition, a possible evolutionary link between present-day *J. virginiana* populations in southern Texas and ancient *J. scopulorum* populations is indicated.

Introduction

Two species of *Juniperus,* eastern redcedar (*J. virginiana* L.) and Rocky Mountain juniper (*J. scopulorum* Sarg.), are of major importance for protective and other environmental plantings throughout the Great Plains region. The natural ranges of the two species, as adapted from Adams [1], Little [2] and Zanoni and Adams [3], overlap in parts of the Great Plains (Fig. 1).

Natural variation in adult populations has been found to be extensive and possibly of hybrid origin [4–7]. Fechner [8] obtained seemingly "good" seed from interspecific crosses of the two taxa but was unable to germinate the seed produced.

Both quantitative and qualitative differences are known to exist among the various species of *Juniperus*. These variations can occur among individuals, within a species, from different geographic origins [1, 7, 9–14] and within an individual tree from season to season [15]. There has been demonstrable environmental influence on terpene expression in *Juniperus* for a particular individual between calendar seasons and maturity levels. Terpene expression, however, has been found to be relatively stable during any given season or age level [13–20]. Enzymatic and chemical compositions in *Juniperus* are the most stable during fall and winter, i.e. periods of dormancy [14, 16–18, 21]. Diurnal variation in *J. scopulorum* trees was found to be less than genotype variation when the trees were growing in a relatively uniform environment [20]. Very few differences in the volatile oil of *J. scopulorum* were attributable to the sex of sample trees [14, 18]. Significant differences were found in the volatile oil of mature vs young leaves of *J. scopulorum* [14, 19] and in *J. virginiana* [14], but not in *J. horizontalis* [14, 22]. The extent of genetic variation of volatile oil constituents in seedling populations, however, is virtually unknown.

In this study, leaf oils of half-sib families representing two species, *J. virginiana* and *J. scopulorum,* from throughout their respective ranges in the Great Plains were analysed. The analysis was made using juvenile foliage of seedlings grown in the "common garden" environment of a nursery unit at the USDA Forest Service Bessey Nursery at Halsey in north-central Nebraska. All seedlings were the same age and exposed to the same cultural practices. Thus, environmental influence over terpene expression was assumed to be minimal for all seedlings.

The objective was to compare the foliage terpenoid patterns and constituents of *Juniperus* seedlings from half-sib families originating from widely diverse geographical areas but grown

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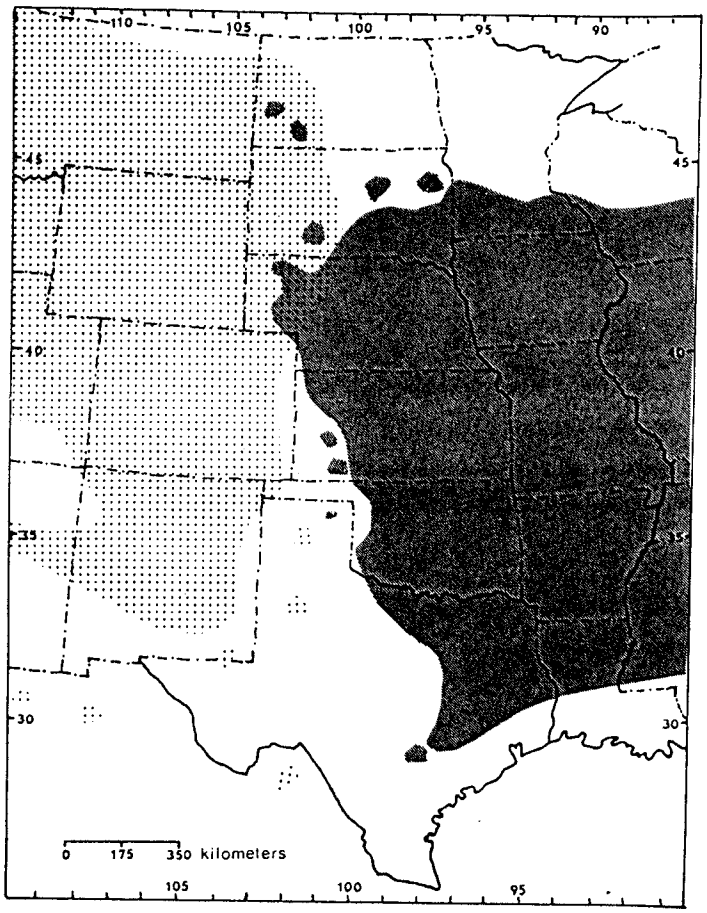

FIG. 1. DISTRIBUTION RANGES OF *JUNIPERUS VIRGINIANA* (GRAY AREAS) AND *J. SCOPULORUM* (STIPPLING) IN THE GREAT PLAINS. Zones of species overlap are indicated by overlaid areas.

under a single environmental regime. Previous studies differ in that they analysed foliage collected on location from mature trees growing on widely separated geographic sites but grown under different environmental regimes.

Results and discussion

Initially, a canonical variate analysis (CVA) was made using 30 characters that had the largest *F* values (among population variance/within population variance) (Table 1) to determine if any of 18 exemplars (samples not included in the populations) could be grouped with one of 17 geographical populations (Fig. 2).

The first three axes of the CVA accounted for 56.28, 19.83 and 5.86%, respectively, of the variance among the 17 populations, with the first two axes being significant. Seven (exemplars 2, 3, 7, 12, 16, 17 and 18) of 18 exemplars were in close association with nearby populations. To improve the sample sizes of the populations, exemplar 18 was added to population MT, exemplars 2 and 3 to WY, exemplar 7 to N1, exemplars 16 and 17 to EN and exemplar 12 to SK (Fig. 2). This resulted in 17 revised geographical populations which were used in subsequent analyses (Fig. 2, Table 2).

The subsequent CVA on the revised 17 populations gave five significant eigenroots accounting for 58.27, 20.51, 5.74, 3.17 and 2.66%, respectively, of the variation among the 17 groups (Table 3).

The first trend shows the separation of the western group of populations (MT, ND, WS, WY and WN) from the eastern group of populations (ST, SO, EO, SK, EK, CK, WK, SN, NN, N1, N2

TABLE 1. THE 30 CHARACTERS USED FOR CANONICAL VARIATE ANALYSIS OF 17 GEOGRAPHICAL POPULATIONS, THEIR IDENTITIES BASED ON MASS SPECTRAL ANALYSIS AND THEIR ASSOCIATED *F* VALUES

Character	*F* value
Per cent yield of oil	25.1523
α-Thujene/α-pinene	7.0523
Sabinene	11.6722
Myrcene	9.2121
α-Terpinene	7.3855
γ-Terpinene	6.5951
Unknown	3.2318
Terpinolene	5.9836
β-Terpeneol isomer	9.6336
Citronellal	4.8443
Isosafrole	7.3897
Unknown (terpene alcohol)	7.7709
Bornyl acetate	3.5975
4-Terpineol	7.0899
Unknown	3.2055
Estragole	5.7917
Piperitone	7.6088
Citronellol	7.7610
(Carane hydrate)	4.4072
Terpene alcohol	6.9638
Safrole	6.3417
(Sesquiterpene)	5.5560
Unknown	5.1071
Methyl eugenol	12.2468
(Alcohol of elemene)	6.0055
Elemicin	15.7391
γ-Eudesmol	9.3172
α-Cadinol isomer	9.7766
α-Eudesmol	4.4612
β-Eudesmol	7.6848

and EN) (Fig. 3). This trend accounted for 58.27% of the variation among the 17 populations based on the 30 chemical characters used.

The two groupings closely parallel the findings of Flake *et al.* [7]. The western group is predominantly in the recognized distribution range of *J. scopulorum*; the eastern group lies within the *J. virginiana* distribution range.

Flake *et al.* [7] showed the division of the two groups to be between populations WN and NN, the same as this study indicated (Fig. 4). Although the division in Fig. 4 is very sharp, there is some indication of a gradation running from WY to WN and then to eastern Nebraska (NN, N2 and EN).

The second axis accounted for 20.51% of the variation among the 17 populations and delineated two groups within the eastern populations (Fig. 3). The first group, the south-eastern group, is composed of populations ST, SO and EO, and the second group contains the remaining eastern populations (SK, EK, CK, WK, SN, NN, N1, N2 and EN). Hall [23] proposed an Ozark race of *J. virginiana* extending from Missouri, south-westerly through eastern Oklahoma, Arkansas and into central Texas. He also proposed a Platte River race which covered most of Kansas, Nebraska and South Dakota, and a Florida race which extended into the south-eastern corner of Texas (Fig. 5). Hall, however, used only six morphological characters and proposed these and other races on the basis of introgression with *J. scopulorum* and *J. ashei* Buch. Introgression of *J. ashei* into *J. virginiana* was not detected using terpenoid characters [9, 10]. Using 19 morphological and 135 terpenoid characters, Adams and Turner [11] found no evidence of introgression into *J. ashei* by *J. virginiana*. Similar results were found [21] even when populations of *J. ashei* were sampled in the Ozarks where that taxon was surrounded by *J. virginiana*.

The north-eastern populations (EN, N1, N2, NN, SN and WK) correspond to the Platte River race [23], while two of the south-eastern populations (SO and EO) corresponds to Hall's Ozark race and the extreme south-eastern population (ST) corresponds to his Florida race (Fig. 5). Flake and Turner [24] found a division which divided the Ozark race into a northern portion (eastern Oklahoma and northern Arkansas through southern Missouri) and a southern portion (east-central Texas). The variation shown from EO to ST populations (Fig. 6) may represent that trend. In southern and central Kansas, the Platte River race may not have the uniformity hypothesized by Hall [23] (see populations CK, EK and SK in Figs. 3 and 6).

A strong indication of a clinal pattern in the distribution of eastern redcedar populations is suggested (Fig. 6). The southernmost populations appear to have close affinities with the more northern populations, but they also have a definite division between their ST and EO–SO groupings.

TABLE 2. LISTING OF THE 17 GEOGRAPHIC POPULATIONS AND THEIR RESPECTIVE NO. OF SAMPLES USED FOR CANONICAL VARIATE ANALYSES

Geographic Population	Code ID	No. of samples Original*	Revised†
Montana	MT	8	9
North Dakota	ND	4	4
Western South Dakota	WS	3	3
Wyoming	WY	5	7
Western Nebraska	WN	3	3
Northern Nebraska	NN	4	4
Nebraska 1	N1	5	5
Nebraska 2	N2	4	5
Eastern Nebraska	EN	8	10
Southern Nebraska	SN	7	7
Western Kansas	WK	5	5
Central Kansas	CK	11	11
Eastern Kansas	EK	4	4
Southern Kansas	SK	4	5
Eastern Oklahoma	EO	4	4
Southern Oklahoma	SO	5	5
Southern Texas	ST	4	4

*CVA used for the first approximation included 17 populations plus 18 exemplars that were not included within the 17 populations.

†CVA used for the second analysis included the original 17 populations with seven exemplars incorporated within the original populations. All remaining exemplars used in the first approximation were deleted from subsequent analyses.

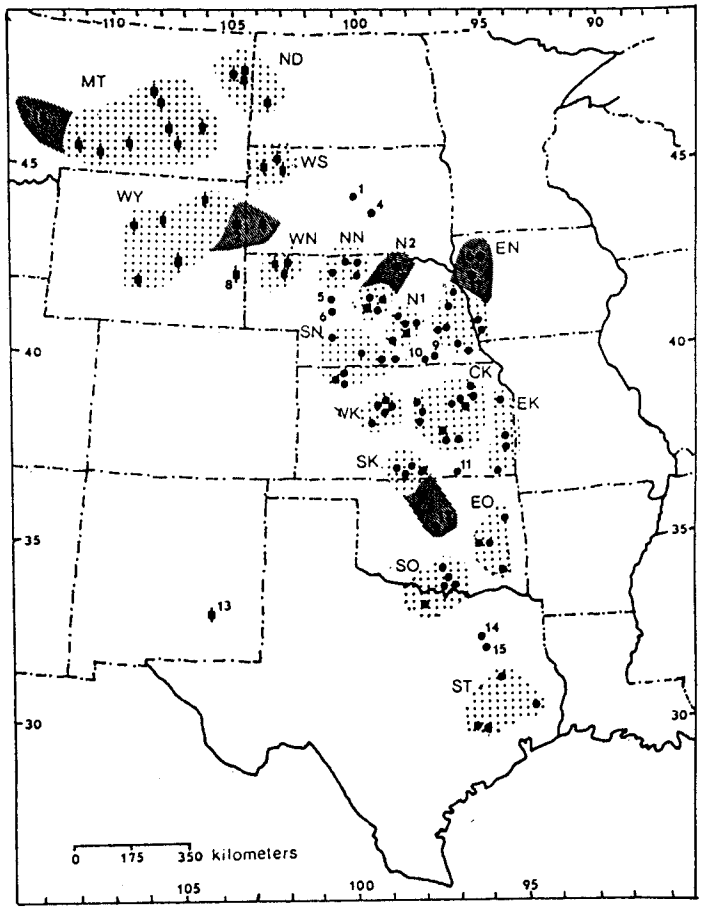

FIG. 2. LOCATIONS OF 106 SAMPLE TREES OF *JUNIPERUS* SEED COLLECTIONS USED IN THE JUVENILE FOLIAGE ANALYSES. ● = *J. virginiana* and ■ = *J. scopulorum*. The 17 populations (stippling) and 18 exemplars (numbers) used in the first canonical variate analysis (CVA) and the 7 exemplars included in the 17 populations (gray areas) used in the second CVA are shown. (See Table 2 for population identity codes.)

The ST samples are more intermediate in characters shared between the two parental taxa. The SO population is intermediate but definitely closely aligned with the *J. virginiana* taxon; whereas the EO population has *J. virginiana* individuals and appears to be exemplary of the Ozark race described by Hall [23].

Barber and Jackson [25] felt that, in regions of great ecological change, simultaneous clinal variations in gene frequencies at a number of loci could be expected. They saw selection as a way to create genetic diversity in local populations of different habitats. Turner [12] and Flake *et al.* [7] concluded that Barber and Jackson interpreted

TABLE 3. THE PERCENTAGE OF VARIABILITY AMONG 17 GEOGRAPHIC POPULATIONS THAT WAS ACCOUNTED FOR BY THE FIRST EIGHT CVA AXES (EIGENROOTS) BASED ON BARTLETT'S TEST OF SPHERICITY

No. of eigenroots removed	Eigenroot value*	Chi-squared value	Degrees of freedom	% of variability among groups	Cumulative % among groups
0	35.8888**	999.60	480	58.27	58.27
1	12.6316**	745.24	435	20.51	78.78
2	3.5331**	561.07	392	5.74	84.51
3	1.9519**	454.52	351	3.17	87.68
4	1.6386**	378.21	312	2.66	90.34
5	1.2602	309.80	275	2.05	92.39
6	1.0279	252.31	240	1.67	94.06
7	0.8595	202.47	207	1.40	95.45

*Significant (**) at the $P = 0.05$ level.

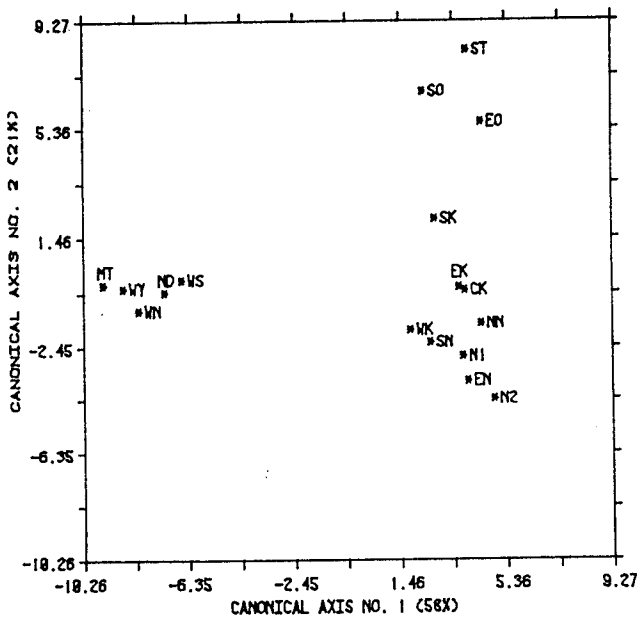

FIG. 3. PLOT OF THE 17 POPULATIONS ALONG THE FIRST (HORIZONTAL) AND SECOND (VERTICAL) CANONICAL VARIATE ANALYSIS AXES FROM THE SECOND CVA. The percentage of among-population variance accounted for by each axis is shown in parentheses. (See Table 2 for population identity codes.)

Hall's [23] descriptions of morphological variation in *J. virginiana* as clinal and not due to hybridization.

The Great Plains Agricultural Council Forestry Committee's GP-13 study was the source of the plant material that was sampled for this hybrid analysis. The seed collection sampling pattern for the GP-13 study was intended to provide a large selection of ecotypes of *Juniperus* to be tested in provenance plantings throughout the Great Plains. Since most of the seed collections were geographically distant from each other, they do not provide the most desirable sampling pattern for detection of regional differentation or hybridization. However, the GP-13 nursery production stock did offer a fortuitous opportunity for a conservative analysis of regional differentation and hybridization of *Juniperus* material which had been grown in a "common garden" environment.

A principal coordinates analysis (PCORD) was run using 30 chemical characters (Table 4) obtained from an ANOVA of two proposed parental populations (based on CVA analysis and author's knowledge) of *J. virginiana* (the 25 samples of EN, CK and EK) and *J. scopulorum* (the 16 samples of MT and WY), with the 17 revised population averages as operational taxonomic units (OTUs) (Fig. 2). The first axis of the PCORD discriminated between the two parental groups, and the resulting

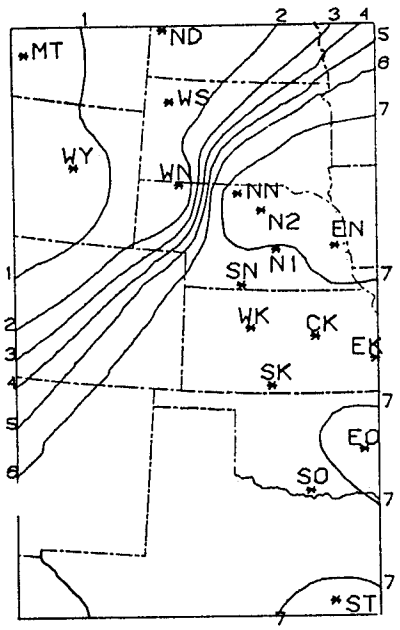

FIG. 4. SIMILARITY CONTOUR INTERVALS BASED ON THE FIRST CANONICAL VARIATE AXIS OF 30 CHEMICAL CHARACTERS SHARED BY 17 POPULATIONS: (See Table 2 for population identity codes.)

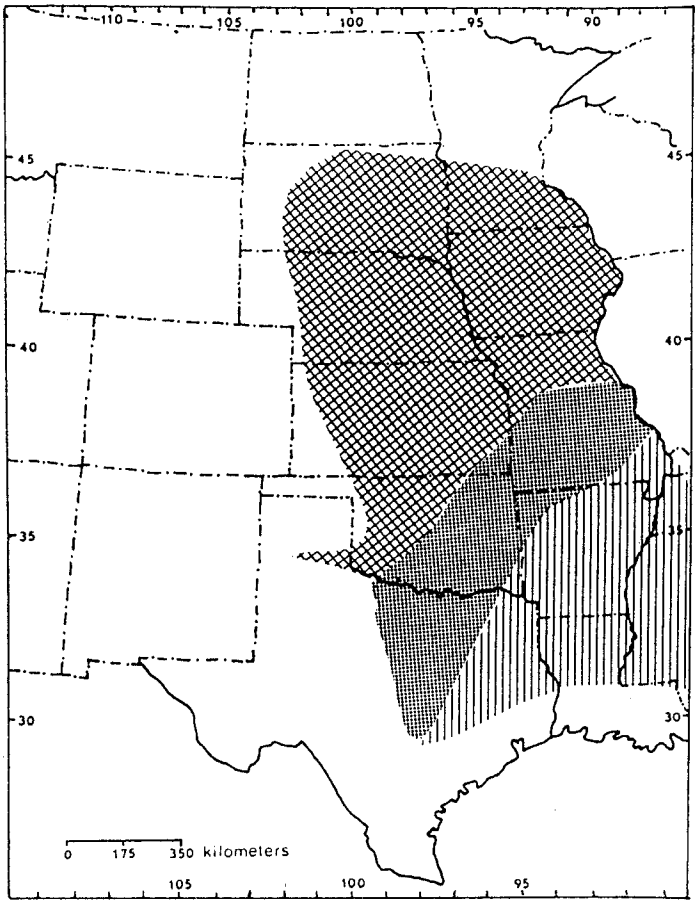

FIG. 5. THE THREE GREAT PLAINS RACES AS DESCRIBED BY HALL. Platte River = cross-hatching; Ozark = stippling; Florida = vertical barring.

contour map of each population's principal coordinate score on axis 1 is shown in Fig. 7. Note the pattern is similar to that of the CVA axis 1 (Fig. 4) in that the sharp break is between populations WN and NN. The most intermediate population is WK (contour below 6). *Juniperus virginiana* also shows intermediacy in populations SN, SK and in all of the southern populations. Some intermediacy is seen in *J. scopulorum* populations WS and WN.

A hybrid distance diagram [26] of the 105 samples based on the 30 characters shared by two parental taxa is shown in Fig. 8. The 16 *J. scopulorum* parental samples clustered in a tight group along with the 11 exemplars from the *J. scopulorum* range. No samples plotted near the point of intermediacy between the two parental groups labelled the synthetic hybrid (F) (Fig. 8). In contrast, the 25 *J. virginiana* samples clustered in a well-defined group, but the 53 exemplars from the *J. virginiana* distribution range did not group tightly around the parental taxon (Fig. 8). The 53 *J. virginiana* exemplars had a number of individuals that plotted in the intermediate zone.

To better visualize the variation in individual populations, the *X* coordinate from Fig. 8 (weighted hybrid distances) was used to generate histograms for the species and populations (Fig. 9). *Juniperus virginiana* (EN, CK and EK) shows a tendency toward bimodality, whereas *J. scopulorum* (MT and WY) has a histogram of tightly clustered individuals. Variable individuals are seen in nearly all populations; however, *J. scopulorum* populations ND, WS and WN have less variation than populations NN, N1, SN, WK, SK, EO, SO and ST in *J. virginiana*. In *J. virginiana*, only population N2 shows a uniform clustering. The *J. virginiana* populations also differ from *J. scopu-*

TABLE 4. THE 30 CHARACTERS INCLUDED IN THE PRINCIPAL COORDINATES ANALYSIS OF TWO POOLED PARENTAL GROUPS AND 12 POPULATIONS USED FOR DISCRIMINATION BETWEEN *JUNIPERUS VIRGINIANA* AND *J. SCOPULORUM*, THEIR IDENTITIES BASED ON MASS SPECTRAL ANALYSIS AND THEIR ASSOCIATED *F* VALUES

Character	*F* value
Per cent yield of oil	244.3676
α-Thujene/α-pinene	35.2408
Camphene	7.2540
Sabinene	106.3249
Myrcene	23.2609
α-Terpinene	31.0793
Limonene	5.5789
γ-Terpinene	22.3718
Unknown	9.4431
Terpinolene	14.1563
β-Terpeneol isomer	66.1084
Citronellal	16.7378
Linalool	5.6580
Isosafrole	67.1132
Unknown (terpene alcohol)	43.0525
Bornyl acetate	8.8118
Estragole	43.1233
Borneol/α-terpineol	5.6471
Unknown	23.7655
Piperitone	73.7968
Unknown	9.2932
Citronellol	35.9480
Safrole	31.9743
Methyl eugenol	41.3369
(alcohol of elemene)	24.0463
Elemicin	133.4802
γ-Eudesmol	70.6994
α-Cadinol isomer	102.5172
β-Eudesmol	94.0046
Acetate II	7.4596

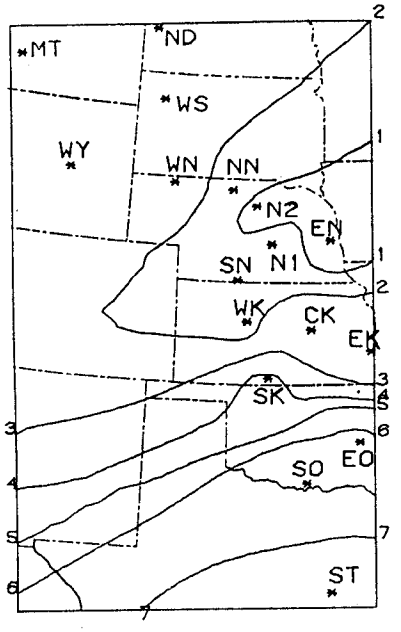

FIG. 6. SIMILARITY CONTOUR INTERVALS BASED ON THE SECOND CANONICAL VARIATE AXIS OF 30 CHEMICAL CHARACTERS SHARED BY 17 POPULATIONS: (See Table 2 for population identity codes.)

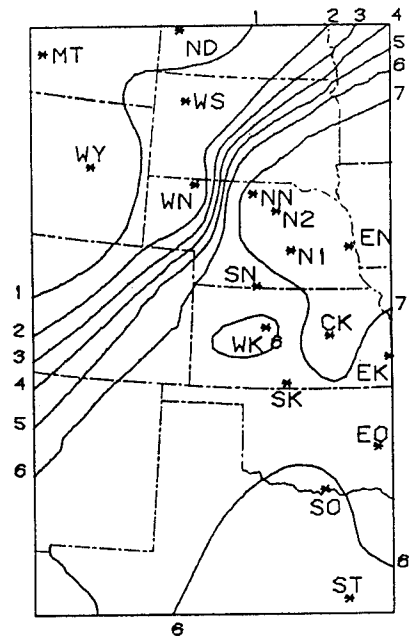

FIG. 7. SIMILARITY CONTOUR INTERVALS BASED ON THE FIRST PRINCIPAL COORDINATES AXIS OF 30 CHEMICAL CHARACTERS SHARED BY THE TWO PROPOSED PARENTAL GROUPS. (See Table 2 for population identity codes.)

lorum in that several of the populations (SN, WK, SO and ST) have individuals that approach intermediacy in contrast to the *J. scopulorum* populations (WS and WN) which show only a slight shift in the mean toward *J. virginiana*. Population WK was the most intermediate in PCORD (Fig. 7), and this was evident in the distance diagrams (Fig. 9), where all WK individuals plot in the hybrid backcross region.

In general, the differentiation among populations seen in the PCORD axes was expressed in the hybrid distance diagrams. The two different methods suggest that *J. scopulorum* germ plasm is moving or has moved eastward into that of *J. virginiana*. This finding is supported by those of Van Haverbeke [6] and Flake *et al.* [7] for the Missouri River Basin.

However, the finding of *J. virginiana* individuals that show similarities to *J. scopulorum* in the ST and SO samples cannot be explained by flow of germ plasm from existing *J. scopulorum* plant material because this flow is discontinuous within this geographical area. Two explanations seem possible. First, the ranges of both *J. scopulorum* and *J. virginiana* were greatly extended during the Pleistocene [21, 27]. The northern Mexico (Serranias del Burro) population of *J. scopulorum*

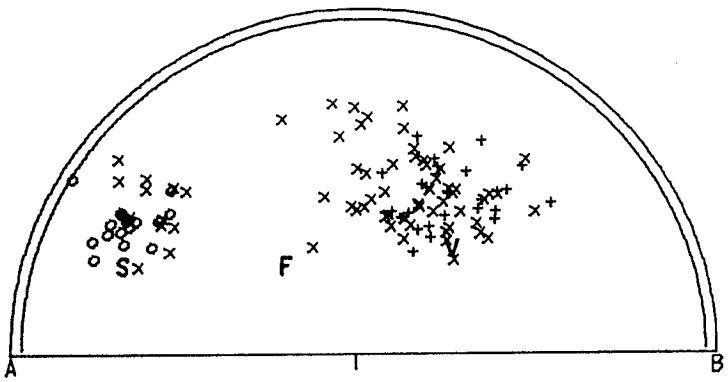

FIG. 8. PLOTTING OF DISTANCE COEFFICIENT COORDINATES FOR 105 SAMPLES. O = *Juniperus scopulorum* parental group sample; + = *J. virginiana* parental group sample; × = non-parental exemplar; F = synthetic hybrid; S = mean for all *J. scopulorum* parental samples; and V = mean for all *J. virginiana* parental samples. All plot points are at the bottom or bottom left of symbol.

[1] could have expanded toward the east into the Edwards Plateau of Texas. If the Edwards Plateau had been covered by a mixed deciduous woodland with conifers [28], this more mesic association, than is presently there, could have supported a western expansion of the range of *J. virginana* (Fig. 1). This would have provided opportunity for sympatry and hybridization, as suggested by Flake *et al.* [10]. Second, the differentiation of the SO and ST populations of *J. virginiana* towards *J. scopulorum* is convergent evolution in response to selection pressure, genetic drift or other evolutionary stimuli.

Experimental

The initial phase of the GP-13 study was completed in the fall of 1977 with the sowing of seed collected from 275 individual juniper tree sources (open-pollinated, half-sib families) selected by co-operators throughout the Great Plains. The seed was sown in August at the USDA Forest Service Bessey Nursery, Halsey, Thomas County, Nebraska.

Seed from all sources was sown in unreplicated single source lots in a completely randomized design within one nursery unit. This design was selected because the nursery unit was considered to have a homogeneous environment. All cultural practices were identical with those practised on other nursery juniper production stock at Bessey Nursery.

Comparisons were made between 28 families of *J. scopulorum* and 78 families of *J. virginiana*. These 106 families represent 37 and 58%, respectively, for the two species, of the available GP-13 seed collected from non-planted (native) parent tree sources. The families were chosen to achieve a geographical representation of the two species within their respective distribution ranges in the Great Plains (Fig. 2).

Composite foliage samples of each of the 106 half-sib families were collected in the nursery, immediately frozen and maintained frozen until steam-distilled. The collections were made during a 3-day period in late November 1979.

Approximately 50–100 g of juvenile foliage from each family was steam-distilled for 2 h using a modified Clevenger-type circulatory apparatus [29], dried over anhydrous sodium sulfate, and stored in a tightly capped storage vial at − 20°.

The individual compounds were separated using a gas/liquid chromatograph (GLC) with a flame ionization detector and a 61 m × 0.508 mm stainless-steel capillary, coated with 5% Carbowax 20M [polyethelene glycol (PEG) 29 0M]. Carrier gas flow was nitrogen (N_2) at 25 cm/s, hydrogen (H_2) at 17 ml/min and air at 300 ml/min. 0.1 μl samples of oil were injected into the GLC for analysis. The chromatograph temperature programming was as follows: isothermal at 7° for 8.2 min; 1°/min linear increase for 8.2 min; 3.5°/min linear increase for 8.2 min; 3°/min linear increase for 32.8 min; 2°/min linear increase for 8.2 min; then isothermal at 220° for 24.6 min. Total time of analysis was 90 min.

Individual peaks were quantified with an electronic digital integrator. Standards were used to produce a reference chromatogram, and each peak on this chromatogram was assigned a reference code number. This reference chromatogram was subsequently used for coding the peaks with the same retention times for data analysis of individual samples. As new or additional peaks were found on the sample chromatograms, they were assigned code numbers and marked on the reference chromatogram.

Identifications of the major terpenoids composing the volatile oil of *J. scopulorum* and *J. virginiana* are based on recent MS identifications [30]. Owing to incomplete resolution, α-pinene and α-thujene are treated as one compound, as are borneol and α-terpineol.

Volatile oil compounds found in quantities less than 0.05% of the total oil were omitted from analyses. Six consecutively associated peaks were deleted because a decomposition peak was present at the same retention time.

Initially, 101 characters (100 terpenoids and phenyl allyl ethers and the per cent oil yield) were checked for frequency of occurrence. Twenty-five compounds found to occur in fewer than 5% of the samples (five sources) were deleted along with 16 compounds that had a maximum value of less than 0.2% of the total oil.

The geographical range of samples was initially subdivided into 17 groups, each containing a minimum of three samples. Individual samples that did not appear to be related to a geographical group were kept separate in the initial analysis

(Fig. 2, Table 2). The original 17 groups were approximations to geographical populations.

The CVA program used in this study was derived from the program CANVAR 2 in ref. [31]. Further modification of this program to get eigenvalues and vectors was accomplished using subroutines DIRNM and HOW after those described in ref. [32]. The test of equality of the eigenroot values used Barlett's test of sphericity [33].

Since the CVA program was capable of handling a maximum of 30 characters, these 30 characters were chosen by doing an analysis of variance (ANOVA) and selecting the 30 characters with the highest F ratios. The CVA for the first approximation included 17 populations plus 18 exemplars that were not included within those 17 populations (Fig. 2, Table 2). A revised population grouping used for the second CVA included the original 17 populations plus 7 of the 18 exemplars of the first approximation. The 7 exemplars were incorporated into the 17 populations (Fig. 2, Table 2). The 30 compounds (characters) utilized in the CVA are given in Table 1.

Based on the results of the CVA of the 17 geographical populations, two geographical groups were identified as representative of the parental populations of *J. virginiana* and *J. scopulorum*. The *J. virginiana* group consisted of the EN, CK and EK populations (25 samples), and the *J. scopulorum* group contained in the WY and MT populations (16 samples) (Fig. 2).

An ANOVA was performed between *J. scopulorum* (16 samples) and *J. virginiana* (25 samples) for 73 chemical characters. The 30 characters with the highest F ratios were then chosen for use in forming a similarity matrix ($F-1$ weighted, Gower metric [34] using the 17 revised population averages. This matrix was then factored by PCORD, and the first PCORD axis scores were contour-mapped [1]. The principal coordinates analysis used was derived from the program PCORD in ref. [31]. Eigenvalues and eigenroots were computed using subroutine HOW from ref. [32].

A graphical hybrid distance method proposed by Wells [26] to test for intermediacy of individuals in populations was conducted on the two parental populations and 64 exemplars as modified for weighting by $F-1$ [35]. Exemplar 13 (Fig. 2) was deleted from this analysis because of its isolated geographical location in relation to the parental taxa.

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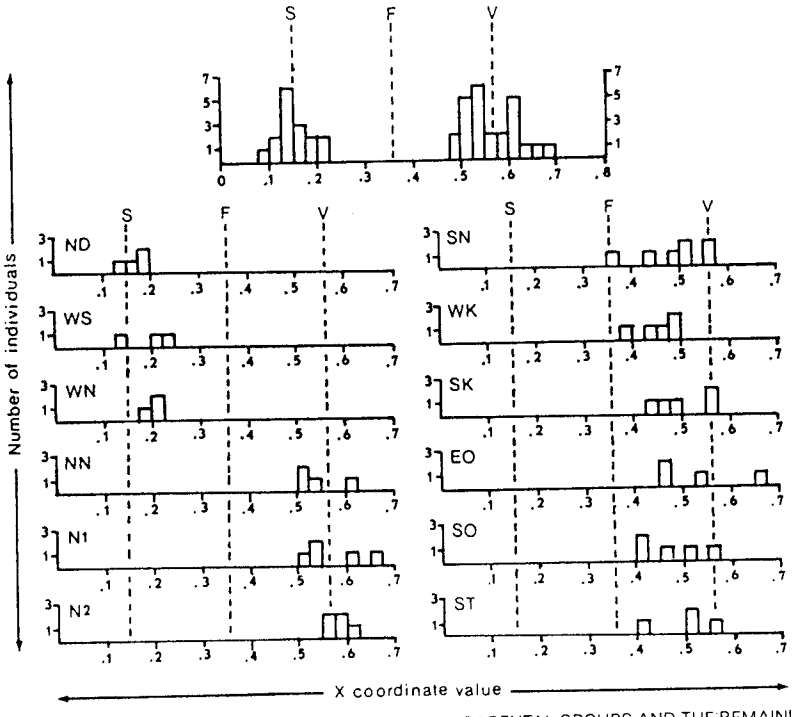

FIG. 9. HISTOGRAMS OF *JUNIPERUS VIRGINIANA* AND *J. SCOPULORUM* PARENTAL GROUPS AND THE REMAINING 12 POPULATIONS USING THE X COORDINATE FROM THE WEIGHTED HYBRID DISTANCES OF FIG. 8. S and V denote the respective means for the two species and F = the synthetic hybrid value.

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