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GEOGRAPHIC VARIATION IN *JUNIPERUS SILICICOLA* AND *J. VIRGINIANA* OF THE SOUTHEASTERN UNITED STATES: MULTIVARIATE ANALYSES OF MORPHOLOGY AND TERPENOIDS

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Summary

Natural populations of *Juniperus silicicola* were sampled from throughout the recorded range along the coast of North America. Additional populations of *J. virginiana* from inland sites were sampled. Morphological characters which have traditionally been used to separate the two taxa were measured along with analyses of the volatile leaf terpenoids. These data were analyzed by canonical variate analysis and contour mapping of the canonical variates. The amount of variation among inland populations of *J. virginiana* was comparable to the divergence of *J. silicicola.* The volatile leaf oils differed only quantitatively for a few components. Characters used in keys (female cone size, leaf tip shape) were not significantly different between the taxa. The populations in Texas, previously treated as *J. silicicola,* were found to be *J. virginiana* in both their morphology and chemistry. Some intergradation was found between the Macon, Georgia and Brunswick, Georgia populations. The coastal, foredune juniper of the southeastern United States (*J. silicicola*), being circumscribed within the range of variation encountered within *J. virginiana,* is treated as a varietas (*J. virginiana* var. *silicicola* (Small) ~~Silba~~ E. Murray).

Introduction

Three species of juniper have generally been recognized for the southeastern United States: *Juniperus communis* L., the circumboreal shrub found on isolated mountains; *J. silicicola* (Small) Bailey, found on the coastal dunes and flood plains; and *J. virginiana* L., the common eastern red cedar of the uplands (Little, 1971). *Juniperus communis,* with its acicular leaves in the subsection *Oxycedrus* of *Juniperus,* has not been a source of taxonomic confusion in this region. The principal point of disagreement has been on the taxonomic status of *J. silicicola* and whether it is a distinct taxon from *J. virginiana.*

In his original recognition of juniper species from the New World, Linnaeus (1753) recognized three species: *Juniperus barbadensis* L. (from the island of Barbados); *J. bermudiana* L. (from the island of Bermuda); and *J. virginiana* (from the eastern United States mainland). Unfortunately it was not clear which figure Linnaeus referred to in his description of *J. barbadensis.* Hemsley (1883) equated *J. barbadensis* with *J. bermudiana,* leaving *J. bermudiana* as the name for all the junipers of the islands of the Caribbean and Bermuda. Sargent (1902) recognized three red cedars in North America: *J. scopulorum* in western North America; *J. virginiana* in eastern United States; and *J. barbadensis* occurring along the Atlantic coast of Georgia to Florida, and also found "on the Bahamas, San Domingo (Dominican Republic), mountains of Jamaica, and on Antigua." *Juniperus silicicola* was originally described by Small (1923) as *Sabina silicicola* Small for the southern red cedar occurring near the edges of marshes and swamps in Florida (based on *J. barbadensis* sensu C. Mohr non Linnaeus). Of course, these are undoubtedly the same plants which Sargent (1902) called *J. barbadensis* from Florida. Small (1913) separated *Sabina barbadensis* (L.)

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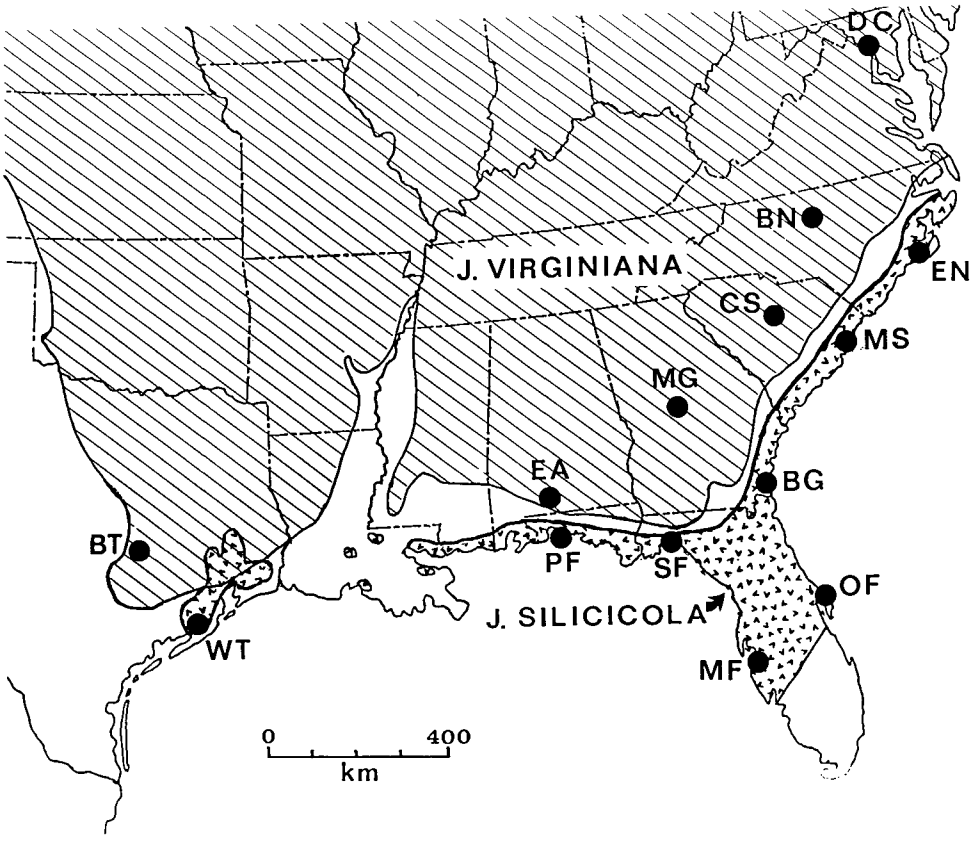

Fig. 1. The distributions of *Juniperus silicicola* and *J. virginiana* based on Little (1971). The populations sampled are shown by the solid circles and two letter acronyms used in this study.

Small [=*Sabina silicicola* Small in Small (1923) and later = *Juniperus silicicola* (Small) Bailey] from *Sabina virginiana* (=*J. virginiana*) in that the former taxon had shorter and thicker leaves, with a blunt apex, staminate aments 4–5 mm long (vs. 3–4 mm in *J. virginiana*) and female cones 3–4 mm long (vs. 5–6 mm long in *J. virginiana*). Correll and Johnston (1970) separated *J. silicicola* from *J. virginiana* on the basis of: branches mostly pendulous (vs. horizontal); ultimate twigs usually less than 1 mm thick (vs. more than 1 mm); leaves bluntly obtuse to acute (vs. acute to acuminate); and female cones 3–5 mm long (vs. 5–8 mm long). Sargent (1922) recognized *J. lucayana* Britton as the southern red cedar (coastal and swamps) treating *J. barbadensis* sensu Sargent as a part of *J. lucayana.* This was in spite of the fact that Britton (1908) originally recognized *J. lucayana* for the Bahamas and reserved *J. barbadensis* L. for the junipers of southern Georgia, Florida and the rest of the West Indies (excluding the Bahamas).

In a recent treatment of *Juniperus,* Zanoni (1978) recognized *J. silicicola* as the juniper of the southeastern United States coastal plain river swamps. Little (1971) records the distribution of *J. silicicola* (Map 29-E) as occurring along the eastern coast from North Carolina southward to mid-Florida and westward along the coast to Louisiana, with disjunct populations in Louisiana and Texas (see Fig. 1). Little (1971) shows the disjunct Texas populations ranging from the coast almost to central Texas (Fig. 1).

Hall (1952) refers to the southeastern coastal juniper as the Florida race of *J. virginiana,* having lax, weeping foliage and small fruits (female cones), blending into *J. barbadensis.*

Flake and Turner (1973), using volatile leaf oils, analyzed 24 populations of *J. virginiana* and found 3 major groups: populations east of the Mississippi River to Washington, DC, an Ozark group, and an East Texas group extending to near Bastrop, Texas. They did not find evidence of a Florida race of Hall; however, their southeasternmost populations were in Burlington, North Carolina; Columbia, South Carolina; Macon, Georgia; and Birmingham, Alabama, which are outside of the recorded range of *J. silicicola.*

Silba (1984) recognized *J. silicicola* as a variety of *J. virginiana* [*J. virginiana* var. *silicicola* (Small) Silba] and Murray (1983) recognized *J. silicicola* as a subspecies [*J. virginiana* subsp. *silicicola* (Small) E. Murray]. Neither Silba nor Murray presented any data to support their taxonomic decisions.

In a recent study of the Caribbean junipers (Adams and Hogge, 1983), six taxa appeared distinct in their volatile leaf oils: *J. bermudiana,* endemic to Bermuda; *J. ekmanii,* endemic to Hispaniola; *J. gracilior,* endemic to Hispaniola; *J. lucayana,* from the Bahamas; *J. silicicola,* Oak Hill, Florida (population OF of this report), and *J. virginiana,* collected near Washington, DC.

An additional study (Adams, 1983a), using both morphology and terpenoids, showed *J. silicicola* to be morphologically similar to *J. lucayana* (Bahamas, Jamaica), *J. gracilior* (Dominican Republic), and *J. ekmanii* (Haiti). Chemically, *J. silicicola* was quite distinct from *J. bermudiana, J. ekmanii, J. gracilior* and *J. lucayana* (Adams, 1983a). The most similar taxon to *J. silicicola,* chemically, is *J. virginiana* (Adams and Hogge, 1983) in that these two taxa were only resolved on the 4th principal coordinate axis after the first 3 coordinates had accounted for 80.7% of the variation among the six taxa.

The purposes of the present study were to determine: if coastal populations of *J. silicicola* were distinct in their morphology and volatile leaf oils from inland populations of *J. virginiana*; if intergradation occurred between the taxa; and the patterns of infraspecific variation in this complex. In order to aid in the comparison with the previous study of Flake and Turner (1973), several of the collections were made from the same general vicinity as those locations sampled by Flake and Turner (Washington, DC; Burlington, NC; Columbia, SC; Macon, GA; and Bastrop, TX).

Materials and Methods

Samples consisted of ten to twelve branchlets, 12 to 15 cm long from the following (Fig. 1) populations (acronym, number of plants sampled): *J. virginiana* (DC, 15), Washington, DC, *Adams 2409–2423,* 29 Jan 1977; *J. virginiana* (BN, 19), Burlington-Greensboro, NC, *Adams 2736–2744, 2865–2874,* 30 Mar 1980; *J. virginiana* (CS, 10), Columbia, SC, *Adams 2745–2754,* 29 Mar 1980; *J. virginiana* (MG, 10), Macon, GA, *Adams 2755–2764,* 29 Mar 1980; *J. virginiana* (EA, 10), Evergreen, AL, *Adams 2825–2834,* 7 Apr 1980; *J. virginiana* (BT, 10), Bastrop, TX, *Adams 2845–2854,* 8 Apr 1980; *J. virginiana* (putative *J. silicicola* of Little) (WT, 10), West Columbia, TX, *Adams 2835–2844,* 8 Apr 1980; *J. silicicola* (EN, 10), Emerald Island, NC, *Adams 2726–2735,* 29 Mar 1980; *J. silicicola* (MS, 10), Murells Inlet, SC, *Adams 2716–2725,* 29 Mar 1980; *J. silicicola* (BG, 10), Brunswick, GA, *Adams 2765–2774,* 31 Mar 1980; *J. silicicola* (OF, 10), Oak Hill, FL, *Adams 2775–2784,* 31 Mar 1980; *J. silicicola* (MF, 10), Mullet Key, FL, *Adams 2795–2804,* 5 Apr 1980; *J. silicicola* (SF, 10), St. Mark Wildlife Refuge, FL, *Adams 2805–2814,* 6 Apr 1980; and *J. silicicola* (PF, 10), Pensacola, FL, *Adams 2815–2824,* 6 Apr 1980.

Foliage samples were frozen in a mobile field trailer and transported frozen to the laboratory, where they were kept frozen (−20 C) until morphological vouchers were taken and the balance of the foliage steam distilled to remove the volatile leaf oils (see Adams, 1975 for details). Voucher specimens are on deposit at the Science Research Center (SRCG).

The volatile leaf terpenoids were removed by steam distillation and analyzed by capillary gas-liquid chromatography (see Adams, 1983a, for details). Peak identifications were based on mass spectral-computer searches previously reported for *J. silicicola* and *J. virginiana*

Table 1. SNK multiple range tests for all 15 morphological characters. Any means underlined by a common line are not significantly different (P = 0.05). Those populations traditionally called *J. silicicola* (Little, 1971) are preceded by "s."

Character: Whip leaf glands visible (WGV) (%); F = 1.90, P = 0.03*

Population:	MG	sBG	sMS	sSF	sOF	CS	sMF	BN	sEN	EA	DC	BT	sPF	sWT
Avg. value:	93.0	87.0	86.0	85.0	85.0	84.0	84.0	82.8	82.0	82.0	78.0	75.0	74.0	65.0
SNK Test:														

Character: Whip leaf margin (WLM); F = 2.92, P = 0.001**

Population:	MG	EN	sBG	sMS	sOF	DC	sPF	BN	CS	sMF	EA	sWT	BT	sSF
Avg. value:	1.16	1.10	1.06	1.05	1.02	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SNK Test:														

Character: Scale leaf glands visible (SGV) (%); F = 2.28, P = 0.009**

Population:	BN	sEN	EA	DC	sPF	MG	CS	sSF	sMF	BT	sOF	sBG	sWT	sMS
Avg. value:	87.2	84.0	82.0	80.0	79.0	79.0	78.0	78.0	77.0	74.0	73.0	71.0	65.0	59.0
SNK Test:														

Character: Scale leaf length (SLL) mm; F = 3.30, P = 0.0004**

Population:	BN	DC	sMF	CS	EA	BT	sWT	sMS	sOF	sBG	MG	sSF	sPF	sEN
Avg. value:	1.65	1.63	1.59	1.57	1.55	1.50	1.45	1.44	1.44	1.43	1.43	1.41	1.32	1.24
SNK Test:														

Character: Scale leaf overlap (LOL) mm; F = 4.68, P = 0.00001**

Population:	sBG	CS	BN	EA	sMF	BT	sWT	MG	sOF	DC	PF	sSF	sMS	sEN
Avg. value:	0.25	0.24	0.24	0.23	0.22	0.22	0.22	0.21	0.21	0.20	0.20	0.19	0.16	0.15
SNK Test:														

Character: Branch width (BRW) mm; F = 3.79, P = 0.0001**

Population:	DC	sOF	sPF	sEN	sBG	sMF	SF	MG	sMS	sWT	CS	BN	EA	BT
Avg. value:	0.93	0.92	0.89	0.89	0.89	0.89	0.88	0.88	0.85	0.85	0.84	0.84	0.83	0.80
SNK Test:														

Character: Scale leaf overlap ratio (SOL) ratio; F = 3.78, P = 0.0001**

Population:	sBG	CS	sPF	sWT	BT	BN	MG	EA	sMF	sSF	sOF	DC	sEN	sMS
Avg. value:	0.17	0.16	0.15	0.15	0.15	0.15	0.15	0.15	0.14	0.14	0.14	0.12	0.12	0.12
SNK Test:														

Character: Scale leaf length/Branch width (L/B) ratio; F = 3.96, P = 0.00007**

Population:	BN	EA	BT	CS	sMF	DC	sWT	sMS	MG	sSF	sBG	sOF	sPF	sEN
Avg. value:	1.94	1.89	1.87	1.87	1.80	1.79	1.72	1.70	1.66	1.61	1.61	1.57	1.48	1.44
SNK Test:														

Character: Scale leaf tip shape (SLT); F = 3.69, P = 0.0001**

Population:	BN	DC	EA	sWT	CS	sMF	sSF	sMS	BT	MG	sPF	sOF	sEN	sBG
Avg. value:	1.97	1.96	1.90	1.89	1.88	1.86	1.76	1.76	1.74	1.74	1.74	1.70	1.64	1.60
SNK Test:														

Character: Branching angle of ultimate twigs (BAN) degrees; F = 7.99, P = 1×10^{-7}**

Population:	DC	sMF	CS	EA	sMS	BT	sEN	sPF	sWT	MG	BN	sBG	sOF	sSF
Avg. value:	34.5	34.5	32.4	32.1	31.9	31.6	31.2	31.0	31.0	29.9	29.7	28.5	27.8	26.7
SNK Test:														

Character: Female cone color (FCO); F = 3.02, P = 0.01**
No cones for MF, PF, SF, WT

Population:	sMS	sEN	BN	sOF	DC	MG	EA	sBG	BT	CS
Avg. value:	5.0	4.58	4.54	4.43	4.34	4.34	4.30	4.19	4.15	4.15
SNK Test:										

Character: Bloom on female cones (BLM); F = 14.70, P = 1×10^{-6}**
No cones for MF, PF, SF, WT

Population:	EA	BT	sBG	CS	sOF	MG	BN	sEN	DC	sMS

Table 1. Continued.

Avg. value:	2.70	2.62	2.61	2.45	2.41	1.97	1.58	1.51	1.43	1.0
SNK Test:										

Character: % female cones with 2 lobes vs. 1 (FLB); F = 1.80, P = 0.1 NS
No cones for MF, PF, SF, WT

Population:	BT	sOF	sBG	CS	BN	sMS	MG	EA	sEN	DC
Avg. value:	16.7	4.3	3.3	3.0	0.0	0.0	0.0	0.0	0.0	0.0
SNK Test:										

Character: Female cone diameter (FDI), mm; F = 5.52, P = 0.0003**
No cones for MF, PF, SF, WT

Population:	EA	DC	BT	BN	MG	sOF	sEN	sBG	CS	sMS
Avg. value:	5.23	5.17	5.06	4.97	4.78	4.73	4.34	4.33	4.29	4.19
SNK Test:										

Character: Seeds per female cone (SPF); F = 8.56, P = 0.00006**
No cones for MF, MS, PF, SF, WT

Population:	BG	sOF	BN	CS	DC	sBG	MG	sEN	EA
Avg. value:	2.00	1.60	1.40	1.20	1.18	1.15	1.10	1.08	1.00
SNK Test:									

(Adams and Hogge, 1983). Canonical variate analysis (CVA) was based on Blackrith and Reyment (1971), Cooley and Lohnes (1971) and Pimentel (1979). Due to the program space limitations CVA of the terpenoids was limited to 30 characters using the 30 terpenoids with the largest F ratios in ANOVA among the 14 populations. Contour mapping of canonical variates follows the previous formulation (Adams, 1970, 1983b).

Morphological characters measured were: whip leaf glands visible (WGV) (scored as percent visible at 10×); whip leaf margin (WLM) (20×, 1 = smooth, 2 = small teeth, 3 = large teeth); scale leaf glands visible (SGV) (scored as with WGV); scale leaf length (SLL) (avg. of five measurements in mm); scale leaf overlap (LOL) (average of five measurements in mm); branch width (BRW) (width of terminal leafy twigs, average of five measurements in mm); scale leaf overlap ratio (SOL) (average ratio of LOL/SLL); scale leaf length divided by branch width (L/B) (average of five ratios); scale leaf tip shape (SLT) (1.0 = obtuse, 2.0 = acute, 3.0 = acuminate); branching angle of ultimate twigs (BAN) (average of five measurements each to nearest 5 degrees); female cone color (FCO) (copper-tan = 1.0, copper-red = 2.0, red-pink = 3.0, blue-violet = 4.0, violet-black = 5.0); bloom on female cones (BLM) (none = 1.0, partially covered = 2.0, covered = 3.0); percent of female cones with 2 lobes versus one lobe (ovoid) (FLB) (0 to 100); female cone diameter (FDI) (average of 10 measurements in mm); and number of seeds per female cone (SPF) (average from 10 cones).

Unfortunately, insufficient female cones were found in populations MF, SF, PF and WT, so the five characters derived from the female cones had to be eliminated from the CVA of the morphology.

Results and Discussion

The principal morphological characters used to separate *J. silicicola* and *J. virginiana* have been: scale leaf length (SLL), scale leaf tip shape (SLT), staminate ament length, female cone diameter (FDI) and branch width of the ultimate twigs (BRW). Scale leaf length (SLL) showed a strong tendency to separate the coastal populations from the inland populations (Table 1), although MG (*J. virginiana,* Macon, Georgia) also had short scale leaves and MF (*J. silicicola,* Mullet Key, Florida) had leaf lengths comparable to *J. virginiana.* Scale tip shape (SLT) did not clearly separate the two taxa (Table 1). Female cone diameter (FDI) showed a tendency for the coastal populations to have smaller female cones (Table 1).

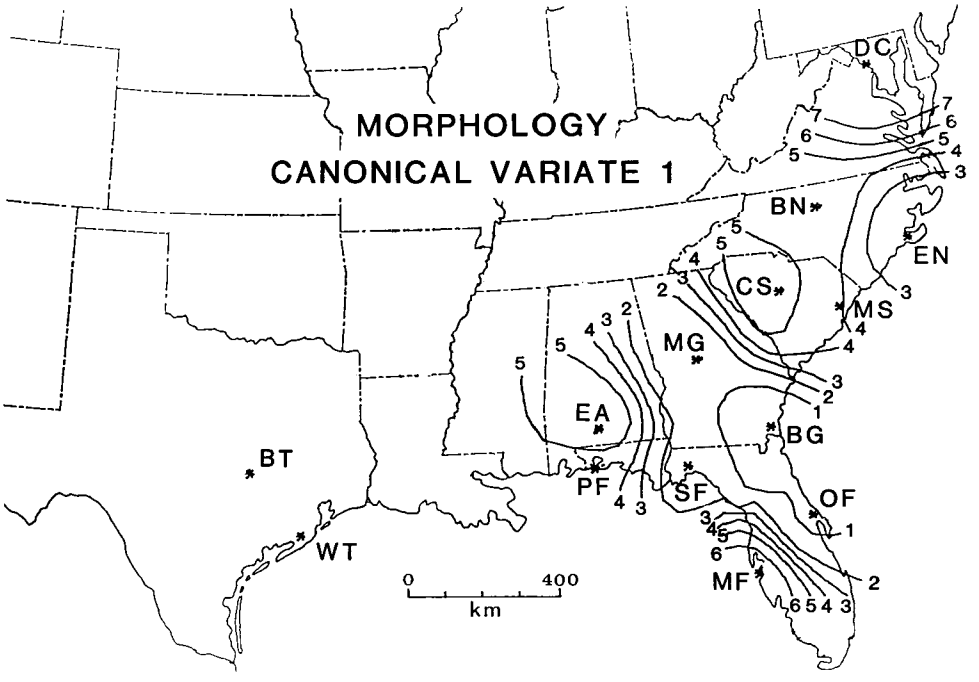

Fig. 2. Contour map of the first canonical variate axis from CVA of 10 morphological characters. Differentiation of the coastal populations EN, MS, BG, OH and SF is shown. Note the similarity of the MG (inland) population to tbe coastal (BG) population and the similarity of the coastal populations, MF and PF to inland *J. virginiana* populations.

although the differences were not significant (P = 0.5) by the SNK test. The values of 3 to 4 mm for *J. silicicola* and 5 to 6 mm for *J. virginiana* could not be verified in this study. The coastal (*J. silicicola*) populations showed a trend toward wider terminal branches, but again no significant differences between taxa (Table 1). Several additional characters were measured, but none resolved the two taxa (Table 1).

To visualize the overall trends, the ten vegetative characters were used in canonical variate analysis (CVA). Unfortunately, the five female cone characters could not be used due to missing data for several populations. The first five eigenroots were highly significant (Bartlet's test of sphericity, Blackrith and Reyment, 1971) and accounted for 32.5, 27.4, 12.3, 8.9 and 6.7% of the variance among the 14 populations (total of 87.7% for the first 5 roots). However, the biological meaning is often lost before the statistical significance (Blackrith and Reyment, 1971). The first canonical variate (Fig. 2) shows the differentiation of coastal populations EN, BG, OF and SF along with MG from the rest of the *virginiana-silicicola* complex. Considerable difference is shown between the coastal populations in Florida (OF, MF, SF, and PF). No differences are seen between the two Texas populations (WT, BT). The second canonical variate revealed (Fig. 3) differentiation between the inland populations (BN, CS) and the coastal populations (EN, MS) as well as differentiation of the DC population. Again, MG (Macon, Georgia) shows sharp differences from adjacent populations. The third canonical variate (Fig. 4) depicts the differentiation of the coastal MS population and minor variations among populations.

In order to gain an overview of the similarities, the first three canonical variates have been plotted on a 3-d ordination (Fig. 5). Several points are obvious from this ordination: coastal populations, previously referred to *J. silicicola,* are not readily resolved from *J.*

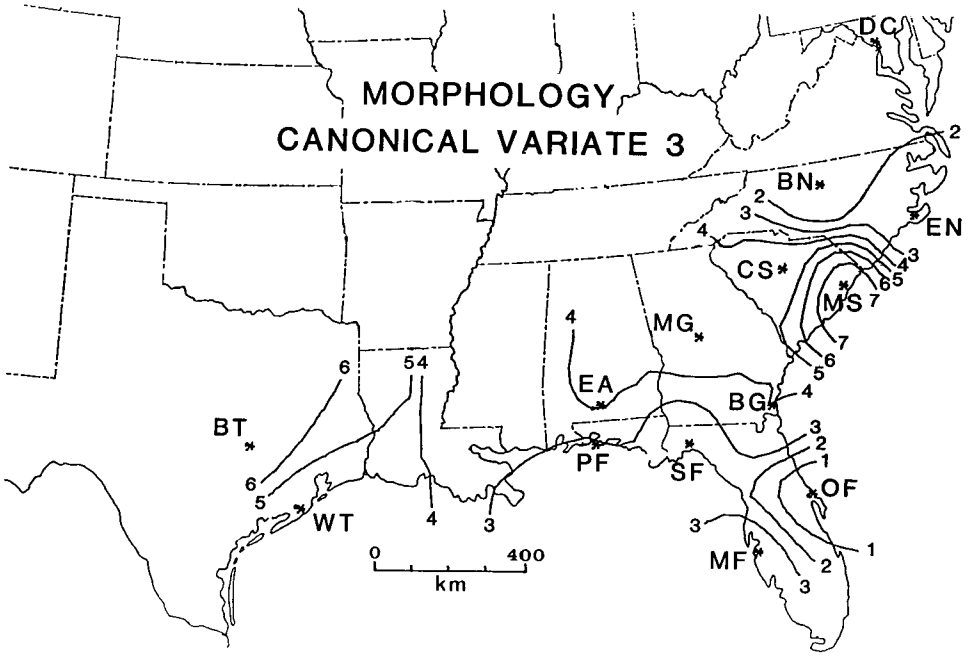

Fig. 3. Canonical variate axis 2, contoured, depicts the differences among the northeastern, coastal populations (EN, MS) and inland populations as well as differences among the inland (*J. virginiana*) populations (DC, BN, CS, MG, EN).

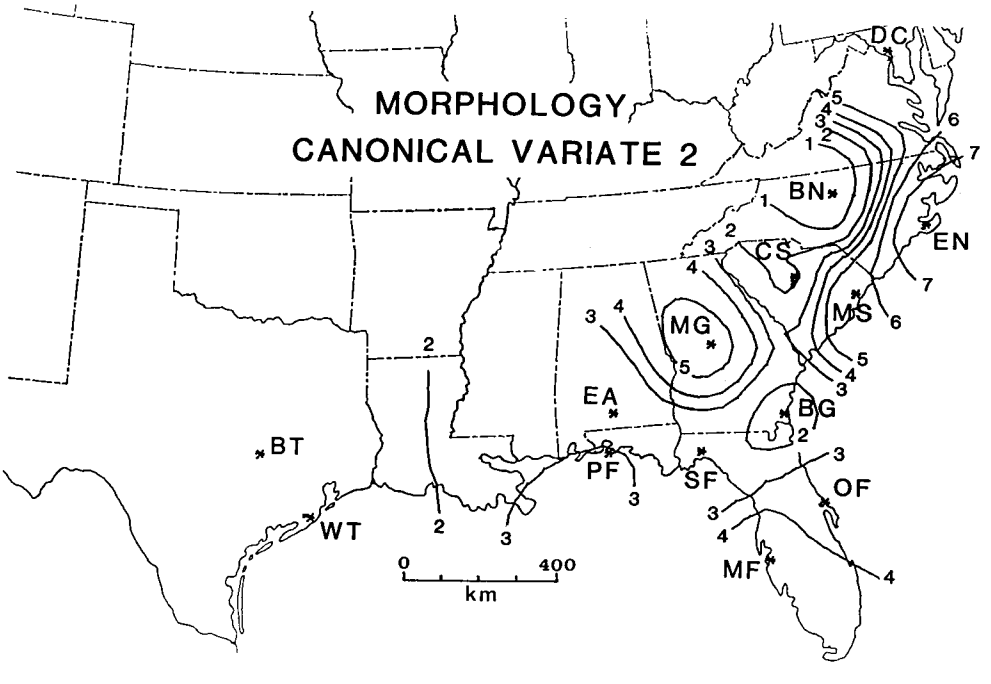

Fig. 4. The third canonical variate presents a northeast (DC) to southwest (BT) cline in the morphology with a variant in the MS population.

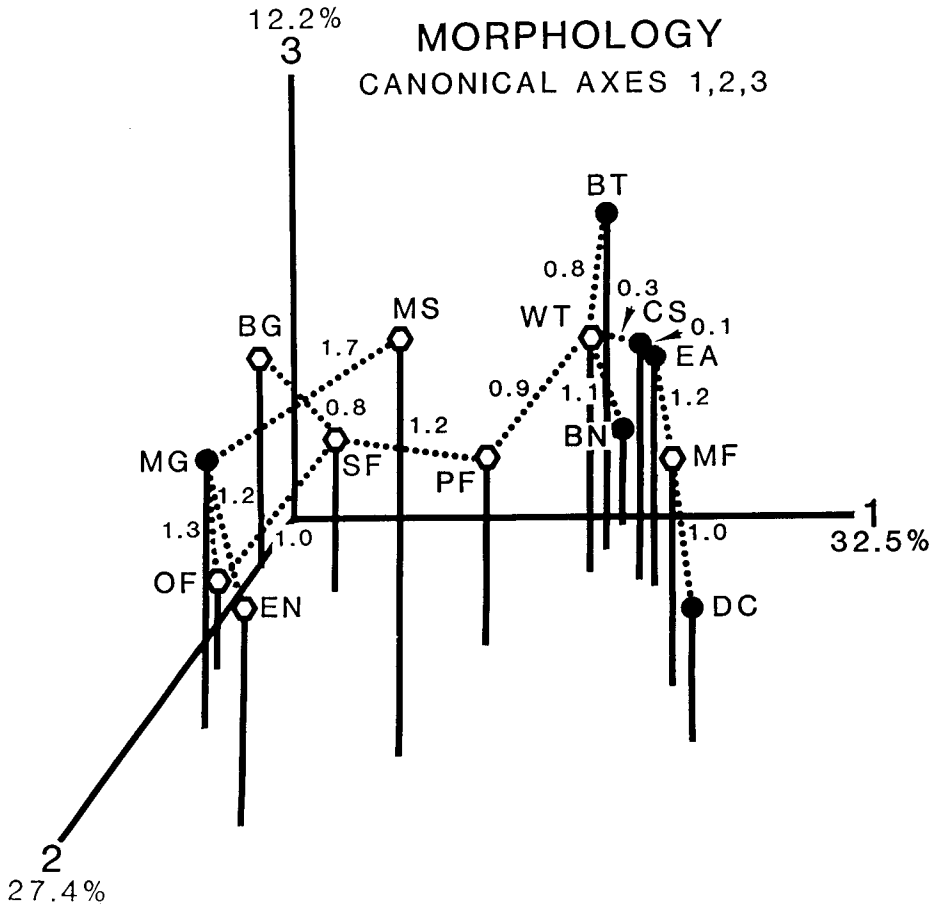

Fig. 5. The overall similarities are shown in a three-dimensional ordination of the populations onto the first three canonical axes. The percentage shown on each axis is the percent of variance. The dotted line is the minimum spanning tree based on euclidian distance using the canonical scores from the first three axes. The solid circles represent inland populations of *J. virginiana* and the open hexagons are coastal populations referred to as *J. silicicola* (Little, 1971). See text for discussion.

virginiana populations; the Macon, Georgia population (MG), clusters closely with coastal (cf. *J. silicicola*) populations; and the Mullet Key, Florida (MF) and West Columbia, Texas (WT) populations cluster closely with *J. virginiana* populations. Obviously, the two taxa are not cleanly separated using these morphological characters, nor are they separated by their female cone characters (see Table 1).

It should be noted that two additional characters were observed in the field: crown shape and bark color. These observations were not quantified but in general, the coastal populations had round to flat-topped crowns among mature trees; whereas inland (*J. virginiana*) mature trees tended to maintain a pyramidal-shaped crown. Interestingly, some of the trees in the Mullet Key, Florida (MF) population were quite columnar as typically seen in fast-growing inland *J. virginiana* trees. Whether the round-flat topped crowns are caused by high winds and salt spray damage or are natural, genetic based characters is not known. Bark color in the coastal populations appeared to be more cinnamon colored as opposed to the brown bark of *J. virginiana* trees. These two characters, if quantified (and genetic based), would tend to separate the coastal populations from the inland populations (with

Table 2. SNK multiple range tests for terpenoids that showed distinct differences among populations. Any means underlined by a common line are not significantly different (P = 0.05). Those populations preceded by an "s" have traditionally been called *J. silicicola* (Little, 1971).

Compound: % yield (% YLD); $F = 16.9$, $P = 0.5 \times 10^{-9}$**														
Population:	CS	BT	sBG	sMS	MG	BN	EA	sOF	sSF	sWT	sPF	sMF	sEN	DC
Avg. value:	0.76	0.72	0.70	0.46	0.46	0.45	0.42	0.40	0.39	0.38	0.35	0.34	0.32	0.21
SNK Test:														
Compound: Tricyclene (TRCY); $F = 31.1$, $P = 0.2 \times 10^{-10}$**														
Population:	sWT	BT	BN	DC	sBG	sMF	EA	CS	sMS	MG	sEN	sSF	sOF	sPF
Avg. value:	0.60	0.52	0.20	0.19	0.16	0.15	0.08	0.04	0.04	0.03	0.03	0.02	0.01	0.01
SNK Test:														
Compound: Sabinene (SBNN); $F = 30.0$, $P = 0.2 \times 10^{-10}$**														
Population:	sWT	BT	DC	sBG	BN	EA	sEN	CS	MG	sMF	sOF	sSF	sPF	sMS
Avg. value:	18.4	17.7	6.72	4.54	4.25	2.41	1.14	1.13	0.97	0.66	0.48	0.47	0.34	0.31
SNK Test:														
Compound: Alpha-terpinene (ATRP); $F = 34.0$, $P = 0.1 \times 10^{-10}$**														
Population:	sWT	BT	DC	BN	sBG	EA	CS	sMF	OF	MG	sEN	sSF	sMS	sPF
Avg. value:	0.97	0.73	0.26	0.24	0.21	0.14	0.10	0.10	0.08	0.08	0.06	0.04	0.04	0.02
SNK Test:														
Compound: Limonene (LMNN); $F = 14.9$, $P = 0.1 \times 10^{-8}$**														
Population:	sMF	sOF	sSF	sEN	EA	BN	sPF	MG	sMS	DC	sBG	CS	sWT	BT
Avg. value:	48.6	33.3	28.8	28.5	27.6	26.3	24.4	24.1	21.8	18.9	18.8	18.1	12.8	3.0
SNK Test:														
Compound: Gamma-terpinene (GTRP); $F = 36.0$, $P = 0.9 \times 10^{-11}$**														
Population:	sWT	BT	DC	BN	sBG	EA	sMF	CS	MG	sOF	sEN	sSF	sMS	sPF
Avg. value:	1.57	1.18	0.45	0.36	0.33	0.21	0.16	0.15	0.12	0.12	0.10	0.09	0.07	0.05
SNK Test:														
Compound: Borneol (BRNL); $F = 4.7$, $P = 0.1 \times 10^{-4}$**														
Population:	DC	BN	sMF	CS	BT	sMS	sEN	sPF	MG	EA	sWT	sSF	sBG	sOF
Avg. value:	0.83	0.34	0.16	0.16	0.10	0.09	0.08	0.05	0.05	0.03	0.02	0.01	0.00	0.00
SNK Test:														
Compound: 4-terpineol (4TRL); $F = 31.4$, $P = 0.2 \times 10^{-10}$**														
Population:	sWT	BT	DC	BN	sBG	EA	CS	sEN	sMF	MG	sOF	sMS	sSF	sPF
Avg. value:	5.08	4.01	1.48	1.30	0.94	0.60	0.45	0.33	0.31	0.30	0.25	0.23	0.18	0.17
SNK Test:														
Compound: Germacrene D (GRMD); $F = 35.5$, $P = 0.9 \times 10^{-11}$**														
Population:	sMF	sPF	sOF	sMS	sSF	sEN	sBG	MG	EA	BN	DC	CS	BT	sWT
Avg. value:	0.96	0.56	0.50	0.40	0.33	0.32	0.31	0.15	0.15	0.11	0.11	0.07	0.05	0.03
SNK Test:														
Compound: Para-menth-1(7),3-diene (PMND); $F = 30.2$, $P = 0.2 \times 10^{-10}$**														
Population:	sWT	BT	DC	BN	sBG	EA	CS	sMF	MG	sEN	sMS	sSF	sPF	sOF
Avg. value:	0.60	0.58	0.39	0.21	0.15	0.09	0.08	0.03	0.03	0.03	0.01	0.00	0.00	0.00
SNK Test:														
Compound: Gamma cadinene (GCDN); $F = 10.7$, $P = 0.1 \times 10^{-7}$**														
Population:	sWT	BT	sEN	BN	sOF	EA	sBG	sSF	MG	sMS	DC	CS	sMF	sPF
Avg. value:	0.96	0.43	0.15	0.12	0.10	0.09	0.08	0.06	0.06	0.04	0.04	0.03	0.02	0.01
SNK Test:														

the exception of West Columbia, Texas, WT, which had light brown bark and roundish crowns not atypical of older *J. virginiana* trees in Texas).

Analyses of the terpenoids from the leaves is shown (Table 2) for several of the compounds that clearly separated populations. The major compounds that separate the Texas popu-

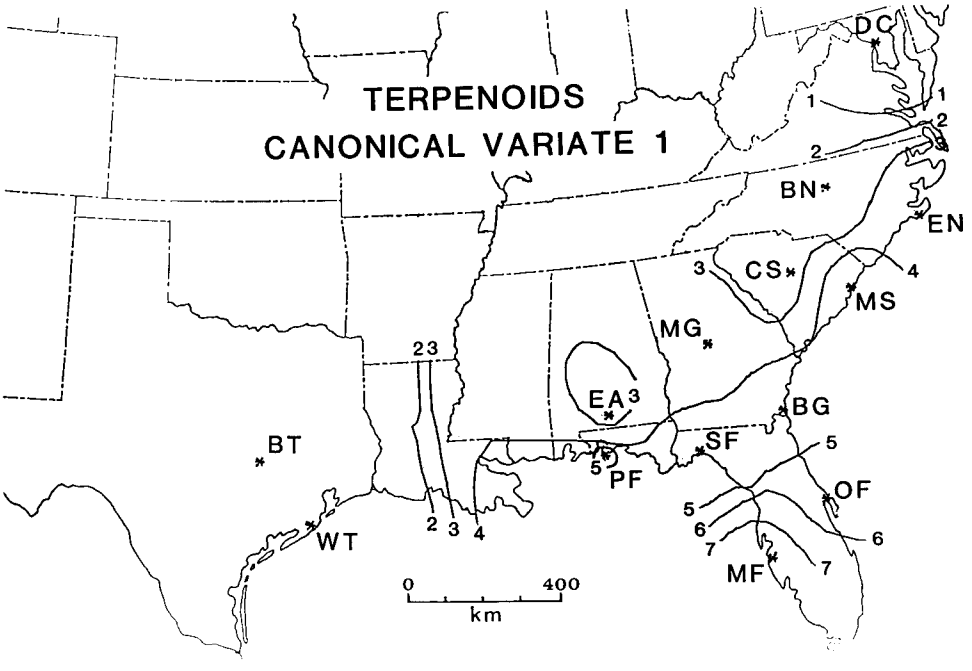

Fig. 6. Contoured canonical variate one for 30 terpenoids. Notice the differentiation of the southeastern coastal populations (EN, MS, BG, OF, MF, SF and PF from inland *J. virginiana* populations. The westernmost populations (BT, WT) show some differentiation from the eastern populations but not between BT and WT.

lations (BT, WT) from the rest of the populations are tricyclene, sabinene, alpha-terpinene, gamma-terpinene, 4-terpineol, paramenth-1(7),3-diene and gamma cadinene. Only germacrene D clearly separates the southeastern coastal populations from the inland populations. Note that the WT (West Columbia, Texas) population is low in germacrene D like the other inland *J. virginiana* populations (Table 2). Several of the other compounds (and of course some not shown) reveal a tendency for the southeastern coastal populations to be separated from the inland populations.

Canonical variate analysis of the terpenoids resulted in nine significant eigenroots. The first five accounted for 37.7, 26.5, 12.2, 7.0 and 4.9% of the variance among populations. The first canonical variate reveals (Fig. 6) a clear differentiation of the southeastern coastal populations (EN, MS, BG, SF, PF, OF and MF) from the inland populations of *J. virginiana.* The Texas populations (BT, WT) are not split but remain similar to the inland (*J. virginiana*) populations (cf. DC, BN, CS).

The second canonical variate presents an east–west trend (Fig. 7) with the Washington, DC (DC) population showing some differentiation, small differences in the southeastern United States populations and a rather sharp differential between the Texas populations and those east of the Mississippi River. This trend is the same one that Flake and Turner (1973) depicted in their fig. 3 (where the population sites sampled in common are: A = DC; B = BN; 8 = CS; 9 = MG; and 14 = BT). The uniformity of populations EA, MG, CS, and BN matches their corresponding pattern exactly. Flake and Turner (1973) showed a slight differentiation of the DC population and considerable differentiation of the Texas populations, just as shown in Fig. 7.

The third canonical variate (Fig. 8) accounted for only 12.2% of the variance among populations and gave a pattern of differentiation of the MF (Mullet Key, Florida) population

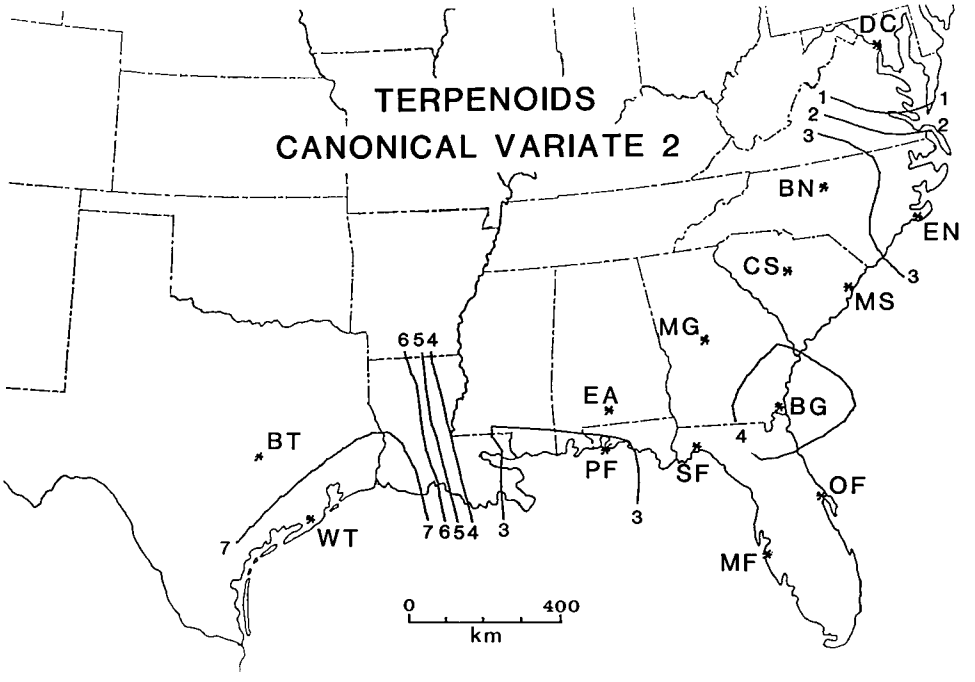

Fig. 7. Canonical variate 2, contoured, presents a northeast–southwest trend with uniformity among the southeastern inland *J. virginiana* populations. This is the same trend that Flake and Turner (1973, fig. 3) found in their terpenoid analysis of *J. virginiana.*

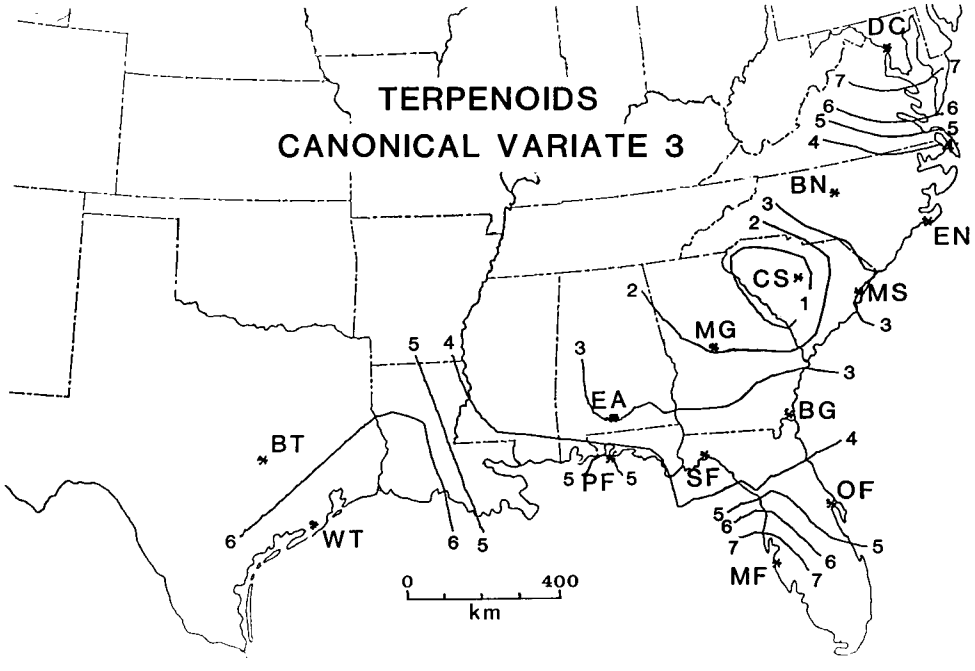

Fig. 8. Contour map of the canonical variate axis 3, terpenoids, depicts the co-differentiation of the MF and DC populations, variation among the inland populations (BN, CS, MG) and additional differentiation of the southwestern populations (BT, WT).

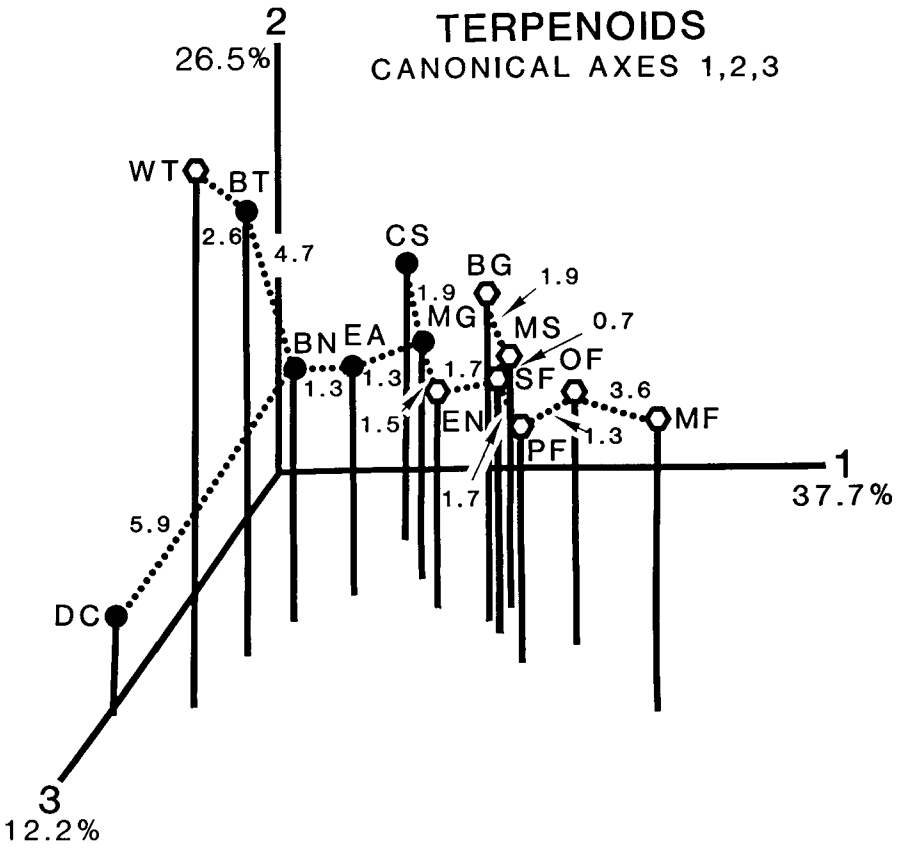

Fig. 9. Ordination of the populations onto the first canonical axes based on CVA of 30 terpenoids. The percentage on each axis is the percent of the variance accounted for that axis. The solid circles denote inland populations of *J. virginiana* and the open hexagons represent the coastal populations referred to as *J. silicicola* (Little, 1971). The dotted line is the minimum spanning tree based on euclidian distances using the canonical score from the first three axes. See text for discussion.

as well as the divergence of the DC population. This trend is similar to the trend obtained from the first canonical variate for the morphology (Fig. 2) except the central inland range of *J. virginiana* is more uniform for the chemical data (Fig. 8).

The overall pattern of relationships is shown in Fig. 9. All of the coastal population (cf. *J. silicicola*) cluster except the West Columbia, Texas (WT) population which clusters with the other Texas population (BT). It should be noted that the West Columbia, Texas (WT) population is not coastal, but in old fields along the Bernard River approximately 44 km from the ocean. This population was called to my attention by the report of their having flat-topped crowns (L. Gilbert, pers. comm.). Since they are in the range of the distribution of *J. silicicola* reported by Little (1971), I included this population in the sample set. It is obvious from the terpenoids (Fig. 9) and morphology (Fig. 5) that the Texas populations (WT, BT) are closely related.

Although the coastal populations (excluding WT) do form a cluster (Fig. 9), there is only a minor gap between the inland *J. virginiana* populations (MG) and the coastal, foredune populations (cf. *J. silicicola,* EN, SF). As previously mentioned, the quantitation of crown shape (if it could be shown to *not* be environmentally induced) and bark color would likely

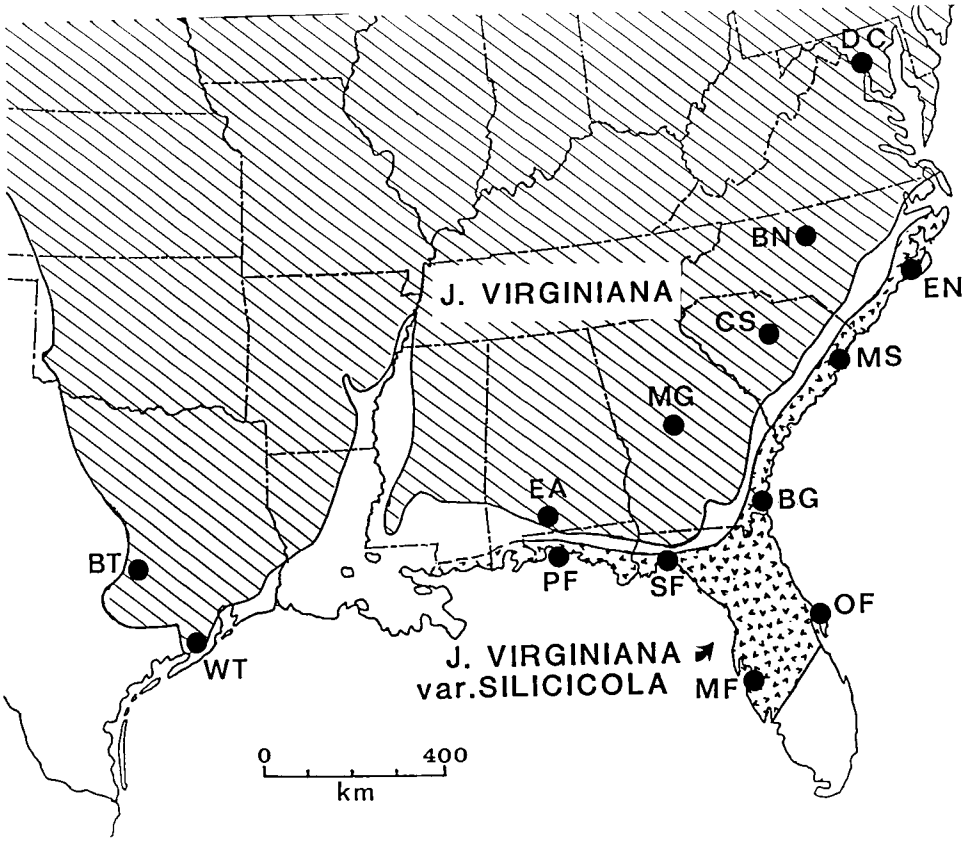

Fig. 10. Revised distributions of *J. virginiana* and *J. virginiana* var. *silicicola,* based on the results from this study. The westward range of *J. virginiana* var. *silicicola* is not precisely known west of PF (Pensacola, Florida). The disjunct populations in Louisiana are most likely *J. virginiana.*

separate the coastal, foredune populations from the inland *J. virginiana* populations. Undoubtedly, the morphological characters historically associated with *J. silicicola* by Small (1913), and by Sargent (1922) in recognizing *J. lucayana* as the southern red cedar (coastal and swamps) imply some level of co-differentiation among coastal (and possibly swamp) populations. One could consider the coastal populations as ecotypes of *J. virginiana.* Their habitat (deep sand and exposure to high wind and salt spray) is certainly unique for *Juniperus* on the North American continent [except for the quite divergent populations of *J. scopulorum* in Puget Sound (Adams, 1983b)]. The edaphic conditions on the foredunes have undoubtedly favored the accumulation of alleles that are physiologically adapted to these conditions. The coastal populations are probably ecotypes of *J. virginiana.* There is no doubt that the coastal juniper populations (*J. silicicola*) in the southeastern United States are very closely related to and derived from *J. virginiana.*

Are these two taxa species? Ownbey (1950) encountered a similar question in *Tragopogon* and listed the following criteria (which I have rephrased as questions): 1. Are the taxa natural groups, characterized by a combination of distinctive morphological features? (and/or chemical features, my addition); 2. Are they reproducing themselves under natural conditions? 3. Is there free gene change between the taxa?

The questionable taxa do appear to be natural groups but they are certainly not well characterized by distinctive morphological (and/or terpenoid) characters. Note that the

differentiation of the Texas (BT, WT) and Washington, DC (DC) populations are greater than that of the coastal *J. silicicola* populations for the terpenoids (Fig. 9). In the previous study of these oils (Adams and Hogge, 1983), six taxa from the Caribbean were compared. The *J. silicicola* samples came from Oak Hill, Florida (OF) and the *J. virginiana* samples came from Washington, DC (DC). Note the difference (Fig. 9) for these two populations (OF, DC). In comparison to *J. bermudiana* (Bermuda), *J. ekmanii* (Haiti), *J. lucayana* (Bahamas), *J. gracilior* (Dominican Republic), we have previously shown (Adams and Hogge, 1983) *J. silicicola* (OF) and *J. virginiana* (DC) to be much more similar to each other than to other taxa from the Caribbean. The two taxa do appear to be reproducing themselves under natural conditions. The question of gene flow cannot be answered from this study except to note the obvious patterns of clinal variation suggestive of introgression.

In striving to recognize taxa at comparable levels of distinctiveness, it appears that these two taxa are not nearly as distinct as the other species of *Juniperus* in the western hemisphere. They differ, principally, by the quantitative amounts of germacrene D. No unique compounds or even large concentration differences are present. The morphological and terpenoid differences are clearly comparable to differences within *J. virginiana* from Washington, DC to Texas.

Should *J. silicicola* be recognized as an infraspecific taxon of *J. virginiana*? Kapadia (1968), among others, has reviewed the three infraspecific categories: subspecies, varietas and formas. He suggested the infraspecific categories be used as a continuation of the principles used in supraspecific classification. Therefore, the subspecies would be a rank between the species and varietas and varietas a rank between subspecies and formas. The rank below a species would be the varietas unless different varietates show patterns of affinities, and then they should be grouped as subspecies. This is the concept I have used in *Juniperus* (also Zanoni, 1978) and appears to be the preferred concept of most present-day North American systematists. Previously I have described and quantified (Adams, 1973) a minor morphological trait that appeared in a few individuals of a population [*J. deppeana* f. *sperryi* (Correll) Adams]. This obviously is not the case for *silicicola-virginiana*. The coastal populations apparently differ from the inland populations by more than a few genes, and these appear to be distributed throughout the populations in all or most of the individuals. Therefore *Juniperus silicicola,* being circumscribed within the range of variation encountered in *J. virginiana* is best treated as a varietas [*J. virginiana* var. *silicicola* (Small) ~~Silba~~]. The populations referred to as *J. silicicola* in Texas (Correll and Johnston, 1970; Little, 1971; and see Fig. 1) are *J. virginiana* and this is reflected in the revised distribution map (Fig. 10). Coastal populations of juniper west of Pensacola, FL (PF) were not located in this study. A tree sampled from the north side of Lake Pontchartrain, Louisiana (*Adams 1642*; 4 July 1976) had low amounts of germacrene D typical of *J. virginiana* and appeared to be, morphologically, more typical of *J. virginiana*. For the aforementioned reasons, the range of *J. virginiana* var. *silicicola* is considered to be along the coast from North Carolina to western Florida and possibly into Mississippi. The disjunct populations of juniper in southern Louisiana and adjacent Texas (Little, 1971) should be considered *J. virginiana* (Fig. 10).

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