

BIOGEOGRAPHY AND EVOLUTION OF THE JUNIPERS OF THE WEST INDIES

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Abstract

The volatile leaf oils of the junipers of the West Indies were examined and comparisons made using principal coordinate analysis and minimum spanning networks. The taxa studied included: *J. barbadensis*, *J. ekmanii*, *J. gracilior*, *J. lucayana*, and *J. saxicola* of the Caribbean as well as *J. bermudiana* from Bermuda and *J. virginiana* var. *silicicola* and var. *virginiana* of the southeastern United States. This is the first report on the composition of the volatile leaf oil of *Juniperus barbadensis* since its recent rediscovery on St. Lucia, BWI. The oil is dominated by limonene (34%) and sabinene (31%) with moderate amounts of α -pinene, 4-terpineol, myrcene, r-terpinene, α -terpinene and terpinolene. Several components normally found only in the heartwood were found in the leaves of this species. *Juniperus barbadensis* has been extinct on Barbados (the type locality) since before 1700 and is now known from only one small population on Petit Piton in St. Lucia, BWI. All of the junipers of the West Indies are in section *Sabina*, series *entire*, and as such are in the North American group related to *J. virginiana*. Examination of the minimum spanning network, based on 70 leaf terpenoids, revealed that the West Indian junipers appear to have arisen from the ancient Appalachian region (*J. virginiana* or its ancestor) and not from the junipers of southern Mexico and Guatemala, which are in series *denticulate* of section *Sabina*. The biogeography of the West Indian junipers supports floristic affinities with the eastern United States rather than affinities with Central America.

Historical treatments of *Juniperus* of the West Indies

Linnaeus (1753) described only three junipers from the New World (*J. virginiana* L., "Virginia and Carolina"; *J. barbadensis*, "America"; and *J. bermudiana*, "America"). However, Hemsley (1883) equated *J. barbadensis* with *J. bermudiana*, adopting *J. bermudiana* as the name for all the junipers of the Caribbean. Sargent (1902) recognized *J. barbadensis* and said it occurred along the Atlantic coast of Georgia and Florida as well as "on the Bahamas, San Domingo (Dominican Republic), mountains of Jamaica and on Antigua." Britton (1908) recognized *J. lucayana* in the Bahamas and reserved *J. barbadensis* for the plants of southern Georgia, Florida and the rest of the Caribbean. Pilger (1913) equated *J. bermudiana* and *J. barbadensis*, but used *J. barbadensis* for the name of

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the common juniper of the Caribbean on the grounds that it was listed first by Linnaeus (1753). Florin (1933) reviewed the junipers of the Caribbean and recognized 5 species: *J. saxicola* Britton and Wilson from Cuba; *J. lucayana* Britton from Cuba, Haiti, Jamaica and the Bahamas; *J. gracilior* Pilger from Haiti and Dominican Republic; *J. ekmanii* Florin from Haiti; and *J. urbaniana* Pilger and Ekman from Haiti. Carabia (1941) recognized *J. barbadensis*, throughout the Caribbean, *J. bermudiana* on Bermuda and *J. virginiana* in the United States. Gillis (1974) treated the Bahamian junipers as *J. bermudiana*. Correll and Correll (1982) recognized the juniper of the Bahamas as *J. barbadensis*. Just from a review of the nomenclatural literature alone, one can sense that the taxa are not very distinct, morphologically.

The recent rediscovery of a small population of *J. barbadensis* at the summit of Petit Piton on St. Lucia, BWI (Adams et al. 1987a) afforded an opportunity to collect fresh foliage and analyze the volatile leaf oils. Although the original populations of *J. barbadensis* on Barbados were apparently cut out before 1700 (Adams et al. 1987a), the rediscovery of the small, relictual population on St. Lucia, only a 150 kilometers from the type locality (Barbados), was very fortuitous. No other natural populations of juniper are known from the lesser Antilles, with the closest natural populations of juniper being *J. ekmanii* in Haiti, *J. gracilior* in the Dominican Republic and *J. lucayana* in Jamaica.

Morphologically all the Caribbean juniper species except *J. bermudiana* and *J. saxicola* are very similar and difficult to distinguish. The variable nature of leaves, even on a single branch, has resulted in confusion in the taxonomy of the junipers of the Caribbean. In fact, it is unlikely that the systematic relationships could ever be determined based solely on morphology. However, the leaf volatile oils have evolved into quite different patterns and the taxa are easy to separate using these chemical data (Adams 1983a; Adams and Hogge 1983; Adams et al. 1987b). In previous studies of the Caribbean junipers, the volatile oil compositions of *Juniperus bermudiana* L., *J. ekmanii* Florin, *J. gracilior* Pilger, *J. lucayana* Britton, *J. saxicola* Britt. & Wils., *J. silicicola* (Small) Bailey and *J. virginiana* L. have been reported and the systematic relationships examined among the taxa (Adams 1983; Adams and Hogge 1983; Adams et al. 1987b). Examination (Adams 1986) of both the volatile leaf oils and morphology of natural populations of *J. virginiana* and *J. silicicola* indicated that these taxa are conspecific and the juniper of the coastal foredunes of the southeastern United States (*J. silicicola*) was therefore treated as a variety of *J. virginiana* L. (i.e., *J. virginiana* var. *silicicola* (Small) E. Murray).

The purposes of this paper are to present the first report on the composition of the volatile leaf oil of *J. barbadensis*, compare its oil with the oils of the other junipers of the West Indies, Bermuda and the southeastern United States to determine if *J. barbadensis* on St. Lucia is conspecific with *J. lucayana* from the Bahamas and Jamaica, and discuss the biogeography and evolution of the junipers of the West Indies, Bermuda and southeastern United States.

Juniper populations examined and status

Figure 1 shows the populations sampled over the past several years. Samples of *Juniperus barbadensis* (BA, Fig. 1) were collected (Adams 5367-5371; Lat. 14° 10' N, Long. 61° 03' W, elev. 730 m, Petit Piton, St. Lucia, BWI). The population consists of approximately 25 trees, all within 30 m of the summit of Petit Piton. The species is

bearing seed and two young trees (ca. 3-6 yrs. old) were found near the top on the west side. No other populations of *J. barbadensis* are known and it must be considered threatened on St. Lucia due to having only one very small population. Nearby islands such as Martinique or Dominica should be reexamined for relictual populations. A visit to Barbados revealed that the habitat has been eliminated (converted to sugar cane fields) over 280 years ago.

Juniperus bermudiana L. (BM, Fig. 1) is endemic to Bermuda. Sometime prior to 1942, two scale insects, *Lepidosaphes newsteadi* and *Carulaspis minima*, were introduced into Bermuda (Bennett and Hughes 1959) from the United States mainland (Groves 1955). These insects infested *J. bermudiana* causing defoliation and death. By 1954, most of the trees of *J. bermudiana* were infected. Biological control was tried with no success. Groves (1955) estimated that 90 percent of the trees were dead by 1955. In 1978, Dr. W. E. Sterner, Director of the Bermuda Biological Station (pers. comm.) estimated that perhaps 99 percent of the original trees had died. The younger trees appear to have some resistance (or perhaps just youthful vigor). The younger trees are now of reproductive age, so perhaps some resistance has developed. The introduction of the resistant *J. virginiana* from the eastern United States into Bermuda should be avoided because the unique germplasm on Bermuda (see below) might be diluted if hybridization occurred with *J. virginiana*.

Juniperus ekmanii Florin (EK, Fig. 1) is endemic to the Morne de la Selle in Haiti. In 1981, only two trees of *J. ekmanii* were found in the Mare Rouge area (Adams 3106, 3107; Mare Rouge, Morne de la Selle, 17 km NE of Seguin, Haiti; Lat. 18° 20' N, Long. 72° 04' W, elev. 1,770 m). Most of this region was logged about 1965. Old stumps of *J. ekmanii* with DBH of up to 2 m are still in the area. Young trees of the species are reported to occur in the Morne la Visite area (Paul Paryski pers. comm.) but their status is threatened by local cutting. *Juniperus ekmanii* must be considered endangered and is most likely headed for extinction before the end of this century.

Juniperus gracilior Pilger (GR, Fig. 1) is endemic to the Dominican Republic and probably Haiti. Collections were made west of Constanza in 1980 (Adams 2785-2794; 14.6 km W of Constanza, Dom. Rep., Lat. 18° 55' N, Long. 70° 50' W, elev. 1,400 m). The species appears to occupy a considerable area west and south of Constanza, Dominican Republic. However the area is heavily utilized and many trees were being cut west of Constanza in 1980. It appears to be the least endangered juniper of Dominican Republic/Haiti at present.

Juniperus lucayana Britton was collected in the Bahama Islands, Cuba and Jamaica. In the Bahamas, *J. lucayana* (LG, Fig. 1) was collected on Great Abaco Island (Adams 2686-2695) where two small populations were found: 5 to 10 trees (55 km south of Marsh Harbour, Lat. 26° 9' N, Long. 77° 12' W, elev. ca. 9 m) on coppice in thick underbrush; and a second site with 15 to 20 trees (5 km N of Hole-in-the-Wall, Lat. 25° 55' N, Long. 77° 14' W, elev. ca. 30 m) on the coppice. On Andros Island (Adams 2696-2705), 15 to 20 trees of *J. lucayana* (LA, Fig. 1) were found scattered in the coppice with pines (5 km S of Andros Town/ Fresh Creek at the junction of the main road and airport road, Lat. 24° 39' N, Long. 77° 48' W, elev. ca. 30 m). On Grand Bahama Island (Adams 2706-2715), 20 to 30 trees of *J. lucayana* (LB, Fig. 1) were found on coppice (23 km W of Freeport and thence 3 km N, Lat. 26° 38' N, Long. 78° 55' W, elev. ca. 3 m). These trees have the

crowns flattened (from wind damage?) and a considerable number of dead branchlet tips. Many dead and partially dead trees were in the area.

With the current travel restrictions in Cuba, it is difficult to assess the status of juniper populations. On a visit in 1985, the author talked with Dr. Antonio Lopez Almirall, who felt that *Juniperus lucayana* has now been largely cut out except in the Sierra de Nipe region, Holquin Province (this region was previously a part of the Oriente Province). All the recent specimens of *J. lucayana* from the mainland of Cuba were examined at the Jardine Botanico Nacional de Cuba (HAJB!). These were found to be from the mountainous region in eastern Cuba (J. Bisse 15775, April 1980, 700-1,000 m, Prov. Holquin, Lat. 20° 29' N, Long. 79° 48' W, HAJB!; J. Bisse, Mayer, Bassler, Alvarez & Gutierrez 35818, Oct. 1972, Loma de Mensura, Prov. Holquin, HAJB! and J. Bisse and Lippold 10222, Oct. 1968, 500-600 m, Pinar de Monte Cristi Sobre, Prov. Guantanamo, Lat. 20° 20' N, Long. Guantanamo, Lat. 20° 20' N, Long. 75° 10' W, HAJB!). Fortunately, samples (Adams 5259-5280) could be obtained two trees of *J. lucayana* are still growing at the Havana Botanical Garden. These trees came from seed collected by J. T. Roig sometime before 1960 from the Cuban mainland (possibly Sierra de Nipe?).

Juniperus lucayana is also found in the swamps in the south-central portion of the Isle of Pines (= Isla de Pinos, = Isla de la Juventud). Dr. Lopez said these populations appear to be stable and not threatened by wood harvesting, etc. A number of trees (15 to 20) of *J. lucayana* have been raised from seed collected from the Isle of Pines and these have been growing at the National Botanical Garden (Jardine Botanico Nacional de Cuba) near Habana since 1977. The female trees are producing female cones that are blue-black, and noticeably flattened. Samples from 2 trees were collected (Adams 5281-5282).

Juniperus lucayana (LJ, Fig. 1) was also collected from Jamaica (Adams 2875-2884), 15 to 20 trees were seen (ridge at the Forestry nursery at Clydesdale and along the road to Hardware Gap, Blue Mtns., Lat. 18° 14' N, Long. 76° 41' W, elev. 1,100 to 1,200 m, St. Andrews Parrish, Jamaica). These trees were very scattered in the forest and their occurrence at high elevations differs greatly from the situation in the Bahamas. Their habitat would seem to be more similar to that of the Sierra de Nipe in eastern Cuba (see above). The plants appeared to be reproducing themselves but the selection of juniper wood to produce tourist souvenirs could easily eliminate *J. lucayana* from Jamaica.

Juniperus saxicola Britt. & Wils. (SX, Fig. 1) is endemic to Cuba where it is only known from the Pico Turquino region at 1,200 to 1,700 m. The species has apparently been fixed by neoteny in the juvenile-leaved growth stage, because even the adult, reproductive individuals have only juvenile leaves (an awn-shaped blade which diverges from the stem at 45 to 60 degrees and a sheath portion that clasps the stem). Normally, in section *Sabina*, only young (up to 4 or 5 years old) junipers have the awn-shaped leaves. The scale (adult) leaves are then produced throughout the life span, except juvenile (awn like) leaves are produced at the tips of branches during a rapid growth period. During the past 20 years the author has examined thousands of junipers in the field and 3 or 4 plants have been found that have juvenile foliage on otherwise mature trees. All the specimens examined of *J. saxicola* have awn-like leaves and no other juniper species have been found from the Pico Turquino region. Thus, it appears that this small region has a reproductive population in which the juvenile leaf gene(s) have become fixed. Pico Turquino is quite isolated from major urban areas and is also somewhat protected by the

government as a memorial because this is the region that Fidel Castro used as a sanctuary in the revolution. However, branches and berries (female cones) are currently being harvested for medicinal use so the endemic population should be considered as possibly threatened. Due to the short amount of time for field work only two trees of *J. saxicola* were sampled (Adams 5284,5285; west slope of Pico Turquino, Lat. 20° 1" N, Long. 76° 51" W, ca. 1,200 m & ca. 1,550 m, Prov. Granma/ Santiago de Cuba boundary, Cuba). No estimate of the population size could be made due to the dense forest growth.

Juniperus virginiana and var. *silicicola* were sampled near Washington, D.C. (Adams 2409-2423; 16 km E of Dulles Airport on I495, Fairfax Co., VA) and Oak Hill, Florida (Adams 2775-2784; 1.6 km E of the jct. of US highway 1 and E. Halifax St, Oak Hill, Volusia Co., FL). *Juniperus virginiana* L., the eastern red cedar, is rapidly increasing the density of plants within its range in the eastern United States by the invasion of old fields. *Juniperus virginiana* var. *silicicola* (Small) E. Murray is confined to coastal fore-dunes and sandy areas near the coast in the southeastern United States. It appears to be stable in population sizes but the populations often consist of only a few hundred trees (or less).

Two additional populations of *Juniperus* were sampled. Examination of Ekman's *J. lucayana* specimens at the Agricultural College, Damien, Haiti (Ekman 3258,3643) revealed that those specimens are similar to *J. lucayana* from the Bahamas. Field trips to St. Michael de l'Attalaye and Bassin Blue have been unsuccessful in locating any naturally occurring, extant trees. The area has been thoroughly cut-over since 1965. Two collections were made near St. Michael. Both are cultivated plants transplanted from the surrounding region about 1965. The first site (NH) is at an abandoned monastery and the second site was in a church courtyard at Ennery. The plants at the church at Ennery were reported to have been obtained about 4 km east of Ennery. Since these plants appeared to have affinities to *J. gracilior* (Adams 1983), this population (NH) is included in this analysis (Adams 2676-2685; 12 km N of Ennery on route 100, at the summit, Lat. 19° 33" N, Long. 72° 28" W, elev. 950 m, Dept. de L'Artibonite, Haiti). As far as is known these junipers exist in only two cultivated locations at present.

A second population of junipers, referred to me by Dr. Tom Zanoni of the Jardine Botanico Nacional of Santo Domingo, is in the Isla de Pelempito region of the Dominican Republic. Samples were collected (Adams 3097-3106; 4 km N of northernmost Alcoa bauxite mine, Lat. 18° 10" N, Long. 71° 36" W, elev. 1,000 to 1,200 m, Pedernales Prov., Dominican Republic). Only 9 live trees and 12 dead trees were found. The area is heavily burned by man-made fires which presents considerable danger to this population. The junipers are found on coppice with eroded limestone at the edge of the pine forests. This population, with affinities to *J. gracilior* and *J. lucayana* (Adams 1983), is referred to in this analysis as PL.

Unfortunately, several unsuccessful attempts have been made to collect *J. urbaniana* Pilger & Ekman, a spreading shrub from near the summit of Pic la Selle, Haiti. The population is apparently restricted to a very small area but still viable in 1984 (Walter Judd pers. comm.). Due to the close similarity in the morphology of *J. ekmanii* and *J. urbaniana*, it would seem likely that they are sibling species. Surprisingly, the very small population of *J. urbaniana* may be the least endangered of any of the junipers in Haiti or Dominican Republic. The site is very inaccessible and above sources of water. The plants are not trees and therefore of no importance for timber or fence posts.

Herbarium vouchers for all of the aforementioned collections are deposited at BAYLU!

Extraction of volatile leaf oils

The volatile leaf oils were extracted by steam distillation of approximately 200 g of foliage for 2 h (Adams 1975a). The oils were concentrated with nitrogen, tightly sealed in glass vials with foil-lined caps and stored at -20° C until analyzed.

Identification of oil components

Mass spectra were recorded with a Finnigan Ion Trap (ITD) mass spectrometer model 700 directly coupled to a Varian 6500 gas chromatograph, using J & W DB5, 0.25 mm x 60 m, 0.25 micron coating thickness, and J & W DB1, 0.25 mm x 30 m, 0.25 micron coating thickness, fused quartz capillary columns. The GC/ITD was operated under the following conditions: Injector temperature: 180°C; temperature programmed for DB1: 60 - 96°C @ 2°/min; 96 - 156°C @ 3°/min; 156 - 230 C @ 6°/min; for DB5: 60 - 240 C @ 3°/min. Carrier gas using DB5 column: He @ 22.9 cm/sec (60°C), 19.1 cm/sec (220°C); using DB1 column: He @ 53.6 cm/sec (60°C), 44.7 cm/sec (220°C), 0.1 ul (20% soln), split 1:50. Tuning values for the ITD were 40, 48, 85, 95 using cedrol as a tuning standard. Cedrol is well-suited for tuning the ITD because its mass spectrum is very sensitive to changes in tuning values. N-octane, n-eicosane and hexadecyl acetate were added as internal standards.

Quantification was made by FID using a DB1 column (see above) in a Varian 6500 gas chromatograph with He as the carrier gas with an average linear velocity of 30 cm/sec (60°C); 25 cm/sec (220°C), 0.1 ul (20% soln.), split 1:30, temperatures as above, except the FID @ 240°C. Identifications were made by comparisons of the mass spectrum of each component in the oils with those of the known terpenes and by searches of spectra from the Finnigan library based on the National Bureau of Standards (NBS) data. Relative retention times (RRT hexadecyl acetate = 1.00) were also compared with the RRT of known terpenoids run under the same conditions. Peak areas were quantitated using a Columbia Scientific Industries Supergrator-2 electronic digital integrator.

Numerical analyses

The chemical data were coded and analyzed by one-way analysis of variance (ANOVA) with 15 treatments (14 df). Compounds that were never larger than a trace (0.5% of the total oil) in the average of any taxon and those with F ratios less than 1.0 were eliminated from use in computing similarity measures. Thus, the initial set of 150 chemical characters was pared to 70 compounds that had F ratios greater than 1.0 and occurred with an average amount greater than 0.5 percent of the total oil in at least one taxon. These 70 compounds (denoted by an asterisk in Table 1) were then used for canonical variate analysis (CVA) and to compute similarity measures among the 15 taxa. The similarity measure used was the Manhattan metric, scaled by the range (= Gower metric, Gower 1971) and weighted by F-1 (from ANOVA) as formulated by Adams (1975b; 1982). Principal coordinate analysis followed the formulation of Gower (1966). Canonical variate analysis followed the formulation of Blackrith and Reyment (1971), Cooley and Lohnes (1971) and Pimentel (1979).

Volatile oil composition of *Juniperus barbadensis*

The compositions of the steam volatile leaf oils from *J. barbadensis* and related species are shown in Table 1. The oil of *J. barbadensis* is pale yellow and yields were 0.6 percent dry wt. (2 hr.) and 2.0 percent (24 hr). *Juniperus barbadensis* leaf oil is dominated by limonene (34%) and sabinene (31%), with moderate amounts of α -pinene, myrcene, α -terpinene, r-terpinene, terpinolene and 4-terpineol. Particularly surprising is the presence of several sesquiterpenoids that have previously been found almost exclusively in the juniper wood oils (cuparene, widdrol, cedrol). The leaf oil of *J. barbadensis* does share a profile somewhat similar to that of *J. lucayana* (LB, LJ, Table 1) in that these taxa contain large amounts of limonene with generally small amounts of sesquiterpenoids. One new unknown (#11), greater than a trace, was found in the oil. Unknown 11, RRT = 1.099, (m/z [%]) MW 272, 131(100), 187(73), 243(40), 43(30), 145(19), 253(13), 188(13), 91(10), a diterpene. All of the other unknown compounds in Table 1 have been previously discussed (Adams and Hogge 1983, Adams et al. 1987b).

Patterns among the junipers of the West Indies

In order to assess the relationships among the junipers of the West Indies, weighted Gower metric similarities were computed among the 15 OTUs using F-1 weighing (F ratio from ANOVA). The resulting similarity matrix was then factored using principal coordinate analysis (PCOOR). First 10 eigenroots (coordinates) accounted for 22.7, 16.3, 9.0, 8.3, 7.8, 6.8, 6.5, 5.1, 4.7 and 4.0 percent (total of 91.4%) of the variation among the 15 OTUs. The first coordinate (22.7%) separates the junipers of Hispaniola (EK, GR, NH, PL) from all the other taxa in the study (Fig. 2). The second coordinate (16%) separates the two varieties of *J. virginiana* (VG, VS) from all the other taxa (Fig. 2). The third coordinate (9%) separates *J. bermudiana* (BM) from the other taxa and also separates the two populations, NH and PL, from *J. ekmanii* (EK) and *J. gracilior* (GR), see Fig. 2. The minimum spanning network that is superimposed (Fig. 2) is based on the distances using the first 10 eigenroots and thus is useful in sensing the distortion of viewing these 15 OTUs in a 3-dimensional projection (see discussion below).

Figure 3 depicts the effects from coordinates 4 and 5. Coordinate 4 (8%) clearly separates *J. saxicola* (SX) from the other taxa (Fig. 3). Coordinate 5 (8%) serves to further separate *J. saxicola* (SX) but it also separates *J. ekmanii* (EK) and *J. gracilior* (GR) from the northern Haiti (NH) and the Pelempito (PL) populations (Fig. 3). Coordinate 6 (7%) appears to further separate the Hispaniola populations, but particularly resolves *J. barbadensis* (BA) from the other taxa (Fig. 4). *Juniperus barbadensis* is further resolved (Fig. 4) on coordinate axis 7 (7%). Coordinates 8, 9, and 10 only accounted for 5.1, 4.7, and 4.0 percent of the variation and only minor separations between the taxa were present.

Variation within *Juniperus lucayana*

Due to the close similarities among the populations of *J. lucayana* (Figs. 2-4), additional analyses were made using the 6 populations of *J. lucayana* (LA, LB, LC, LG, LJ, LP) in ANOVA. Forty compounds were found with F ratios greater than 1.0 and a population average greater than 0.5 percent of the total oil. Similarities were calculated as above and principal coordinate analysis performed on the similarity matrix. Principal

coordinate analysis resulted in 5 eigenroots that accounted for 43.4, 23.8, 14.1, 12.7, and 5.9 percent of the variation (total of 100%) among the 6 taxa.

The first coordinate accounted for the major trend among the populations (43%) by separating the Cuban junipers (LC, LP) from the other populations (Fig. 5). The second coordinate (24%) was due to the differentiation of the Jamaica population (LJ) from the other population (Fig. 5). The third coordinate (14%) revealed minor differences between the Cuban populations (LC, LP; Fig. 5) as well as small differences among the populations from the Bahama Islands (LA, LB, LG; Fig. 5). Coordinates 4 (12.7%) revealed additional differentiation of the Isle of Pines population (LP) from the other populations. Coordinate 5 (5.9%) was due to a minor separation between the Grand Bahama (LB) and Great Abaco (LG) populations. The overall minimum spanning network (based on the combined distance along all 5 coordinate axes) is shown in Fig. 5. This analysis revealed only a minor shift of LA (Andros Island) to link with LG (Great Abaco) instead of with LB (Grand Bahama Island) [cf. Figs. 5 and 2].

It might be noted that canonical variate analysis (CVA) was also performed using the same 70 compounds (by 15 taxa) as analyzed by principal coordinates (see above). The first 10 canonical variates accounted for 31.39, 25.36, 9.76, 8.91, 7.56, 5.28, 4.14, 3.36, 2.22, and 0.71 percent (total of 96.69%) of the variation among the 15 OTUs. All 10 canonical variates were highly significant from zero (Bartlett's test of sphericity). The results from CVA were similar to PCOOR except the taxa were not as well resolved on individual axes. The minimum spanning network derived from distances on canonical axes was not as amenable to interpretation in view of the geological facts (see discussion below). Pimentel, in his discussion of canonical variate analysis (1979:222), states "...the best criterion for any decision is that it makes good biological sense." Thus, in the case of the junipers of the Caribbean, it appears that canonical variate analysis at the species level was not as useful as F-weighted, principal coordinate analysis. The removing of correlation between variables in CVA appears to obscure some of the relationships among the taxa. It appears that the patterns of correlation among the original variables (terpenoids in this case) are very important in defining relationships between taxa (see examples in *Juniperus* and sunfish, Adams 1982). A second problem is that CVA's assumption of equal sample sizes and equal variances are not met and may seldom be met when sampling natural populations. For example, only two mature trees of *J. ekmanii* (endemic to Haiti) are known to exist; therefore, obtaining an adequate sample set was not possible.

Minimum spanning network analyses

The minimum spanning network based on the distances on the first 10 principal coordinates using 70 terpenoids, is shown in Fig. 6. Note the central nature of *J. lucayana* populations (LA, LB, LC, LG, LJ, LP) in the network. The junipers appear to be divided into 6 groups: *J. barbadensis*, BA; *J. bermudiana*, BM; the Hispaniolan junipers, EK, GR, NH, PL; the *J. lucayana* junipers, LA, LB, LC, LB, LJ, LP; *J. saxicola*, SX; and the eastern United States junipers, VG, VS. *Juniperus virginiana* var. *virginiana* (VG) is linked to the West Indian junipers through *J. lucayana* from Andros Island (LA, 82.9). However, notice that var. *silicicola* (VS, dashed line in Fig. 6) is almost equally linked to *J. lucayana* from Grand Bahama Island (83.4, Fig. 6). *Juniperus saxicola* is linked through *J. lucayana* (LP, 74.4) from the Isle of Pines but the next shortest link is with *J. lucayana* from Grand Bahama Island (LB, 75.1, link not shown). The linkage of the Hispaniola junipers is

through the Pelempito population (PL) to either the Isle of Pines (LP, 72.3, Fig. 6) or the Cuba mainland (LC, 72.5, Fig. 6, dashed line).

Superimposition of the minimum spanning network onto the geographical map of the populations sampled is shown in Fig. 7 (one should bear in mind that the origin of LC [*J. lucayana* from the Havana Botanical Garden] cannot be precisely located and may well have come from eastern Cuba). One is immediately impressed with the great distances that separate *J. barbadensis* from the nearest extant junipers (over 1,200 km) and *J. bermudiana* from the Bahamas (1400 km). A second important feature is the degree of divergence among the populations of juniper in Hispaniola (note distances of 61 [EK-NH] and [EK-GR]). There is a definite north-south tendency in the network which may reflect bird migration patterns. Juniper seeds are very effectively transported by birds (Livingston 1972; McAtee 1947; Phillips 1910; Poddar and Lederer 1982). Several birds commonly feed on juniper berries (i.e. female cones) such as cedar waxwings, crows, bluebirds, robins, and starlings (Livingston 1972; McAtee 1947; Phillips 1910; Poddar and Lederer 1982). These and other birds' migration pathways need to be further examined.

Speciation of *Juniperus* into the West Indies

The genus *Juniperus* is divided into 3 sections: *Caryocedrus*, *Oxycedrus* and *Sabina* (Gausson 1968). The junipers of the Western Hemisphere are found in two sections: section *Oxycedrus* with only one circumboreal species, *J. communis* in North America; and section *Sabina* with 38 taxa in North America (Zanoni 1978). The section *Sabina* has been divided into 2 informal series (Gausson 1968) based on the leaf margins: entire and denticulate (at 40x magnification). The series denticulate likely originated in the highlands of Mexico as a part of the Madro-Tertiary geoflora and radiated out into the arid and semi-arid regions of the southwestern United States and throughout the highlands of Mexico as far south as northern Guatemala (Fig. 8). The southernmost species in the continental North America (*J. comitana* Martinez, *J. gamboana* Martinez, *J. standleyi* Steyermark) are now found in the highlands of Chiapas, Mexico and Guatemala (Fig. 8) at elevations ranging from 1,300 to over 3,000 m (Zanoni and Adams 1979, Adams et al. 1985). These species are all in the denticulate group (or series) and appear to have been part of the radiation and adaptation from the ancestral denticulate junipers (Fig. 8). The series entire is composed of *J. blancoi* Martinez, *J. horizontalis* Moench, *J. scopulorum* and *J. virginiana* (and var. *silicicola*) on the continental North America as well as all the taxa in the West Indies and Bermuda (Fig. 8). The series entire on continental North America appears to have arisen from *J. virginiana* (or its ancestor) from the ancient land mass of Appalachia (Anderson 1953, Flake et al. 1969). Elements of the eastern North American flora are thought to be closely related to the Old World (Fernald 1931) and this is certainly true between *J. virginiana* of the eastern United States and *J. sabina* of southern Europe.

Juniperus scopulorum, a sibling species of *J. virginiana*, has been treated as a variety (*J. virginiana* var. *scopulorum* [Sarg.] Lemmon, Handb. West-Amer. Cone Bearers ed. 4, 114, 1900; *J. virginiana* var. *montana* Vasey, Rep. U. S. Commiss. Agric. 1875, 184, 1876; Zanoni 1978). Several studies have confirmed hybridization between these taxa (Fassett 1944; Van Haverbeke 1968; Schurtz 1971; von Rudloff 1975; Flake, von Rudloff, and Turner 1978; Adams 1983b; Comer, Adams and Van Haverbeke 1982). *Juniperus scopu-*

lorum is postulated (Adams 1983b) to have arisen from *J. virginiana* (Fig. 8). *Juniperus horizontalis* is closely related to both *J. scopulorum* and *J. virginiana* and has been treated as a variety, *J. virginiana* var. *prostrata* (Persoon) Torrey (Fl. New York 2, 235, 1843). *Juniperus horizontalis* hybridizes in several areas with *J. virginiana* (Fassett 1945a,b; Schurtz 1971; Palma-Otal et al. 1983). *Juniperus horizontalis* also hybridizes with *J. scopulorum* (Fassett 1945c; Schurtz 1971; von Rudloff 1975; Adams 1983b). *Juniperus horizontalis* is postulated to have been derived from *J. virginiana* or its ancestor (Fig. 8). *Juniperus blancoi* is very closely related to *J. scopulorum* (Adams 1983b) and is confined to a few locations in central and northern Mexico along flowing streams. It is postulated to have been derived from *J. scopulorum* (in fact it may be conspecific, see Adams 1983b). The only other member of series entire is *J. virginiana* var. *silicicola* which is barely distinct from *J. virginiana* (Adams 1986) and may have been derived as recently as the Pleistocene (Fig. 8).

Speciation of *Juniperus* into the West Indies is postulated to have occurred by long distance dispersal of *J. virginiana* (or its ancestor) by birds to the Bahama Islands and then to Bermuda, Cuba, Jamaica, and Hispaniola. *Juniperus saxicola* most likely evolved from a *J. lucayana* ancestor in eastern Cuba from seeds carried into the Pico Turquino region. Either by a chance founder's effect or by genetic drift, the gene(s) for controlling the conversion from juvenile (awn-like) to adult (scale-like) leaves become fixed such that all adults now have only juvenile leaves. *Juniperus barbadensis* appears to have arisen from *J. lucayana*, possibly from Cuba. The large distance from Cuba to St. Lucia and the lesser Antilles render this postulate somewhat tentative. The alternative mode, island hopping from Hispaniola is less attractive because suitable habitat would seem unlikely on many of the intervening islands.

The situation in Hispaniola is still far from resolved, except to say that *J. lucayana* appears to have been involved in colonization. *Juniperus ekmanii* and *J. gracilior* probably were derived from a *J. lucayana*-like ancestor. *Juniperus urbaniana*, although not sampled in this study, would appear to be very closely related to *J. ekmanii* and probably arose from *J. ekmanii* or its ancestor. Additional studies (in progress) may resolve the apparent diversity in Hispaniola.

The introduction of *J. bermudiana* to Bermuda must have been relatively recent as Bermuda's soil was only formed during the first interglacial period of the Pleistocene (1 million yBP; Sayles 1931; Bryan and Cady 1934; Cox 1959). Considering the genetic bottleneck that the Bermuda junipers have gone through in their current fight for survival, we cannot be sure that extant trees fairly represent the gene pool that evolved on Bermuda. This may account in part, for the divergence of *J. bermudiana* from the Bahama junipers.

Significance to floristic affinities of the West Indies

This study of the Caribbean junipers may shed some light on the origin of the vegetation of the Caribbean Islands. Howard (1973) suggests that the major vegetation affinities of the Antilles lie with Central America and then to the northern part of South America. Rosen (1975) came to a similar conclusion based primarily on fresh water fish distributions. He even postulated that continental drift accounts for the affinities by proposing that the Caribbean islands are part of the Pacific plate, which pushed its way between North and South America, northeasterly to its present position. This would have

allowed contact between the proto-Antilles land mass and the southern Mexico-Guatemala (to the north) and the South American land mass (to the south). Thus, according to Rosen, the flora and fauna from Central America and South America could have easily transferred to the proto-Antilles land mass and rode the drift to the present position in the Caribbean.

However, Khudoley and Meyerhoff (1973) were firmly opposed to the idea of continental drift in explaining the origin of the Antilles. Interestingly though, they (Khudoley and Meyerhoff 1973) state "Faunal and floral similarities between Central America and the Greater Antilles suggest that direct land connections existed, perhaps via western Cuba or via the Cayman Ridge and Nicaragua Rise." It should be also be noted however, that Khudoley and Meyerhoff (1973) are diametrically opposed on the origin of the Antilles with Khudoley believing that "the area of the present Caribbean Seas was a land mass until Cretaceous time", and Meyerhoff believing that "the whole of the Greater Antilles was a late Jurassic through early Tertiary island arc...". If Rosen (1975) or Khudoley (Khudoley and Meyerhoff 1973) are correct then the land mass has been large and contiguous for a long time whereas if Meyerhoff (Khudoley and Meyerhoff 1973) is correct, one would expect to find more endemic species on the various islands.

This study favors the Meyerhoff theory in that each island has seemed to spawn a new taxon of *Juniperus*. All of the junipers of the Caribbean have smooth leaf margins (series entire) and no junipers from the denticulate (serrate) leaf margined junipers (series denticulate). Only the denticulate leaf margined junipers are found in southern Mexico and Guatemala (the southern-most range of *Juniperus* in the continental western hemisphere). There are therefore no affinities between the Caribbean junipers and those of Central America. The spread of the junipers across the Caribbean islands has most likely been by birds from eastern North America. The differentiation of these island populations has been affected both by selection and founder's effects. Genetic drift may have also played a part in the diversity of the island junipers because of the expansion and contraction of their ranges during the Tertiary and Pleistocene. According to Curran (1965), the Caribbean sea level dropped approximately 122 m, about 19,000 yBP as well as another drop in sea level of 146 m at 40,000 yBP. Rosen (1978) shows that these drops in sea level would unite several of the Bahamian Islands. Conversely, a rise in the ocean level of only a few meters would inundate many juniper sites in the Bahamas where *J. lucayana* often occurs at 1 to 2 m above sea level. Broecker (1965) reported evidence for higher levels about 80,000 yBP in the Bahamas. Thus, there is ample evidence of changes in available juniper habitat, which in turn has probably led to local extinctions as well as range expansions. This, coupled with limited gene flow between the islands, has led to the considerable amount of diversity and differentiation in the leaf oils of the Caribbean junipers.

The results from this study indicate that *Juniperus barbadensis* is quite distinct from the other junipers in its leaf oil. It is most similar to *J. bermudiana* and *J. lucayana*, but does not appear to be conspecific. The West Indies junipers appear to have arisen from *J. virginiana* (or its ancestor) in eastern North America, with the West Indies having been populated by long distance dispersal of seeds by birds.

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Table 1. Composition of the Volatile Leaf Oils of *Juniperus barbadensis* from St. Lucia, BWI along with the volatile leaf oils of other Caribbean junipers previously reported (Adams 1983; Adams and Hogge 1983). Compounds are listed in order of their elution from a DB1 column. BA = *J. barbadensis*, St. Lucia, BWI; LJ = *J. lucayana*, Jamaica; LB = *J. lucayana*, Bahama Islands; BM = *J. bermudiana*, Bermuda; EK = *J. ekmanii*, Haiti; GR = *J. gracilior*, Dominican Republic; VS = *J. virginiana* var. *silicicola*, Florida, USA; and VG = *J. virginiana* var. *virginiana*, Washington, D.C. USA. Those 70 components denoted with an asterisk (*) were utilized in principal coordinate analysis. Compositional values in parenthesis indicate that a compound runs at that retention time but no mass spectrum was obtained. Compound names in parenthesis are tentatively identified. T indicates the compound was present in trace amounts (less than 0.5% of the total oil).

Compound	% total oil							
	BA	LJ	LB	BM	EK	GR	VS	VG
Percent Yield*	0.6	0.6	0.2	0.3	1.4	0.8	0.4	0.2
Unknown 1*, RRT=0.143	-	-	T	-	(T)	0.8	-	(T)
Unknown 2*, RRT=0.151	-	-	T	-	(T)	0.8	-	T
Tricyclene + p-Thujene*	0.9	0.6	0.5	T	1.9	1.4	T	T
α -Pinene*	7.4	49.1	33.0	22.3	1.3	1.8	2.4	1.4
Camphene*	T	T	T	0.7	1.9	1.2	T	T
Sabinene*	31.0	9.7	8.3	2.8	5.0	10.1	T	6.7
β -Pinene*	T	1.1	1.2	0.6	T	T	T	T
1-Octen-3-ol*	-	T	T	1.0	T	T	0.9	-
Myrcene*	3.8	3.2	4.0	2.9	2.5	1.9	0.9	0.9
2-Carene	-	T	T	-	T	-	T	T
α -Phellandrene	T	-	-	T	-	T	-	-
3-Carene	-	-	-	T	-	-	T	(T)
α -Terpinene*	1.7	T	T	T	0.9	1.7	T	T
p-Cymene*	T	T	T	0.5	0.5	1.4	T	-
β -Phellandrene	T	-	-	-	-	-	-	T
Limonene*	34.2	25.9	18.0	35.3	9.6	7.3	33.3	18.9
trans-Ocimene*	0.7	T	-	T	-	-	-	(T)
γ -Terpinene*	2.7	0.8	0.7	0.7	1.7	3.5	T	T
(p-menth-1(7),3-diene)*-	T	-	T	-	-	-	T	
(cis-p-menth-2-ene-ol)*0.9	-	T	-	0.9	1.1	-	T	
Terpinolene*	1.2	1.0	0.8	0.8	0.6	0.9	(T)	0.5
(trans-p-menth-2-ene-ol)*	0.7	-	-	-	-	T	-	-
4-Terpinenyl acetate	T	T	-	-	-	-	-	T
Linalool*	-	-	T	1.1	0.6	2.6	1.5	4.4

Table 1 Continued

Unknown 3, RRT=0.337*	-	-	-	(T)	1.6	2.0	-	-
(3-Cyclopentene-1-acetaldehyde, 2,2,3-tri-methyl)	(T)	T	T	T	-	-	-	-
cis-Sabinene hydrate	-	T	T	T	-	-	-	T
(cis-Dihydrocarveol)*	T	-	-	-	0.5	0.8	-	-
Camphor*	(T)	T	T	6.5	5.8	1.1	T	3.7
trans-Pinocarveol*	-	-	-	1.1	-	-	-	-
(trans-Dihydrocarveol)*	T	T	(T)	-	(T)	0.7	-	-
trans-Sabinene hydrate	-	-	-	-	-	-	-	T
Camphene hydrate*	-	-	(T)	1.4	2.2	1.4	T	T
Borneol*	T	T	T	2.1	5.1	2.0	-	0.8
4-Terpineol*	6.5	1.6	2.5	1.4	6.3	11.6	T	1.5
Myrtenal*	-	-	(T)	0.7	-	-	T	T
α -Terpineol*	T	T	T	T	0.8	0.9	-	T
Estragol*	-	-	-	-	-	-	0.5	T
(p-Cymen-9-ol)	-	T	T	T	-	-	T	T
cis-Piperitol*	T	-	-	-	T	T	-	-
trans-Piperitol	T	-	-	-	-	-	-	-
Unknown 4, RRT=0.426*	-	-	-	-	(T)	1.2	-	-
Carvone*	T	T	(T)	1.0	(T)	T	T	T
Citronellol*	T	T	0.9	T	(0.6)	0.6	T	2.3
Piperitone*	-	-	0.6	-	-	T	T	(T)
Isosafrole*	(T)	-	(T)	(T)	-	-	3.6	6.7
Bornyl acetate*	T	0.6	4.1	4.2	43.9	35.7	T	2.1
Safrole*	(T)	T	(T)	-	-	(T)	13.7	10.9
Sabinyl acetate*	(T)	-	T	0.8	(T)	(T)	-	-
Methyl eugenol*	-	T	(T)	(T)	-	T	8.2	2.9
Caryophyllene	T	T	T	T	T	T	T	T
Thujopsene*	T	-	(T)	2.1	(T)	T	(T)	T
α -Cadinene*	-	-	T	-	T	T	-	T
Germacrene isomer 2*	(T)	-	T	-	T	T	T	T
Germacrene D*	T	0.6	T	T	-	-	(T)	T
Cuparene	T	-	-	-	-	-	-	-
β -Cubebene*	-	-	0.8	-	T	T	-	-
Unknown 5, RRT=0.658*	-	-	0.9	-	-	-	-	-
α -Muurolene	(T)	T	-	T	T	T	T	T
T-Cadinene*	T	-	2.8	-	T	-	T	T
δ -Cadinene*	T	T	0.7	T	T	T	0.7	0.8
Unknown 6, RRT=0.692*	-	-	0.6	-	-	-	T	T
Elemicin*	-	-	-	-	T	T	-	T
Elemol*	(T)	T	T	T	-	-	12.1	8.2
Cadinol isomer 1*	T	T	-	-	-	-	-	-

Table 1 Continued

Unknown 7, RRT=0.715*	(T)	-	1.9	-	-	-	0.9	T
Cadinol isomer 2*	-	T	0.9	-	(T)	(T)	(0.8)	0.7
Unknown 8, RRT=0.732*	T	T	2.2	T	-	-	0.7	2.0
Widdrol	T	-	-	-	-	-	-	-
Cedrol	T	-	-	-	-	-	-	-
(Cubenol)*	-	-	1.2	T	T	T	(0.7)	0.9
γ -Eudesmol*	-	-	-	-	-	-	3.4	2.8
r -Cadinol*	-	T	-	-	T	T	2.0	T
r -Muurolol*	-	T	1.6	T	T	-	-	2.4
β -Eudesmol*	-	-	-	-	-	-	2.8	1.7
Cadinol isomer 4*	-	0.5	-	-	-	-	-	-
α -Cadinol*	T	-	-	-	-	-	-	-
α -Eudesmol*	-	-	-	-	-	-	3.4	3.1
Unknown 9, RRT=0.769*	T	-	2.3	T	(T)	T	-	-
Unknown 10, RRT=0.791*	T	T	0.9	T	T	T	T	-
Acetate II*	-	-	-	-	-	-	1.8	3.5
Abietatriene	T	-	T	T	-	T	T	-
Manool*	(T)	-	T	-	-	-	T	(T)
(Kaur-16-ene)*	T	-	T	0.7	-	T	-	-
Unknown 11, RRT=1.099*	0.6	-	-	-	-	-	-	-

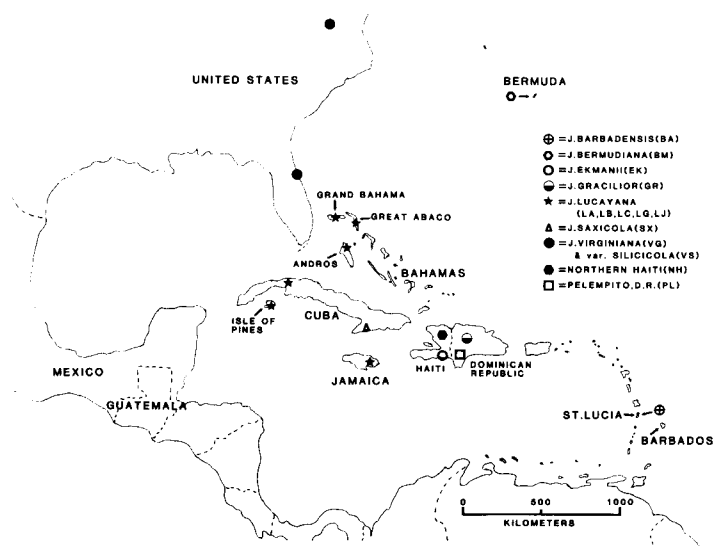


Figure 1. Population vicinity map of the study area with population locations. The endemic juniper, *J. urbaniana* occurs near *J. ekmanii* in Haiti but was not sampled in this study. Additional populations of *J. lucayana* (not sampled) occur on a few of the islands of the Bahamas and in eastern Cuba.

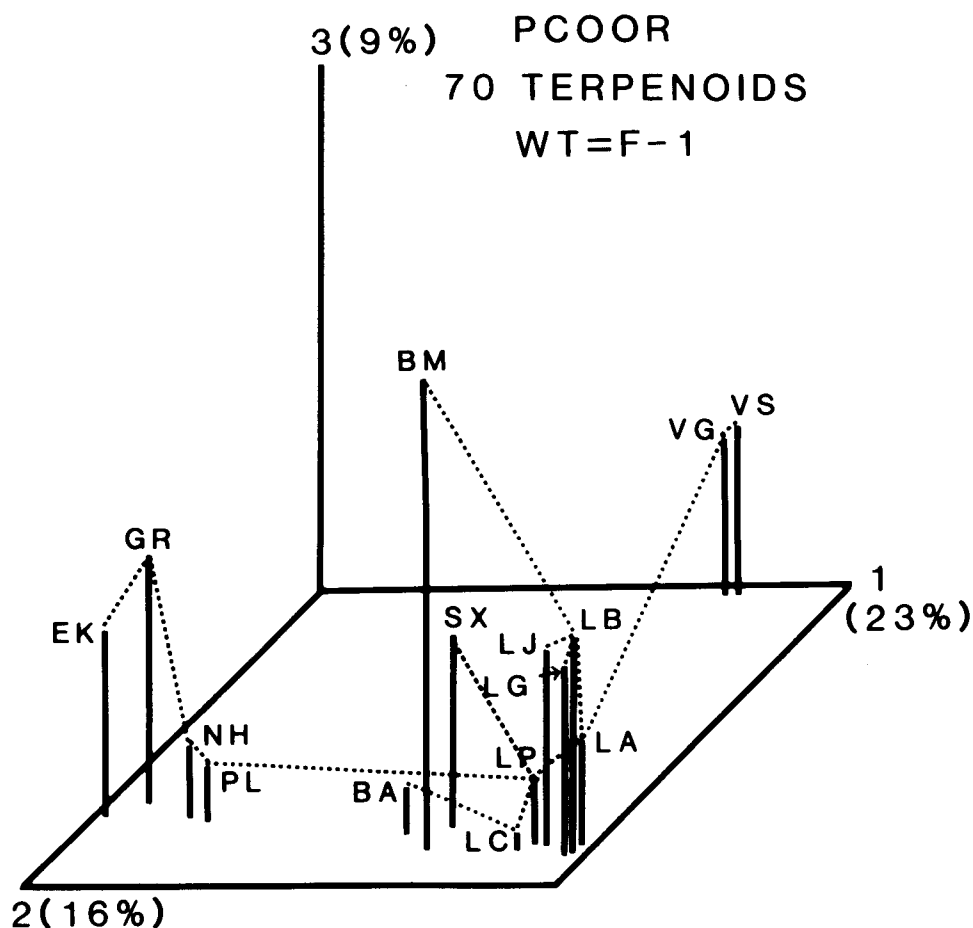


Figure 2. Principal coordinate analysis using 70 terpenoids from the volatile leaf oils. The individual components were weighted by F-1 (F from ANOVA of the 15 OTUs) in the similarity measure. The minimum spanning network (dashed line) distances are based on the first 10 principal coordinates. The OTU codes are: BA = *J. barbadensis*, St. Lucia; BM = *J. bermudiana*, Bermuda; EK = *J. ekmanii*, Haiti; GR = *J. gracilior*, Dominican Republic; LA, LB, LC, LG, LJ, and LP = *J. lucayana*, from, respectively, Andros Island, Grand Bahama Island, Cuba (mainland), Jamaica, Great Abaco Island, and Isle of Pines; NH = northern Haiti; PL = Pelempito region of Dominican Republic; SX = *J. saxicola*, Cuba; VG = *J. virginiana*, Washington, D.C.; and VS = *J. virginiana* var. *silicicola*, Florida, USA. The percentage number on each axis is the percent of the total variation among the OTUs accounted for by that axis.

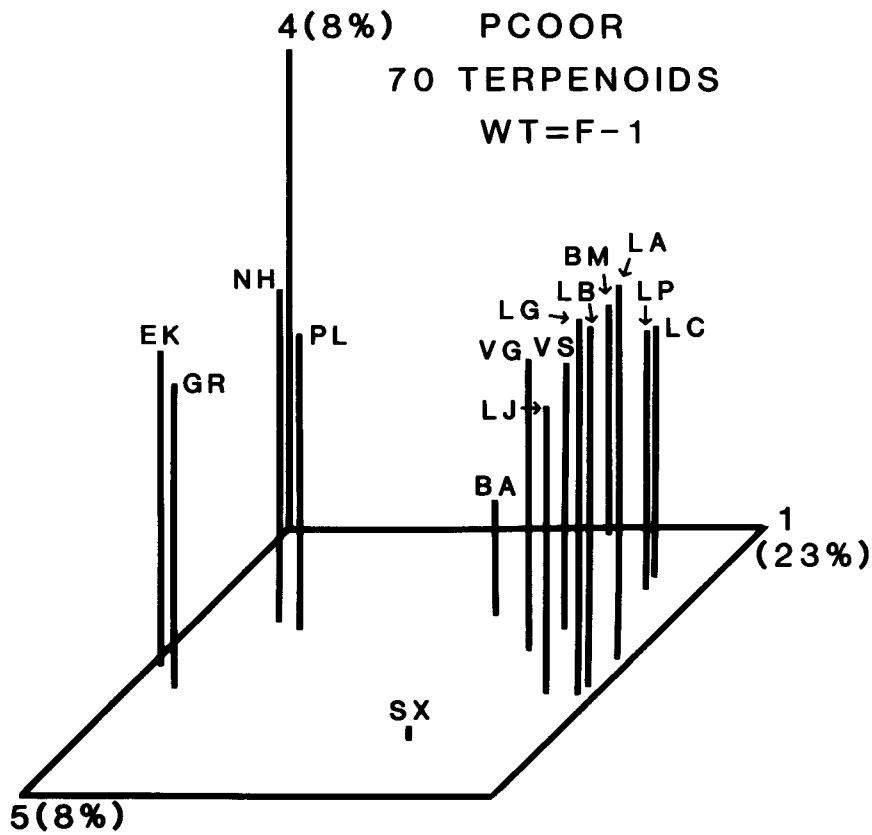


Figure 3. Principal coordinate analysis based on terpenoids. See Fig. 2 for OTU codes. Note the separation of SX (*J. saxicola*) and BA (*J. barbadensis*) on axis 4. Axis 5 primarily separates EK, GR from NH, PL and *J. saxicola* (SX) from the other junipers.

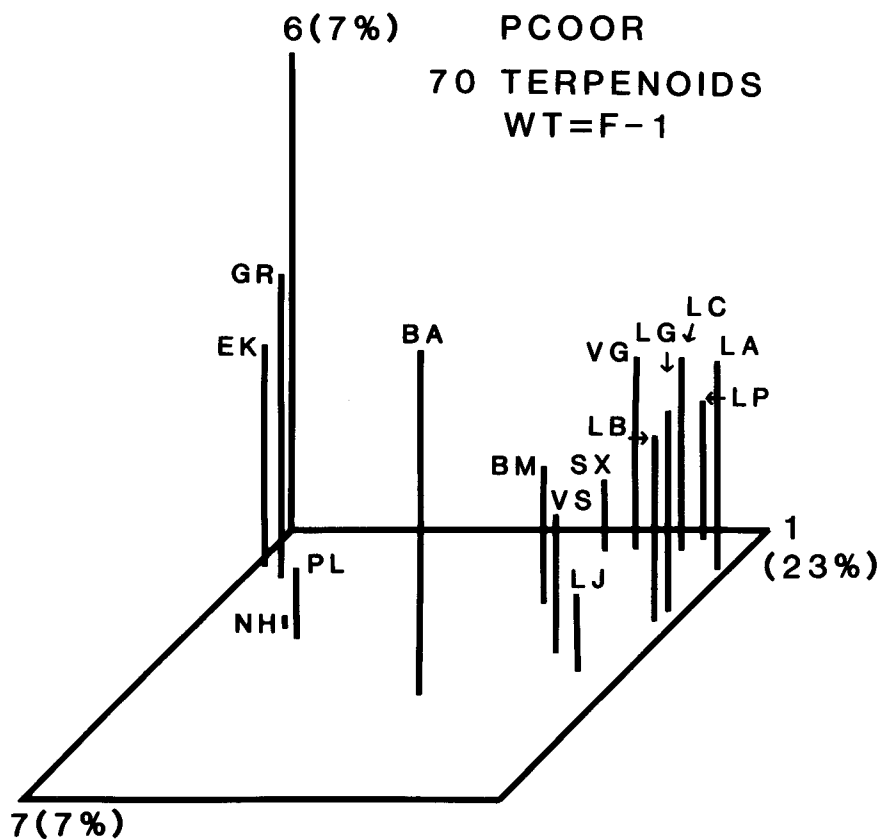


Figure 4. Principal coordinate analysis for coordinates 1, 6, and 7. Coordinate 6 further separates the populations from Hispaniola into EK, GR and NH, PL as well as separating the two varieties of *J. virginiana*, VG and VS.

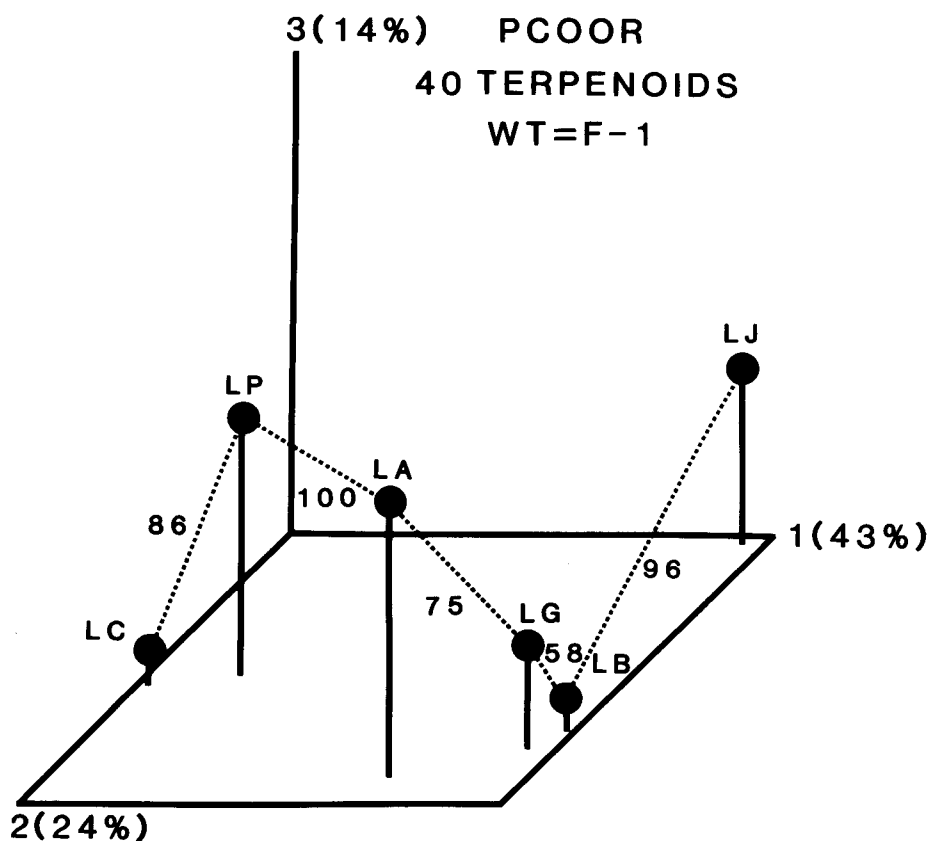


Figure 5. Principal coordinate analysis of the six *J. lucayana* populations (see Fig. 2 caption for codes) using 40 terpenoids. The first coordinate primarily separates the two Cuban populations (LC, LP) from the other populations. The second axis separates the Jamaica population (LJ). The third axis separates the two Cuban populations (LC, LP) from each other and separates out two of the Bahamian populations (LG, LB). The dashed line is the minimum spanning network based on distances on the first 5 principal coordinates.

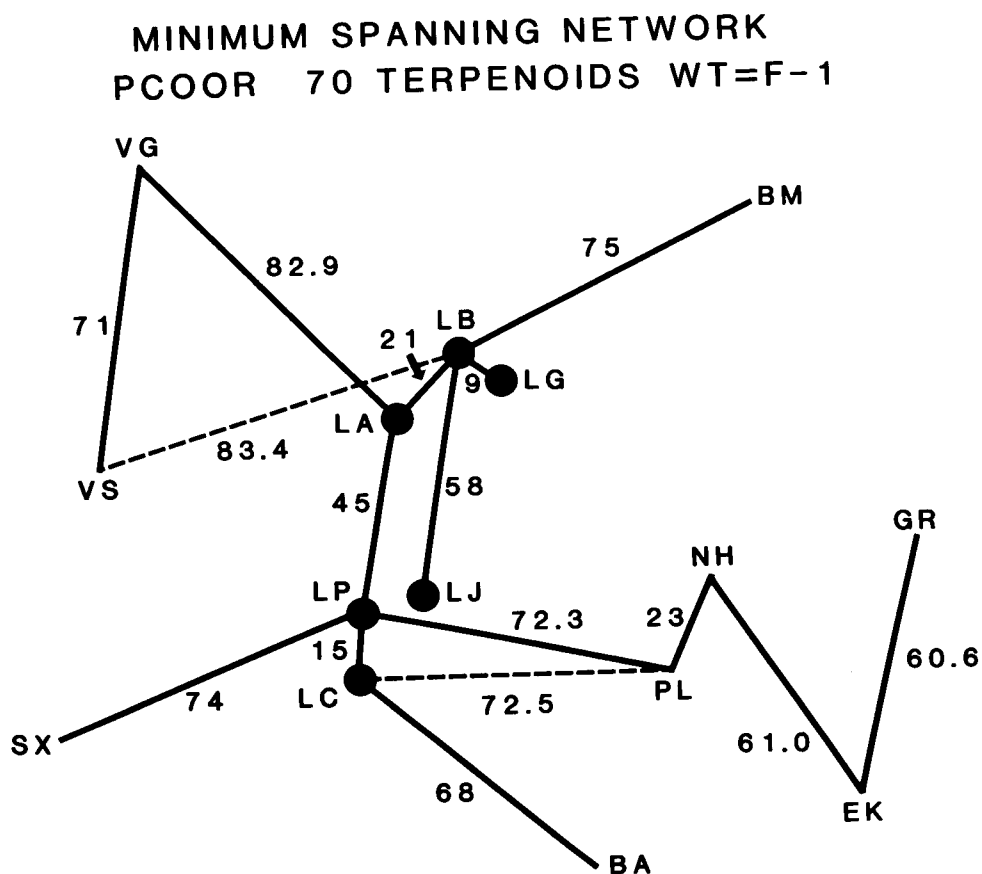


Figure 6. Minimum spanning network based on the first 10 coordinates from PCOOR using 70 terpenoids and 15 OTUs. All the distances have been scaled by 100 to eliminate most of the decimals. The dashed line from VS to LB is the smallest distance from VS (*silicicola*, Florida) to any OTU off the mainland. The dashed line from PL to LC is the second shortest distance to an OTU not on Hispaniola. OTU codes are as defined in Fig. 2.

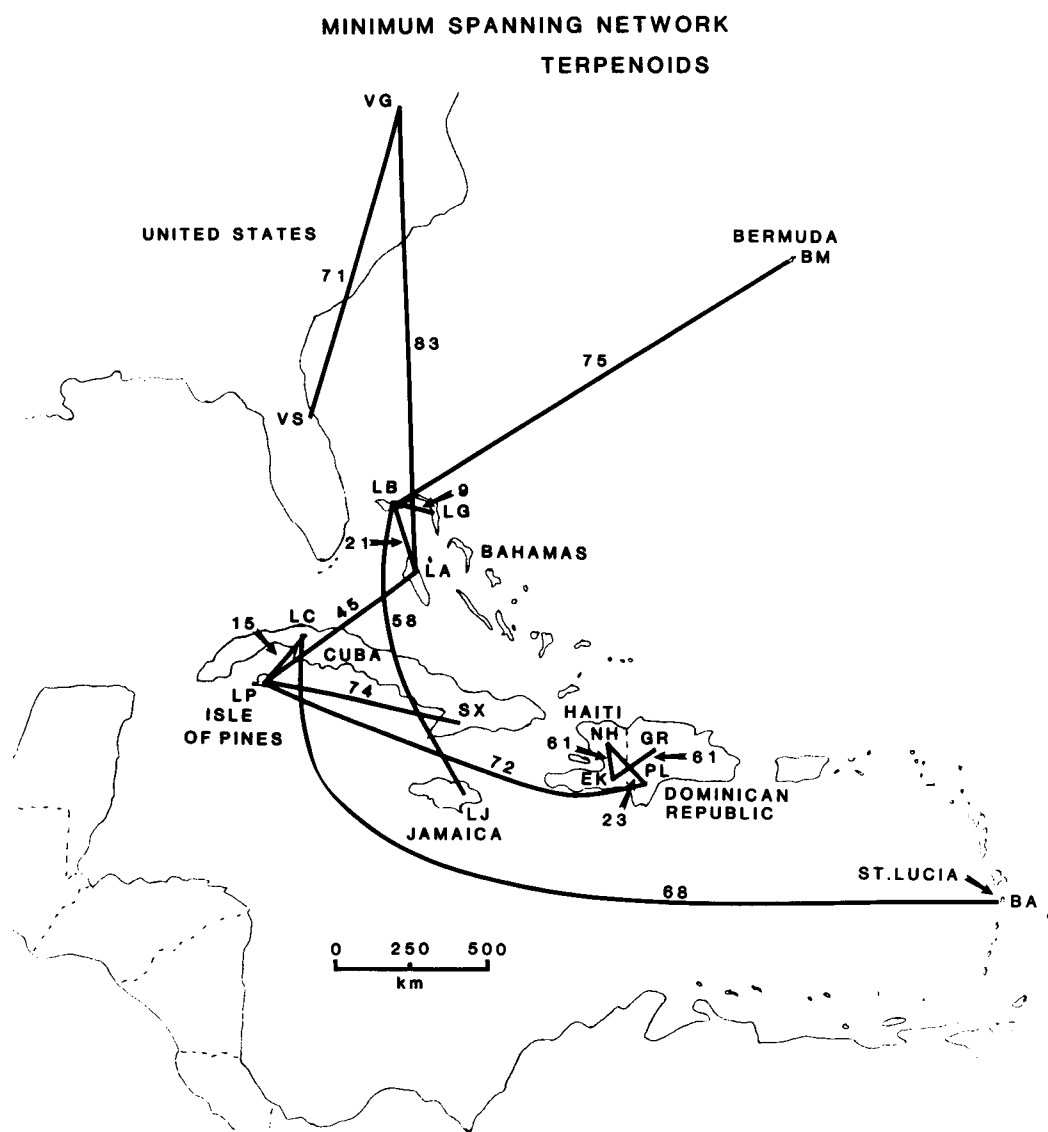


Figure 7. Minimum spanning network (from Fig. 6) mapped onto the geographical map of the West Indies and surrounding region. OTU codes are as defined in Fig. 2. See text for discussion.

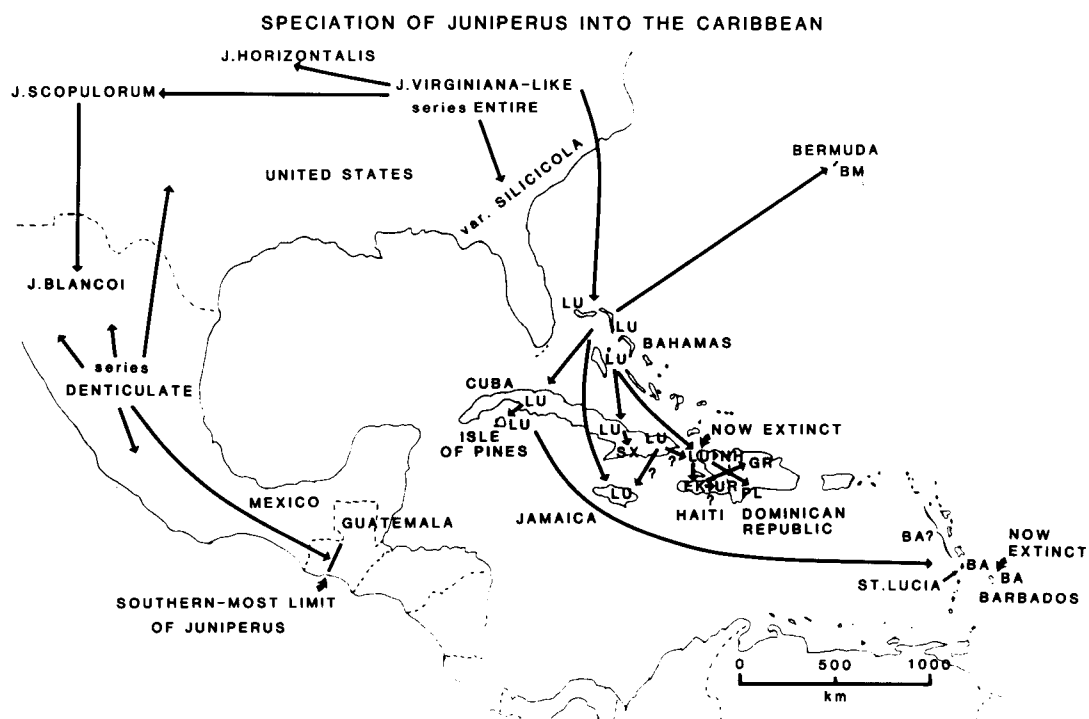


Figure 8. Proposed Speciation of *Juniperus* into the Caribbean. Note especially that the junipers from the southern Mexico/ northern Guatemala area are in series denticulate, whereas all the junipers of the Caribbean, Bermuda and eastern United States are in series entire. See text for additional discussion.