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Variation among *Cupressus* species from the western hemisphere based on random amplified polymorphic DNAs

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Abstract

Random amplified polymorphic DNAs (RAPDs) data were analyzed from all the taxa of *Cupressus* from the western hemisphere. Populations of *Cupressus* from Arizona and Texas, USA, were found to cluster in the two groups delimited by Wolf (1948): *C. arizonica* and *C. glabra*. These data suggest that these taxa might be better recognized at the specific level as per Wolf (1948), rather than at the varietal level (Farjon, 1998) or not at all (Bartel, 1994). A second analysis, which included *Chamaecyparis nootkatensis* (= *Cupressus nootkatensis*) and all the taxa of *Cupressus* from the western hemisphere, revealed four major groups: (1) *C. benthamii* and *C. lindleyi* from central Mexico; (2) *C. macrocarpa*, *C. guadalupensis*, *C. nootkatensis*, *C. forbesii*, and *C. bakeri*; (3) *C. goveniana*, *C. pigmaea*, *C. sargentii*, *C. abramsiana*, *C. nevadensis*, *C. arizonica*, and *C. montana* (= *C. arizonica* var. *montana*); and (4) *C. glabra*, *C. stephensonii*, and *C. macnabiana*. This analysis supports the placement of *Ch. nootkatensis* into *Cupressus* (*C. nootkatensis*). Trees identified by Wolf (1948) as *C. sargentii* from Santa Barbara Co., proved to be quite distinct in their RAPDs from *C. sargentii* populations growing north of this county. Additional field studies are being conducted to resolve the specific status of these plants. Individuals of *C. forbesii* showed considerable variation within and among populations, suggesting possible hybridization or micro-differentiation.

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1. Introduction

Wolf (1948) recognized 15 species with two subspecies of *Cupressus bakeri* in his treatment of New World *Cupressus* (Table 1). However, in an epilogue, he accepted Martinez's (1947) treatment of Mexican cypress, which would recognize *Cupressus benthamii* and *Cupressus lindleyi* in place of *Cupressus lusitanica*. Essentially employing Wolf's (1948) "drastic treatment of the New World species of *Cupressus*", Little (1970) accepted eight species recognized by Wolf and treated the remaining species as varieties of three species (Table 1). Little (1970) and subsequent authors have treated *C. bakeri* as a monotypic (no infraspecific taxa) species (Bartel, 1993; Eckenwalder, 1993; Rafii and Dodd, 1994). In 'the more conservative end of the spectrum', Eckenwalder (1993) included seven species in his treatment of *Cupressus* north of Mexico, with one species treated as a variety of *Cupressus guadalupensis* (Table 1). Farjon (1998) recognized eight *Cupressus* species with 11 varieties of four of the recognized species in the western hemisphere (Table 1). Farjon (1998) included *Cupressus pigmaea* within *Cupressus goveniana* and *Cupressus nootkatensis* within *Chamaecyparis nootkatensis*. Using DNA sequencing, Gadek et al. (2000) concluded that *Ch. nootkatensis* was best placed within *Cupressus*. Farjon (1998) treated *C. lindleyi* as a synonym of *C. lusitanica* (Table 1) and *C. benthamii* as a variety (*C. lusitanica* var. *benthamii*). Despite the complicated variation in the four treatments in Table 1, the authors differ principally in rank and in the recognition, or lack thereof, of a few taxa (i.e. *C. benthamii*, *Cupressus matthewsii*, and *C. pigmaea*). Moreover, all of the published treatments since 1948 have been derived from Wolf's comprehensive monograph.

In recent studies, Rushforth et al. (2002) found *C. benthamii* and *C. lindleyi* to be distinct and more similar in their random amplified polymorphic DNAs (RAPDs) than to *C. lusitanica*, but that study did give some support for the origin of *C. lusitanica* from the New World. In an analysis of the taxa of the eastern hemisphere, Rushforth et al. recognized 14 species (Adams et al., 1993). They found considerable variation among small isolated populations that appear to be relictual. Nearly every species was characterized by having small, disjunct populations often clinging for survival in unusual soil/rock substrates. In the eastern hemisphere, *Cupressus* seems to persist most commonly in small populations or as a result of human cultivation (e.g. *Cupressus sempervirens*).

In the western hemisphere, most of the *Cupressus* species occur on the west coast of the US. Exceptions are *Cupressus arizonica* (from Arizona to Texas and into northern Mexico), *C. benthamii* and *C. lindleyi* (central Mexico to central America mountains). Worldwide, *Cupressus* species seem to be headed for extinction as most populations are small and relictual.

It is interesting to contrast *Cupressus* and its nearest phylogenetic relative, *Juniperus* (junipers). Gadek et al. (2000), using matK and rbcL sequence data, recently confirmed that *Cupressus* and *Juniperus* are 'sister' genera. *Juniperus* is the second largest genus (68 species, 36 varieties; Adams 1999, 2000a–d, 2001; Adams et al., 2001a,b) of the conifers, exceeded in diversity only by *Pinus* (pines). In North Amer-

Table 1
Comparison of four taxonomic treatments of *Cupressus* from the western hemisphere

Specific or infraspecific epithet	Wolf (1948)	Little (1970)	Eckenwalder (1993)	Farjon (1998)
<i>C. abramsiana</i>	<i>C. abramsiana</i> C.B. Wolf	<i>C. goveniana</i> var. <i>abramsiana</i> (C.B. Wolf) Little	(= <i>C. goveniana</i> Gordon)	<i>C. goveniana</i> var. <i>abramsiana</i> (C.B. Wolf) Little
<i>C. arizonica</i>	<i>C. arizonica</i> Greene	<i>C. arizonica</i> Greene var. <i>arizonica</i>	<i>C. arizonica</i> Greene	<i>C. arizonica</i> Greene var. <i>arizonica</i>
<i>C. bakeri</i>	<i>C. bakeri</i> Jeps. ssp. <i>bakeri</i> (= <i>C. lusitanica</i> Mill.)	<i>C. bakeri</i> Jeps.	<i>C. bakeri</i> Jeps.	<i>C. bakeri</i> Jeps.
<i>C. benthamii</i>		(= <i>C. lusitanica</i> Mill.)	[not addressed]	<i>C. lusitanica</i> var. <i>benthamii</i> (Endl.) Carr.
<i>C. forbesii</i>	<i>C. forbesii</i> Jeps.	<i>C. guadalupensis</i> var. <i>forbesii</i> (Jeps.) Little	<i>C. guadalupensis</i> var. <i>forbesii</i> (Jeps.) Little	<i>C. guadalupensis</i> var. <i>forbesii</i> (Jeps.) Little
<i>C. glabra</i>	<i>C. glabra</i> Sudw.	<i>C. arizonica</i> var. <i>glabra</i> (Sudw.) Little	(= <i>C. arizonica</i> Greene)	<i>C. arizonica</i> var. <i>glabra</i> (Sudw.) Little
<i>C. goveniana</i>	<i>C. goveniana</i> Gordon	<i>C. goveniana</i> Gordon var. <i>goveniana</i>	<i>C. goveniana</i> Gordon	<i>C. goveniana</i> Gordon var. <i>goveniana</i>
<i>C. guadalupensis</i>	<i>C. guadalupensis</i> S. Watson	<i>C. guadalupensis</i> S. Watson var. <i>guadalupensis</i>	[not addressed]	<i>C. guadalupensis</i> S. Watson var. <i>guadalupensis</i>
<i>C. lusitanica</i>	<i>C. lusitanica</i> Mill.	<i>C. lusitanica</i> Mill.	[not addressed]	<i>C. lusitanica</i> Mill. var. <i>lusitanica</i>
<i>C. macnabiana</i>	<i>C. macnabiana</i> A. Murray bis	<i>C. macnabiana</i> A. Murray bis	<i>C. macnabiana</i> A. Murray bis	<i>C. macnabiana</i> A. Murray bis
<i>C. macrocarpa</i>	<i>C. macrocarpa</i> Hartweg	<i>C. macrocarpa</i> Hartweg	<i>C. macrocarpa</i> Hartweg	<i>C. macrocarpa</i> Hartweg
<i>C. matthewsii</i>	<i>C. bakeri</i> ssp. <i>matthewsii</i> C.B. Wolf	(= <i>C. bakeri</i> Jeps.)	(= <i>C. bakeri</i> Jeps.)	(= <i>C. bakeri</i> Jeps.)
<i>C. montana</i>	<i>C. montana</i> Wiggins	<i>C. arizonica</i> var. <i>montana</i> (Wiggins) Little	[not addressed]	<i>C. arizonica</i> var. <i>montana</i> (Wiggins) Little
<i>C. nevadensis</i>	<i>C. nevadensis</i> Abrams	<i>C. arizonica</i> var. <i>nevadensis</i> (Abrams) Little	(= <i>C. arizonica</i> Greene)	<i>C. arizonica</i> var. <i>nevadensis</i> (Abrams) Little
<i>C. nootkatensis</i>	[not addressed]	[not addressed]	[not addressed]	<i>Chamacyparis nootkatensis</i> (D. Don) Spach
<i>C. pigmaea</i>	<i>C. pigmaea</i> (Lemmon) Sarg.	<i>C. goveniana</i> var. <i>pigmaea</i> Lemmon	(= <i>C. goveniana</i> Gordon)	(= <i>C. goveniana</i> Gordon var. <i>goveniana</i>)
<i>C. sargentii</i>	<i>C. sargentii</i> Jeps.	<i>C. sargentii</i> Jeps.	<i>C. sargentii</i> Jeps.	<i>C. sargentii</i> Jeps.
<i>C. stephensonii</i>	<i>C. stephensonii</i> C.B. Wolf	<i>C. arizonica</i> var. <i>stephensonii</i> (C.B. Wolf) Little	(= <i>C. arizonica</i> Greene)	<i>C. arizonica</i> var. <i>stephensonii</i> (C.B. Wolf) Little

ica, some *Juniperus* species have become weedy and invaded millions of acres of rangeland and abandoned farms (Adams et al., 1998; Adams and Turuspekov, 1998). *Juniperus* species range from sea level (e.g. *Juniperus virginiana* var. *silicicola*, *Juniperus lutchuensis*, *Juniperus procumbens*) to above timberline (e.g. *Juniperus monticola* var. *compacta*).

Juniperus species have evolved a fleshy female cone in which the cone scales are fused. These cones are often referred to as 'fruits' or 'berries'. Juniper cones are especially consumed by birds and small mammals (Phillips, 1910; McAtee, 1947; Holthuijzen and Sharik, 1985; Santos et al., 1999). In fact, the long-distance dispersal by birds has resulted in *Juniperus* being found on Atlantic islands, such as Bermuda and the Azores. Throughout North America, *Juniperus* is flourishing and expanding its range.

In contrast, *Cupressus* has evolved a round, woody cone that opens to release nearly wingless seeds. With only gravity and water as the apparent seed dispersal agents, long-distance dispersal (i.e. seed 'migration') seems highly unlikely. Although animals may act to disperse cones and seeds (i.e. external carriage, frugivory), the smooth, nearly wingless seeds have limited abilities to move into open habitats (Stebbins, 1980). In contrast to *Juniperus*, *Cupressus* shows no evidence of becoming weedy and expanding its present range. As an aside, nearly all *Juniperus* species are dioecious, whereas all *Cupressus* species are monoecious.

From the fossil and palynological record, *Cupressus* previously occupied substantial portions of the west coast in the recent past. With the lowering of the forest zones by 500–1000 m during the Pleistocene (ca. 12,000–18,000 ybp, Graham, 1999), *Cupressus* may have occupied large areas of the west coast as recently as 12,000 ybp. If the present populations are relictual from a recent widespread Pleistocene distribution, then one might expect to find very low variation within populations. Due to the long generation times in *Cupressus* and the recent age of the putative, relictual disjunct populations (12,000–18,000 ybp), one might not expect much differentiation between these disjunct populations.

The present study was performed to analyze all the *Cupressus* taxa of the western hemisphere to provide a basis for more detailed population analysis in the future.

2. Materials and methods

The following specimens were utilized: *Cupressus abramsiana* C.B. Wolf, Bartel 1567A, B, Santa Cruz Co., CA, USA; *C. arizonica* Greene, Adams 9268-9269, Brewster Co., TX, USA; Bartel 1580A, B, Pima Co., AZ, USA; Bartel 1581A, B, Dragoon Mtns., Cochise Co., AZ, USA; Bartel 1582A, B, Pedregosa Mtns., Cochise Co., AZ, USA; Bartel, 1583A, B, Greenlee Co., AZ, USA; *C. bakeri* Jepson, Bartel 1572A, B, Shasta Co., CA, USA; *C. benthamii* Endl., Adams 8710, 8711, Hidalgo, Mexico; *Cupressus forbesii* Jepson, Bartel 1588, Orange Co., CA, USA; Bartel 1589A, B, Los Angeles Co., CA, USA; Bartel 1576A, B, Otay Mtn., San Diego Co., CA, USA; Bartel 1577A, B, Guatay Mtn., San Diego Co., CA, USA; *Cupressus glabra* Sudw., Bartel 1584A, B, Matzatzal Mtns., Gila Co., AZ, USA; Bartel 1585A,

B, Tonto Basin, Gila Co., AZ, USA; Bartel 1586A, B, Yavapai Co., AZ, USA; *C. goveniana* Gordon, Bartel 1565A, B, C, Monterey Co., CA, USA; *C. guadalupensis* S. Watson, Berkeley Bot. Garden, ex. Guadalupe Isl., Baja California Norte, Mexico, Martin Grantham collection, ref. spec, Adams 8417; *C. lindleyi* Klotzsch ex. Endl., Adams 8706, 8707, Chihuahua, Mexico; *Cupressus macnabiana* A. Murray bis, Bartel 1569A, B, Napa Co., CA, USA; Bartel 1573A, B, Amador Co., CA, USA; *Cupressus macrocarpa*, Bartel 1566A, B, Monterey Co., CA, USA; *Cupressus montana* Wiggins, Bartel 1590A, B, 1591A, B, Baja California Norte, Mexico; *Cupressus nevadensis* Abrams, Bartel 1574A, B, Greenhorn Mtns., Kern Co., USA; Bartel 1575A, B, Piute Mtns., Kern Co., CA, USA; *C. nootkatensis* D. Don in Lambert, Adams 9086, Seattle, WA, USA; Adams 9273, Mill Bay, BC, Canada; *C. pigmaea* (Lemmon) Sarg., Bartel 1568A, B, Mendocino Co., CA, USA; *Cupressus sargentii* Jepson, Bartel 1564A, B, C San Luis Obispo Co., CA, USA; Bartel 1570A, B, 1571A, B, Napa Co., CA, USA; Bartel 1578A, B, Santa Barbara Co., CA, USA; *Cupressus stephensonii* C.B. Wolf, Bartel 1579A, B, San Diego Co., CA, USA. Adams' specimens are deposited at BAYL herbarium, Waco, Texas. Bartel's specimens are held in his personal herbarium, Carlsbad, California.

One gram (fresh weight) of foliage was placed in 20 g of activated silica gel and transported to the lab, then stored at -20°C until the DNA was extracted. DNA was extracted from the leaves by use of the Qiagen DNeasy Mini-plant extractors. Ten-mer primers were purchased from the University of British Columbia (5'–3'): 131, GAA ACA GCG T; 153, GAG TCA CGA G; 204, TTC GGG CCG T; 212, GCT GCG TGA C; 218, CTC AGC CCA G; 239, CTG AAG CGG A; 244, CAG CGA ACC G; 250, CGA CAG TCC C; 327, ATA CGG CGT C; 338 CTC TGG CGG T; 346, TAG GCG AAC G; 347, TTG CTT GGC G; 389 CGC CCG CAG T; 413, GAG GCG GCG A.

PCR was performed in a volume of 15 ml containing 50 mM Tris–HCl (pH 9), 2.0 mM MgCl_2 , 0.01% gelatin and 0.1% Triton X-100, 0.2 mM of each dNTPs, 0.36 mM primers, 0.3 ng genomic DNA, 15 ng BSA and 0.6 unit of Taq DNA polymerase (Promega). A control PCR tube containing all components, but no genomic DNA, was run with each primer to check for contamination. DNA amplification was performed in an MJ Programmable Thermal Cycler (MJ Research, Inc.). The thermal cycle was: 94°C (1.5 min) for initial strand separation, then 40 cycles of 38°C (2 min), 72°C (2 min), 91°C (1 min). Two additional steps were used: 38°C (2 min) and 72°C (5 min) for final extension. Bands that occurred once or did not show fidelity within the two replicated samples of each taxon were eliminated. It should be noted that these bands contain very useful information for the study of genetic variance and individual variation, but are merely 'noise' in the present taxonomic study. Bands were scored in four classes: very bright (6); medium bright (5), faint (4) and absent (0). See Adams and Demeke (1993) for details on electrophoresis and RAPD band scoring.

Similarity measures were computed using absolute character state differences (Manhattan metric), divided by the maximum observed value for that character over all taxa (Gower metric, Gower, 1971; Adams, 1975).

3. Results and discussion

In an effort to determine the extent of geographic variation in *C. arizonica*/*glabra* and *C. goveniana*/*abramsiana*/*pigmaea*/*sargentii*, a preliminary study using 125 RAPD bands was conducted. This study indicated (Fig. 1) that *C. pigmaea* appears to be distinct from *C. goveniana*, which is contrary to Farjon's (1998) submersion of *C. pigmaea* within *C. goveniana* (Table 1). On the other hand, *C. abramsiana* and *C. goveniana* appeared less distinct, which lends support to Farjon's treatment of *C. abramsiana* as a variety of *C. goveniana* (Table 1). In addition, *C. glabra* (Table 1) was found to be a quite distinct from *C. arizonica* (Fig. 1). All of the *C.*

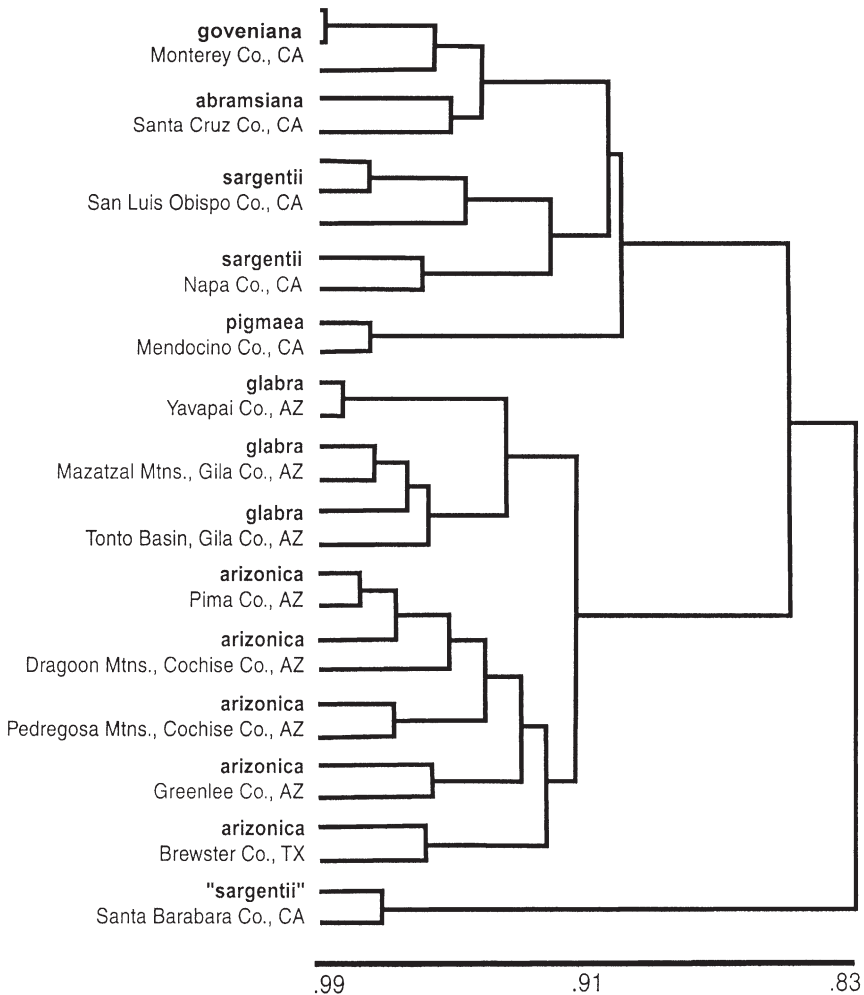


Fig. 1. Minimum spanning network based on 125 RAPD bands of populations of *C. goveniana*, *C. abramsiana*, *C. sargentii*, *C. pigmaea*, *C. glabra* and *C. arizonica*.

arizonica samples formed a group with the samples from the Chisos Mountains in Texas clustering last (Fig. 1). The most surprising result was the unusual clustering of the putative '*C. sargentii*' from Santa Barbara Co., CA (Fig. 1). This analysis indicated that this material is neither similar to *C. sargentii*, nor to any taxon in the preliminary study using 125 RAPD bands. Based on these data, two individuals were chosen as exemplars from each taxon to be used in a larger study of all the taxa from the western hemisphere: *C. goveniana* (Monterey Co., CA); *C. abramsiana* (Santa Cruz Co., CA); *C. sargentii* (San Luis Obispo and Napa Cos., CA); *C. pigmaea* (Mendocino Co., CA); *C. glabra* (Gila and Yavapai Cos., AZ); *C. arizonica* (Cochise and Pima Cos., AZ). Also included were the putative '*C. sargentii*' plants from Santa Barbara Co.

RAPD analysis resulted in 215 bands that displayed fidelity among individuals within taxa. A minimum spanning network based on these bands revealed four major groups (Fig. 2).

3.1. Group 1

C. benthamii/lindleyi—the taxa of the Mexican/central American mountains. These taxa appeared quite distinct (Fig. 2), suggesting that they are species, not merely varieties. Recognition at the specific level is consistent with Martinez's (1947) treatment of Mexican cypress. However, Rushforth et al. (2002) also found *C. lusitanica* to be distinct, so the resolution of the taxonomy of this group remains undetermined.

3.2. Group 2

Subgroup A: *C. macrocarpa/guadalupensis/nootkatensis*—clearly *C. nootkatensis* (= *Ch. nootkatensis*) fits nicely into *Cupressus*. Interestingly, the so-called inter-generic hybrid *Cupressocyparis leylandii* (Jack. and Dall.) Dall. (Rushforth, 1987) had putative parents of *C. macrocarpa* and *C. nootkatensis*, and both of these taxa are found in this group (Fig. 2). Subgroup B: It is composed of *C. forbesii* plants. These individuals were found to be extremely variable in their DNA banding. A number of bands were missing and a number of unique bands were present (but not used in computations). Additional field work is in progress to extend the analysis of *C. forbesii*. The positioning of *C. forbesii* as a variety of *C. guadalupensis* (see Table 1 and Little, 1970; Eckenwalder, 1993; Farjon, 1998) is not supported by these data, but rather its classical recognition as a species (Wolf, 1948; Munz, 1968; Bartel, 1993). *C. bakeri*, clusters in group 2 (Fig. 2).

3.3. Group 3

C. goveniana/pigmaea/sargentii/abramsiana/nevadensis/arizonica/ montana—*C. goveniana* is the most distinct in this group (Fig. 2). *C. pigmaea* has been treated as synonymous with *C. goveniana* (Farjon 1998), but in this analysis it appears to be closely allied with *C. sargentii* (Fig. 2). This analysis gives some support for its recognition as a separate species (Wolf 1948; Munz 1968) or as a variety of *C.*

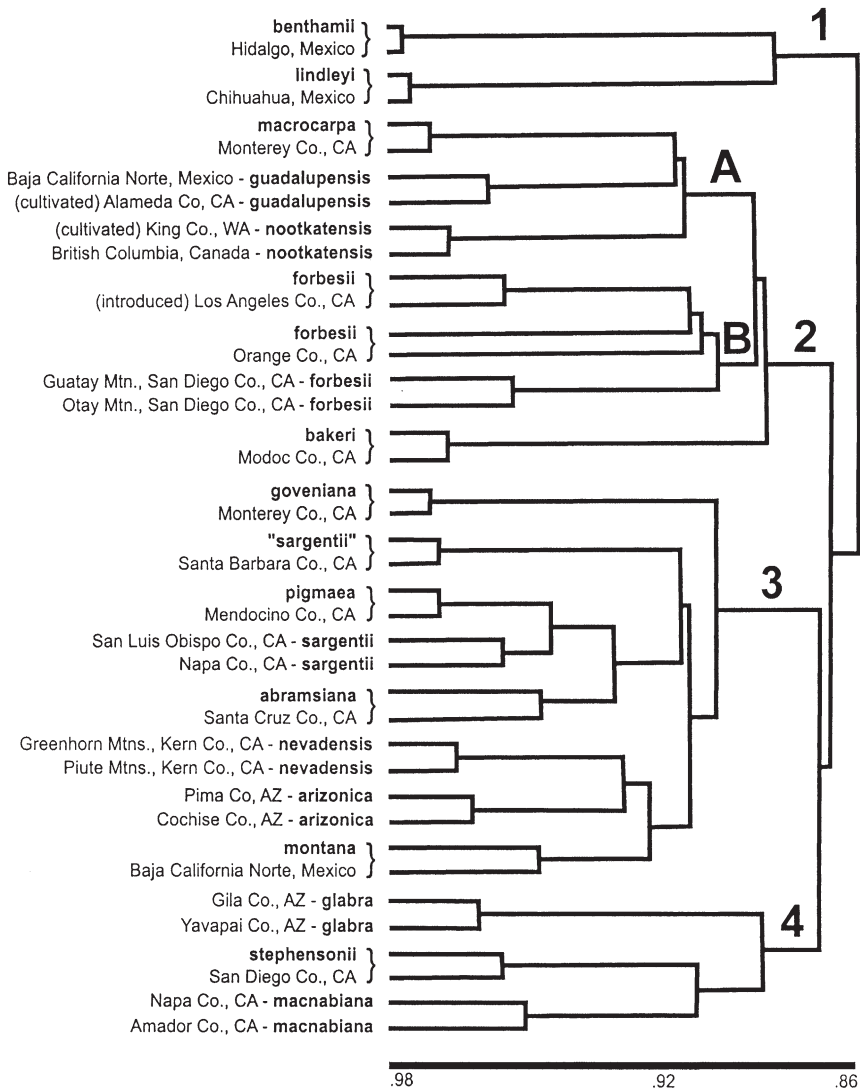


Fig. 2. Minimum spanning network based on 215 RAPD bands for all taxa of *Cupressus* in the western hemisphere. The numbers 1–4 identify the four groups of taxa. Within group 2 are two distinct clusters labeled A and B. See text for discussion.

sargentii. The purported *C. sargentii* plants from Santa Barbara Co., do not link with *C. sargentii* (Fig. 2). Additional field and lab work is needed to ascertain their biological status. In contrast to the preliminary study using 125 RAPD bands, *C. abramsiana* would appear to be better treated as a species or variety of *C. sargentii* rather than as a variety of *C. goveniana*. *C. nevadensis/arizonica/montana* form a subset of group 3 (Fig. 2). Little (1970) and Farjon (1998) recognized *C. nevadensis* as a

variety of *C. arizonica* (Table 1) and these data support relationship of *C. nevadensis* with *C. arizonica*. *C. montana* was collected from Baja, Mexico, and displays considerable divergence from *C. arizonica* (Fig. 2), lending some support for specific recognition as a full species (Wolf, 1948).

3.4. Group 4

Glabra/stephensonii/macnabiana—this group is diverse, but distinct from other *Cupressus* (Fig. 2). Interestingly, *C. glabra* and *C. stephensonii* have been treated as varieties of *C. arizonica* (Little, 1970; Farjon, 1998). This analysis does not support a close relationship of *C. glabra* and *C. stephensonii* with *C. arizonica*.

Overall, it seems that each population sampled seemed to carry some unique genetic differences, often at the level of differences between varieties and/or species. This suggests that there is very limited gene flow between populations. Certainly, there is very limited seed dispersal between populations. If one accepts *C. macrocarpa*, *C. nootkatensis*, and *C. guadalupensis* (group 2, Fig. 2) as distinct species, then it is interesting to note that these cluster at a similarity of about 0.92 (Fig. 2). Examination of taxa in Fig. 2 that are distinct at 0.92 or less gives the following 13 taxon groupings: *bentharii*, *lindleyi*, *macrocarpa*, *guadalupensis*, *nootkatensis*, *forbesii*, *bakeri*, *goveniana*, *pigmaea/sargentii/abramsiana*, *nevadensis/arizonica/montana*, *glabra*, *stephensonii*, *macnabiana* and ‘*sargentii*’ from Santa Barbara. Of course, these are but one kind of data and additional data needs to be taken into consideration before specific status is accorded to the taxa sampled. It is clear, however, that a taxonomic revision of this group is needed. Additional field and lab work is planned to better understand the variation in *C. forbesii* and the nature of the ‘*C. sargentii*’ plants from Santa Barbara Co., CA.

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