GEOGRAPHIC VARIATION IN THE LEAF ESSENTIAL OILS OF *TAXODIUM* (CUPRESSACEAE)

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ABSTRACT

Volatile leaf oils of *Taxodium distichum*, *T. d.* var. *imbricarium* and *T. mucronatum* were found to be high in α-pinene (27-83%), except from the Texas Hill country, where the oil was lower in α-pinene (5-17%) and very high in β-phellandrene (59-78%). Both *T. d.* var. *distichum* and var. *imbricarium* appear to have chemical races: high/low α-pinene and low/high limonene/β-phellandrene. Based on the leaf terpenoids, *T. mucronatum* in Mexico appears to have two variants: Durango and Oaxaca-Guatemala. The oils of *T. distichum* have two regional groups: South Central USA and Texas Hill Country - Rio Grande Valley. The oil of the putative *T. mucronatum* from Bolleros, MX was found to be more similar to *T. distichum* than to any *T. mucronatum* in the study. Putative *T. d.* var. *imbricarium* from Fowl River, AL was found to have oil like *T. d.* var. *distichum*, not like *T. d.* var. *imbricarium* from Tampa, FL. *Phytologia 94(1): 53-70 (April 2, 2012).*

KEY WORDS: *Taxodium distichum*, *T. d.* var. *imbricarium* (*T. ascendens*), *T. mucronatum*, terpenes, leaf essential oil composition, geographic variation.

Taxodium Rich. is a small genus with one to three species. Britton (1926), Dallimore & Jackson (1966) and Rehder (1940) all recognized three species: bald cypress, *T. distichum* (L.) Rich., pond cypress, *T. ascendens* Brongn. and Montezuma or Mexican bald cypress, *T. mucronatum* Ten. Watson (1985) treated *T. ascendens* as *T. d.* var. *imbricarium* (Nutt.) Croom. Both Farjon (2005) and Eckenwalder (2009) recognized *T. distichum*, *T. d.* var. *imbricarium* and *T. mucronatum*. Denny (2007) treated the genus as monotypic with one species, *T. distichum* and two varieties: var. *imbricarium* and var. *mexicanum* (Carr.) Gord. (= *T. mucronatum*). Denny (2007) and Denny and Arnold (2007) give a lucid discussion of the historical nomenclature of the genus.

There has been surprisingly little research on the leaf essential oils of *Taxodium*. A very early paper on the volatile oil from the seed cones of *T. distichum* (Odell, 1912) reported dextro pinene (85%), dextro limonene (5%), a "pseudo terpene alcohol (2%), carvone (3%) and a tricyclic sesquiterpene (3%) with a yield of 1-2%. Flamini et al. (2000) examined the essential oils from seed cones, leaves and branches from cultivated trees of *T. distichum* in North Tuscany, Italy. They found the oils from seed cones, leaves and branches were dominated by α-pinene (71.3, 79.9, 57.3%, respectively). The oils shared most components, but the seed cones were higher in limonene (18.7%). El Taunawy et al. (1999) reported that essential oil from seed cones of *T. distichum* grown in Giza, Egypt contained α-pinene (87.3%), camphene (1.0%), β-pinene (1.7%), myrcene (2.0%), limonene (1.3%) and thujopsene (3.7%) with 38 trace components. Ogunwande et al. (2007), in a study of cytotoxic effects of *T. distichum* seed cone and leaf oils from a tree cultivated in Ibaden, Nigeria, reported 60.5% α-pinene, 17.6% thujopsene, and 29 other compounds in seed cones, but only 0.9% α-pinene in leaves! In fact, α-pinene accounted for nearly all the monoterpene fraction.

No study of leaf oils of *Taxodium* from native materials in the United States, Mexico and Guatemala was found in the literature. The purpose of this study was to report on leaf essential oils of *Taxodium distichum*, *T. d.* var. *imbricarium* and *T. mucronatum* and examine geographic variation in these oils.

MATERIALS AND METHODS

Plant material: Seeds were collected by Denny (2007) in late summer and fall, 2003 and germinated and grown in containers in spring, 2004. Subsequently, seedlings were transplanted to the Texas A & M University Horticulture Farm, College Station, Texas (30°37'38.222" N, 96°22'18.505" W). The site soil was a Boonville Series, fine, smectitic, thermic chromic vertic albaqualf, with a mean soil pH of 6.4. From the 22 *Taxodium* collection sources, 9 were sampled for this study (Fig. 1) as follows:

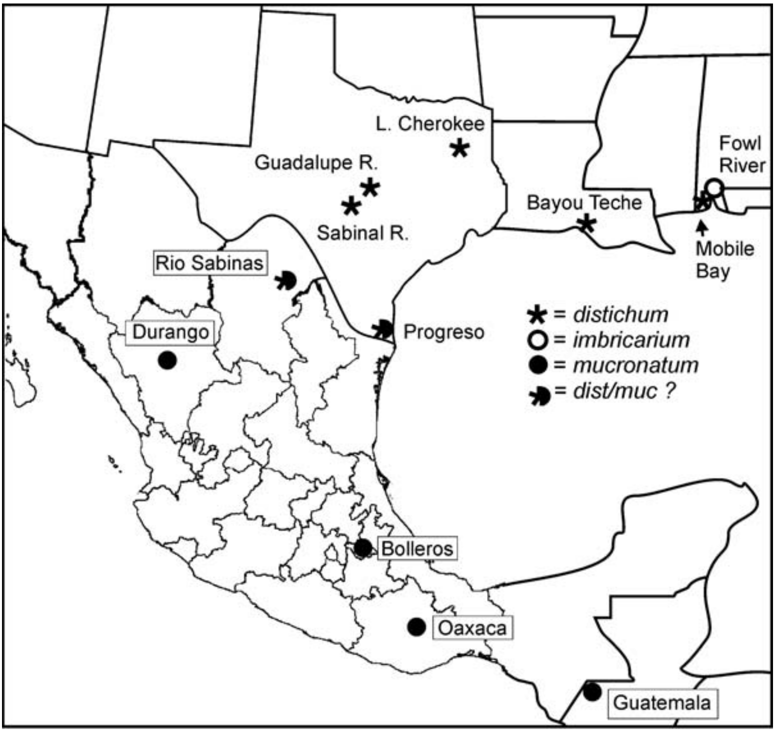

Figure 1. Locations of populations sampled for this study. Sites at Tampa, FL not shown, see text for details.

T. mucronatum: Rio Nazas, Durango, MX, MX2M, 25º 18' 36" N, 104º 38' 24" W, *Adams 12833-12837*; Rio Sabinas, Coah., MX, *Adams 13039-13043*, Bolleros, DF, MX, MX3M, 19º 30' 0" N, 98º 54' 36" W, *Adams 12838-12842;* Progreso, TX, MX5M, 26º 4' 12" N, 97º 54' 36" W, *Adams 12843-12847*.

T. distichum: Guadalupe River, TX, TX2D, 30º 4' 12" N, 99º 17' 24" W, *Adams 12848-12852*; Sabinal River, TX, TX5D, 29º 9' 36" N, 99º 28' 12" W, *Adams 12853-12857;* Lake Cherokee, TX, EP1D, 32º 20' 24" N, 94º 42' 0" W, *Adams 12858-12862;* Bayou Teche, LA, EP3D, 29º 5' 24" N, 91º 12' 6" W, *Adams 12863-12867*; Mobile Bay, AL, EP4D, 30º 36' 0" N, 87º 54' 36" W, *Adams 12868-12872*.

T. distichum var. *imbricarium*: Fowl River, AL, EP5I, 30º 27' 0" N, 99º 06' 36" W, *Adams 12873-12877*.

In addition, samples were collected from natural populations as follow:

T. mucronatum: KM 295 on Pan-American Highway, 42 km S of Guatemala-Mexico border, Guatemala, 15º 24' 05" N, 91º 41' 33" W, *Adams 6857*, Rio del Oro, 36 km S of Oaxaca on hwy 190, Oaxaca, MX, 16º 55' 52" N, 96º 25' 31" W, *Adams 6873*;

T. distichum: Hillsborough River, Hillsborough Co., FL, 28º 09' 05.15" N, 82º 13' 37.24" W, *Adams 12828*, Hillsborough River, Hillsborough Co., FL, 28º 01.164' N, 82º 27.881' W, *Adams 12829-12830,* Hillsborough River, Hillsborough Co., FL, 27º 59.796' N, 82º 28.010' W, *Adams 12831-12832*;

T. d. var. *imbricarium*: edge of swamp, Hillsborough Co., FL, 28º 11' 39.80" N, 82º 30' 54.09" W, *Adams 12823-12827*. Voucher specimens are deposited in the Herbarium, Texas A & M University (for plot materials) and Baylor University (for Adams field collected materials).

Isolation of Oils - Fresh leaves (200 g) were steam distilled for 2 h using a circulatory Clevenger-type apparatus (Adams, 1991). Oil samples were concentrated (ether trap removed) with nitrogen and the samples stored at -20ºC until analyzed. Extracted leaves were oven dried (100ºC, 48 h) for determination of oil yields.

Chemical Analyses - Oils from 10-15 trees of each of the taxa were analyzed and average values reported. Oils were analyzed on a

HP5971 MSD mass spectrometer, scan time 1/ sec., directly coupled to a HP 5890 gas chromatograph, using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column (see Adams, 2007 for operating details). Identifications were made by library searches of our volatile oil library (Adams, 2007), using the HP Chemstation library search routines, coupled with retention time data of authentic reference compounds. Quantitation was by FID on an HP 5890 gas chromatograph using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column using the HP Chemstation software.

Data Analysis - Terpenoids (as percent total oil) were coded and compared among the taxa by the Gower metric Gower (1971). Principal coordinate analysis was performed by factoring the associational matrix using the formulation of Gower (1966) and Veldman (1967).

RESULTS AND DISCUSSION

The volatile leaf oils of *Taxodium distichum*, *T. d.* var. *imbricarium* and *T. mucronatum* (Table 1) were found to be high in α-pinene (27-83%), except from the Texas Hill Country, where the oil was lower in α-pinene (5-17%) and very high in β-phellandrene (59-78%). The leaf terpenoids of *T. mucronatum* in Mexico appears to be of two geographic variants: Durango and Oaxaca-Guatemala, with the oil from Durango being very distinct (Table 1). Population samples from Bolleros, Durango, Progresso, Sabinal River, Guadalupe River and Fowl River had very little variation. Therefore, average component values were used for these populations in the numerical analyses. Both *T. d.* var. *distichum* and var. *imbricarium* (FL) appear to have chemical races based on high/low α-pinene and low/high limonene/β-phellandrene (LMNN/BPHL).

PCO analysis revealed (Fig. 2) that the oils of *T. distichum* appear to be composed of two regional groups: South Central USA and Texas Hill Country - RGV (Rio Grande Valley). Putative *T. mucronatum* from Bolleros, MX is more similar to *T. distichum* than to any *T. mucronatum* in the study. Rio Sabinas samples consisted of four low α-pinene samples that were very similar to the Hill Country/ RVG samples and one high α-pinene tree that has affinities to the Durango and Bolleros trees (Fig. 2). Guatemala - Oaxaca plants form a group (Fig. 2). Durango trees have the most distinct oil (Tab1e 2, Fig. 2).

The low α-pinene trees from the South Central USA cluster with Texas Hill Country - RGV trees (Fig. 2), but have a link to the high α-pinene South Central USA plants. It may be that these low α-pinene trees represent a genotype transplanted from the Hill Country, introgression or a chemical polymorphism. The Progresso, TX and Rio Sabinas (low α-pinene) trees cluster with the Texas Hill country trees (Sabinal R., TX; Guadalupe R.) and not with any *T. mucronatum* in the study (Fig. 2).

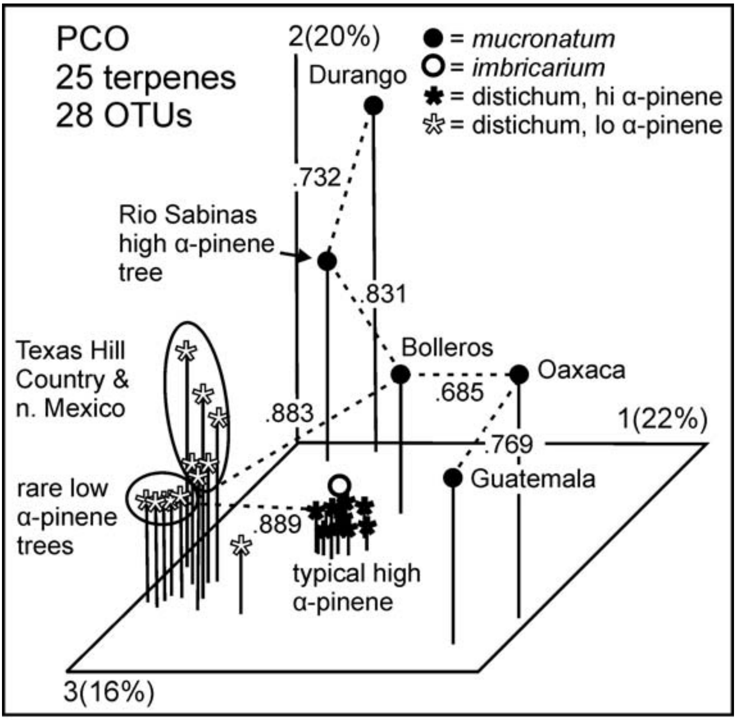

Figure 2. PCO based on 25 terpenes. Numbers next to dotted lines (minimum links) are similarities.

The imbricate leafed trees (cf. *T. distichum* var. *imbricarium*) from Fowl River, AL, have a leaf oil like that of *T. d.* var. *distichum* (Fig. 2).

To supplement the aforementioned samples, additional materials of *T. d.* var. *imbricarium* and *T. d.* var. *distichum* were collected from near Tampa, FL. Surprisingly, the oils of var. *imbricarium* contained both hi- and low α-pinene types (Table 2). A minimum spanning network without the intermediate oils, shows that the oils of var. *imbricarium* (FL) have a distinctive terpene pattern (Fig. 3, Table 1, see germacrene D, α-muurolene, δ-cadinene, α-cadinol). However, *imbricarium* (AL) is essentially the same as var. *distichum* from the South Central USA.

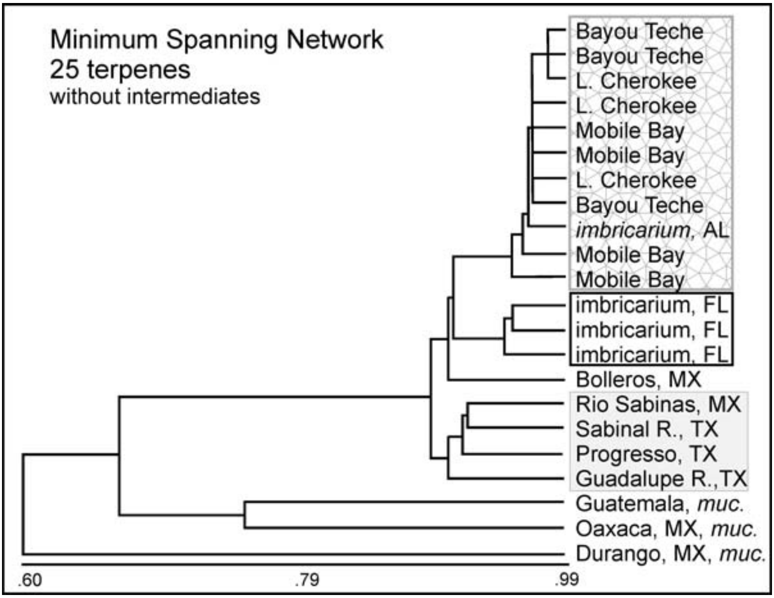

Figure 3. Minimum spanning network showing the placement of var. *imbricarium*, FL.

PCO of these 22 OTUs (Fig. 4) shows that the oils of the Florida var. *imbricarium* trees are most similar to var. *distichum* from the South Central USA. The Texas Hill Country-n Mexico oils are quite distinct, as are the Durango and Guatemala-Oaxaca oils (Fig. 4).

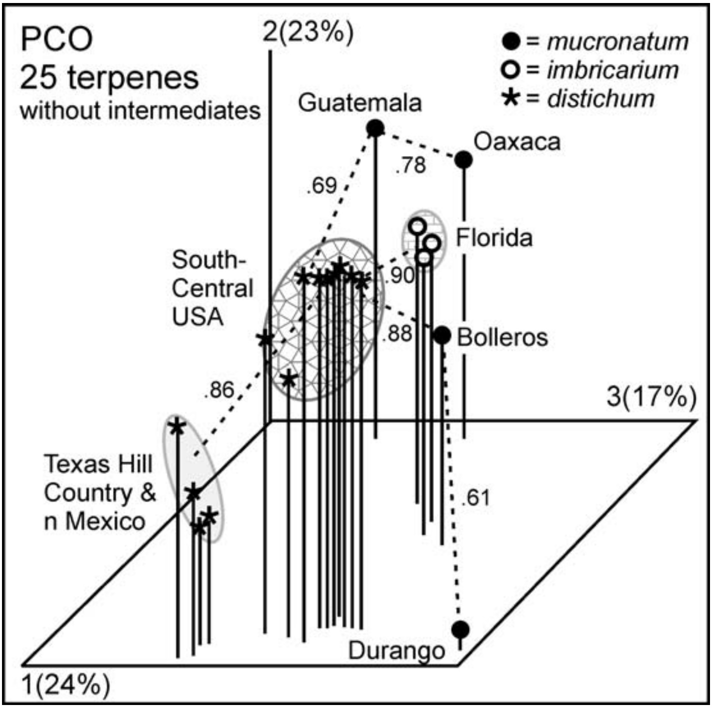

Figure 4. PCO of 22 OTUs based on 25 terpenes. Note the linkage of var. *imbricarium*, Florida with the South Central USA, var. *distichum* trees.

All of the trees analyzed in the Texas Hill Country-RGV-Rio Sabinas populations (20 trees) were very uniform and low in α-pinene, except one unusual individual at Rio Sabinas. However, all the Central South region populations contained mostly high α-pinene trees with one or two low α-pinene trees (Fig. 5). PCO of these individual *T. distichum* trees (Fig. 5) clearly separates low and high α-pinene trees (axis 1, 40%). Four low α-pinene individuals [Lake Cherokee (2), Bayou Teche (1), Mobile Bay (1)] cluster with typical Texas Hill Country - n Mexico trees (Fig. 5). No intermediate oil types are seen in

Fig. 5, suggesting that these individuals are not hybrids or introgressants, but more likely a chemical polymorphism. Additional sampling will be necessary to fully address this problem.

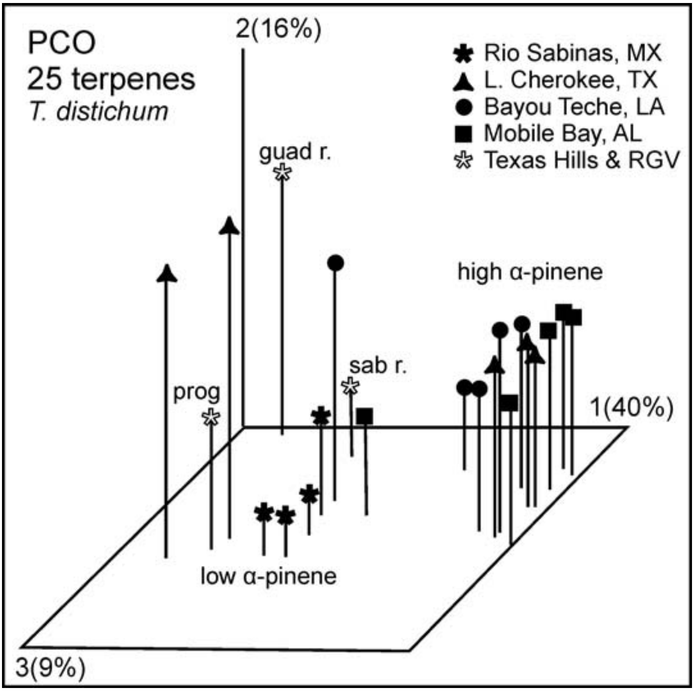

Fig. 5. PCO ordination of individuals of *T. distichum* based on 25 terpenes.

The *Taxodium* from near Tampa, Florida present an interesting problem. *Taxodium d.* var. *imbricarium* has adult foliage with imbricate leaves. Examination of trees on the edge of a swamp north of Tampa revealed that young trees first appear to produce alternate, lanceolate leaves, then produce adult, imbricate leaves. Many of the putative *T. d.* var. *distichum* trees, growing in the river rapids and at streamside on the Hillsborough River, had typical alternate, lanceolate leaves, but some trees had imbricate leaves. This heteroblastic change has also been observed during nursery production of *T. d.* var.

imbricarium seedlings. It appears that var. *distichum* and *T. mucronatum* are fixed in neoteny for the alternate, lanceolate leaves. This is similar to the situation in *Juniperus saxicola* Britt. and P. Wilson that is fixed for juvenile (whip or decurrent) leaves, as opposed to having the adult, scale-like leaves found on the adult foliage of the other *Juniperus* L. in section Sabina (Adams, 2011).

PCO analysis of var. *imbricarium* (Florida), var. *distichum* (Florida) and other var. *distichum* (AL and LA) shows (Fig. 6) the distinctness of var. *imbricarium* (FL) from var. *distichum*. In addition,

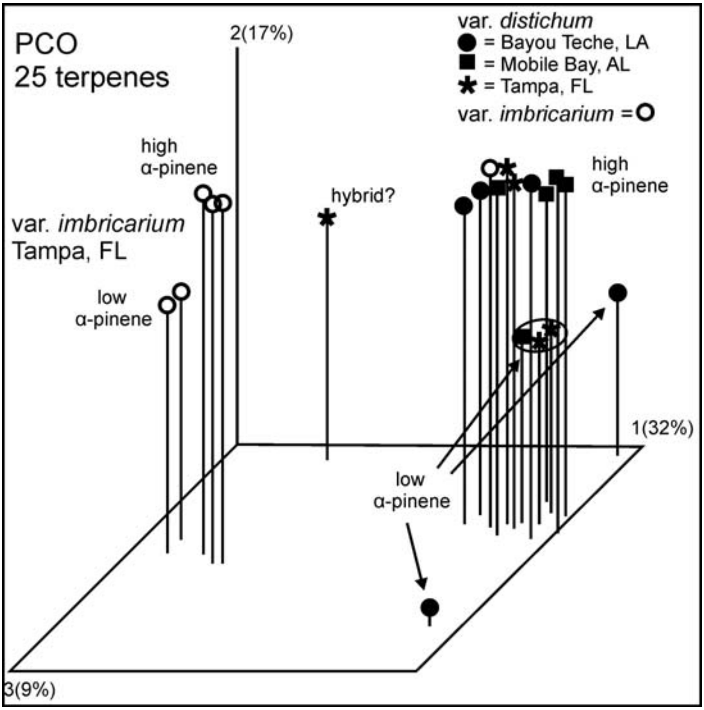

Figure 6. PCO of var. *imbricarium* (Florida) and var. *distichum* plants.

high/ low α-pinene var. *imbricarium* form a loose cluster, as do high/ low α-pinene var. *distichum* plants. Two trees from the Bayou TecheTeche population with low α-pinene are ordinated as outliers. These may be just trees with unusual oils. In addition, one of the var. *distichum*, Tampa, FL ordinates in a hybrid position midway between var. *distichum* and var. *imbricarium*.

Contouring the clustering order reveals (Fig. 7) the South Central USA, *T. distichum* group, the Texas Hill Country-northen Mexico group and the affinity of the Bolleros, MX population to *T. distichum*. These data suggest that *T. distichum* may extend into eastern Mexico.

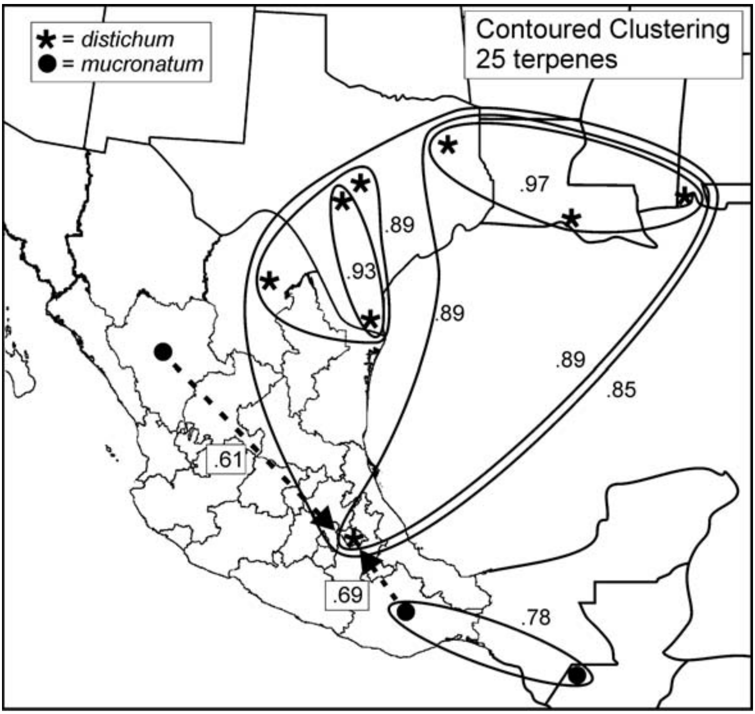

Figure 7. Contoured clustering based on 25 terpenes.

Of course, the Bolleros, MX population, with oils like var. *distichum* might have been derived from germplasm of var. *distichum* introduced from the USA (Fig. 7).

Based on analyses of the oils, it appears that *T. distichum* var. *distichum* from the South Central USA is distinct from var. *imbricarium* in Florida, but individuals with imbricate leaves from Fowl River, AL (cf. var. *imbricarium*) had oil patterns like var. *distichum*. *Taxodium d*. var. *distichum* appears to have 2 geographic chemical groups in the area studied: South Central USA and Texas Hill Country-northern Mexico (Fig. 7). Two types of oil patterns appear to be indigenous to Mexico: Durango and Oaxaca-Guatemala (Fig. 7). Additional research (in progress) using DNA sequencing will be needed to resolve these relationships.

ACKNOWLEDGEMENTS

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Table 1. Leaf essential oil composition of populations of *Taxodium*. muc Dur = *mucronatum*, Durango, MX; muc Oax = *mucronatum*, Oaxaca, MX; muc Bol = *mucronatum*, Bolleros, MX; dist Guad = *distichum*, Guadalupe River, TX, dist Mob = *distichum*, Mobile Bay, AL, imb FL = var. *imbricarium*, Tampa, FL. Compounds in boldface appear to separate taxa and were used in numerical analyses. KI = Kovats Index (linear) on DB-5 column. Compositional values less than 0.1% are denoted as traces (t). Unidentified components less than 0.5% are not reported. For unknown compounds, four ions are listed, with the largest ion underlined.

KI	compound	muc Dur	muc Oax	muc Boll	dist Guad	dist Mob	imb FL
921	tricyclene	0.2	0.6	0.3	t	0.2	0.3
924	**α-thujene**	**1.1**	**-**	**-**	**0.4**	**t**	**-**
932	**α-pinene**	**27.3**	**42.9**	**76.6**	**5.3**	**72.8**	**79.3**
946	camphene	0.9	0.2	1.0	t	0.7	0.4
969	**sabinene**	**16.9**	**0.4**	**0.2**	**1.9**	**0.2**	**0.3**
974	**1-octen-3-ol**	**-**	**-**	**-**	**-**	**-**	**0.6**
974	β-pinene	0.9	1.2	3.0	0.3	2.1	1.4
988	myrcene	3.8	2.2	4.2	3.9	3.0	2.3
1002	α-phellandrene	0.2	t	t	t	t	t
1014	**α-terpinene**	**4.4**	**t**	**0.1**	**0.9**	**t**	**0.1**
1020	**p-cymene**	**0.5**	**1.2**	**1.9**	**0.1**	**t**	**t**
1024	**limonene**	**1.2**	**0.6**	**1.0**	**t**	**6.0**	**0.9**
1025	**β-phellandrene**	**1.2**	**0.6**	**0.9**	**61.5**	**5.0**	**0.6**
1044	(E)-β-ocimene	t	-	-	t	-	-
1054	**γ-terpinene**	**7.3**	**0.1**	**0.1**	**1.6**	**0.1**	**0.2**
1065	cis-sabinene hydrate	0.3	-	-	t	-	-
1086	**terpinolene**	**2.3**	**0.3**	**0.5**	**0.8**	**0.4**	**0.9**
1098	linalool	-	t	t	-	-	-
1098	**trans-sabinene hydrate**	**0.3**	**-**	**-**	**t**	**-**	**-**
1100	n-nonanal	-	-	-	t	-	-
1102	perrilene	t	-	-	-	-	-
1114	endo-fenchol	t	-	-	-	-	-
1118	**cis-p-menth-2-en-1-ol**	**0.9**	**-**	**-**	**0.2**	**-**	**-**
1122	α-campholenal	-	t	t	-	-	-
1135	trans-pinocarveol	-	t	t	-	-	t
1136	**trans-p-menth-2-en-1-ol**	**0.5**	**-**	**-**	**0.1**	**-**	**-**
1141	camphor	-	t	t	-	-	t
1145	camphene hydrate	-	t	t	-	-	t

KI	compound	muc Dur	muc Oax	muc Boll	dist Guad	dist Mob	imb FL
1165	borneol	t	0.2	0.1	-	-	-
1166	p-mentha-1,5-dien-8-ol	-	-	-	t	t	0.1
1174	**terpinen-4-ol**	**15.5**	**0.2**	**0.3**	**3.3**	**0.2**	**0.4**
1186	**α-terpineol**	**1.1**	**0.8**	**0.8**	**0.3**	**0.8**	**1.0**
1195	**cis-piperitol**	**0.2**	**-**	**-**	**-**	**-**	**-**
1207	**trans-piperitol**	**0.3**	**-**	**-**	**t**	**-**	**-**
1215	trans-carveol	-	-	-	t	-	-
1287	**bornyl acetate**	**-**	**1.7**	**1.2**	**0.1**	**0.6**	**0.4**
1298	trans-pinocarvyl acetate	0.1	0.2	0.2	t	0.1	t
1324	myrtenyl acetate	-	-	-	-	t	0.1
1339	trans-carvyl acetate	-	-	-	0.2	t	-
1345	α-cubebene	-	t	t	-	-	-
1346	α-terpinyl acetate	t	-	-	-	-	-
1373	α-ylangene	-	t	-	-	-	-
1374	α-copaene	-	t	-	-	-	-
1387	β-bourbonene	-	0.1	t	-	-	-
1390	β-elemene	-	0.2	t	-	-	-
1396	duvalene acetate	t	-	-	0.2	0.2	t
1410	α-cedrene	t	-	-	t	-	-
1419	β-cedrene	0.1	0.2	0.1	t	-	-
1417	**(E)-caryophyllene**	**-**	**1.6**	**0.2**	**0.9**	**0.9**	**1.0**
1429	**cis-thujopsene**	**3.3**	**6.9**	**3.2**	**1.7**	**-**	**-**
1452	α-humulene	-	0.3	t	0.1	0.1	0.2
1476	β-chamigrene	0.2	-	-	t	-	-
1478	γ-muurolene	-	1.2	0.2	-	-	0.1
1480	**germacrene D**	**0.2**	**0.8**	**-**	**-**	**-**	**4.0**
1495	γ-amorphene	-	0.3	-		-	-
1500	**α-muurolene**	**-**	**0.8**	**0.3**		**-**	**0.1**
1500	β-himachalene	0.3	-	-	0.1	-	-
1502	α-chamigrene	0.1	-	-	-	-	-
1504	**cuparene**	**0.2**	**0.4**	**0.2**	**0.2**	**-**	**-**
1505	β-bisabolene	-	t	-	-	-	-
1512	α-alaskene	t	-	-	-	-	-
1513	γ-cadinene	-	0.8	t	-	-	0.1
1522	**δ-cadinene**	**t**	**1.9**	**t**	**-**	**-**	**0.5**
1532	**γ-cuparene**	**0.2**	**-**	**-**	**t**	**-**	**-**
1533	**trans-cadina-1,4-diene**	**-**	**0.4**	**t**	**t**	**-**	**-**
1537	**α-cadinene**	**-**	**0.1**	**-**	**-**	**-**	**-**
1542	δ-cuparene	t	-	-	t	-	-

KI	compound	muc Dur	muc Oax	muc Boll	dist Guad	dist Mob	imb FL
1550	occidenol	-	0.2	-	-	-	-
1561	(E)-nerolidol	t	-	-	0.1	-	-
1562	β-calacorene	-	t	-	-	-	-
1574	germacrene D-4-ol	-	-	-	-	-	t
1582	**caryophyllene oxide**	**0.2**	**1.1**	**0.3**	**7.3**	**3.6**	**0.2**
1589	allo-cedrol	0.1	-	-	0.2	-	-
1599	**widdrol**	**2.0**	**0.6**	**0.7**	**1.2**	**-**	**-**
1600	**cedrol**	**0.8**	**1.2**	**1.5**	**1.3**	**-**	**-**
1607	β-oplopenone	0.1	-	-	-	-	-
1608	**humulene epoxide II**	**-**	**0.1**	**t**	**0.8**	**-**	**-**
1618	junenol	-	-	-	-	-	t
1638	epi-α-cadinol	-	0.5	-	-	-	0.2
1638	epi-α-muurolol	-	0.5	-	-	-	0.2
1639	**caryophylla-4(12),8(13) -dien-5-α-ol**	**-**	**-**	**-**	**0.6**	**0.3**	**0.3**
1644	α-muurolol	-	0.3	-	-	-	0.1
1649	β-eudesmol	-	0.2	-	-	-	-
1652	**α-cadinol**	**0.3**	**2.0**	**t**	**-**	**-**	**1.0**
1653	**3-thujopsenone**	**-**	**-**	**-**	**0.3**	**-**	**-**
1662	**<u>43</u>,79,187,220**	**-**	**-**	**-**	**0.6**	**0.2**	**0.3**
1674	**<u>43</u>,79,187,220**	**-**	**-**	**-**	**0.6**	**0.3**	**0.4**
1683	**epi-α-bisabolol**	**0.4**	**0.4**	**0.3**	**0.4**	**-**	**-**
1685	**germacra-4(15),5,10(14) -trien-1-al**	**0.1**	**0.6**	**-**	**-**	**-**	**0.6**
1905	isopimara-9(11),15-diene	0.1	-	-	0.2	0.1	0.2
1959	**hexadecanoic acid**	**-**	**1.7**	**0.2**	**-**	**-**	**-**
1978	manoyl oxide	t	-	0.1	0.3	-	t
2055	abietatriene	t	0.3	0.1	0.2	t	t
2056	manool	-	0.2	-	-	-	-
2087	abietadiene	t	-	-	-	-	-
2132	**linoleic acid**	**-**	**1.7**	**-**	**-**	**-**	**-**
2184	sandaracopimarinol	-	t	-	-	-	-
2231	diterpene, **41**,81,273,318	-	0.7	-	-	-	-
2268	diterpene, **41**,81,273,318, iso.	-	0.8	-	-	-	-
2329	**6,7-dehydro-ferruginol**	**-**	**1.1**	**t**	**t**	**t**	**t**
2331	**trans-ferruginol**	**-**	**7.5**	**0.1**	**t**	**0.2**	**0.3**
2350	diterpene acid,41,55,301,316	-	1.4	-	-	-	-
2365	communic acid	-	0.4	-	-	-	-

Table 2. Leaf essential oil composition plants with high/low amounts of α-pinene /low/high limonene-β-phellandrene (LMNN/BPHL). dist Prog = *distichum*, Progresso, TX, dist Guad = *distichum*, Guadalupe R., Mob hi LI = Mobile Bay, high LMNN/BPHL, Mob hi AP = Mobile Bay, high α-pinene, imb hi AP = *imbricarium* (FL), high α-pinene, imb hi LI = *imbricarium* (FL)/, high LMNN/BPHL.

KI	compound	dist Prog	dist Guad	Mob hi LI	Mob hi AP	imb hi AP	imb hi LI
921	tricyclene	t	t	0.1	0.2	0.3	0.1
924	**α-thujene**	**0.3**	**0.4**	t	**t**	**-**	**t**
932	**α-pinene**	**5.1**	**5.3**	**25.6**	**72.8**	**79.3**	**51.0**
946	camphene	t	t	0.4	0.7	0.4	0.3
969	**sabinene**	**1.4**	**1.9**	**0.4**	**0.2**	**0.3**	**0.2**
974	β-pinene	0.2	0.3	1.2	2.1	1.4	1.8
988	myrcene	3.4	3.9	2.8	3.0	2.3	3.8
1002	α-phellandrene	t	t	t	t	t	**t**
1014	**α-terpinene**	**0.2**	**0.9**	**0.1**	**t**	**0.1**	**0.1**
1020	p-cymene	t	0.1	t	t	t	**t**
1024	**limonene**	**t**	**t**	**29.0**	**6.0**	**0.9**	**11.0**
1025	**β-phellandrene**	**78.2**	**61.5**	**28.7**	**5.0**	**0.6**	**10.0**
1054	**γ-terpinene**	**1.2**	**1.6**	**0.3**	**0.1**	**0.2**	**0.2**
1086	**terpinolene**	**0.6**	**0.8**	**0.4**	**0.4**	**0.9**	**0.9**
1118	**cis-p-menth-2-en-1-ol**	**t**	**0.2**	**-**	**-**	**-**	**-**
1174	**terpinen-4-ol**	**2.6**	**3.3**	**0.5**	**0.2**	**0.4**	**0.3**
1186	α-terpineol	0.3	0.3	0.5	0.8	1.0	1.0
1287	bornyl acetate	0.3	0.1	0.8	0.6	0.4	0.4
1298	trans-pinocarvyl acetate	t	t	t	0.1	t	**t**
1396	duvalene acetate	0.1	0.2	0.3	0.2	t	**t**
1417	(E)-caryophyllene	0.3	0.9	0.6	0.9	1.0	0.2
1429	**cis-thujopsene**	**t**	**1.7**	**-**	**-**	**-**	**-**
1452	α-humulene	t	0.1	t	0.1	0.2	0.2
1478	**γ-muurolene**	**-**	**-**	**-**	**-**	**0.1**	**0.4**
1480	**germacrene D**	**-**	**-**	**-**	**-**	**4.0**	**4.5**
1500	**α-muurolene**	-	-	-	**-**	**0.1**	**0.2**
1504	cuparene	-	0.2	-	-	-	-
1513	**γ-cadinene**	**-**	**-**	**-**	**-**	**0.1**	**0.3**
1522	**δ-cadinene**	**-**	**-**	**-**	**-**	**0.5**	**0.9**
1574	germacrene D-4-ol	-	-	-	-	t	0.2
1582	**caryophyllene oxide**	**2.5**	**7.3**	**3.6**	**3.6**	**0.2**	**t**
1589	allo-cedrol	-	0.2	-	-	-	-

KI	compound	dist Prog	dist Guad	Mob hi LI	Mob hi AP	imb hi AP	imb hi LI
1599	**widdrol**	**t**	**1.2**	-	**-**	**-**	-
1600	**cedrol**	**t**	**1.3**	-	**-**	**-**	-
1608	**humulene epoxide II**	**0.3**	**0.8**	**-**	**-**	-	**-**
1638	**epi-α-cadinol**	-	**-**	**-**	**-**	**0.2**	**0.5**
1638	**epi-α-muurolol**	-	**-**	**-**	**-**	**0.2**	**0.4**
1639	**caryophylla-4(12),8(13) -dien-5-α-ol**	**t**	**0.6**	**0.3**	**0.3**	**0.3**	**-**
1644	α-muurolol	-	-	-	-	0.1	0.2
1652	**α-cadinol**	**-**	**-**	-	**-**	**1.0**	**2.3**
1653	**3-thujopsenone**	**t**	**0.3**	**-**	**-**	**-**	**-**
1662	**43,79,187,220**	**t**	**0.6**	**0.2**	**0.2**	**0.3**	**-**
1674	**43,79,187,220**	**t**	**0.6**	**0.3**	**0.3**	**0.4**	**-**
1683	**epi-α-bisabolol**	**-**	**0.4**	**-**	**-**	**-**	**-**
1685	**germacra-4(15),5,10(14) -trien-1-al**	-	**-**	**-**	**-**	**0.6**	**1.1**
1789	1-octadecene	t	t	0.2	t	-	-
1905	isopimara-9(11),15-diene	0.2	0.2	0.2	0.1	0.2	t
1978	**manoyl oxide**	**0.2**	**0.3**	**-**	**-**	**t**	**-**
2055	**abietatriene**	**0.1**	**0.2**	**t**	**t**	**t**	**-**
2105	**isoabienol**	**-**	**-**	**-**	**-**	**-**	**1.0**
2184	**sandaracopirmarinal**	**-**	**-**	**-**	**-**	**-**	**0.5**
2329	**6,7-dehydro-ferruginol**	t	**t**	**0.2**	**t**	**t**	t
2331	**trans-ferruginol**	t	**t**	**0.3**	**0.2**	**0.3**	**1.7**