Leucaena: species diversity & genetic resources

Colin Hughes

Institute of Systematic & Evolutionary Botany
University of Zurich
Switzerland
colin.hughes@systbot.uzh.ch

Universität Zürich

1983 – 1997

Fieldwork in Central America, northern South America, Mexico & the U.S.A.
The Oxford Forestry Institute, University of Oxford – funded by the U.K. Department for International Development

1998

Monograph of Leucaena – Systematic Botany Monographs
& Leucaena Genetic Resources Handbook, Tropical Forestry Paper

2001-2003

Department of Plant Sciences, University of Oxford with post-doc Donovan Bailey, funded by The Royal Society & The Leverhulme Trust

2004 onwards

Inputs to a series of projects on phylogenetics and genomics of Leucaena led by Donovan Bailey, New Mexico State University, U.S.A.

SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 55

Monograph of Leucaena
(Leguminosae-Mimosoideae)

Colin Hughes

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS
9 November 1998

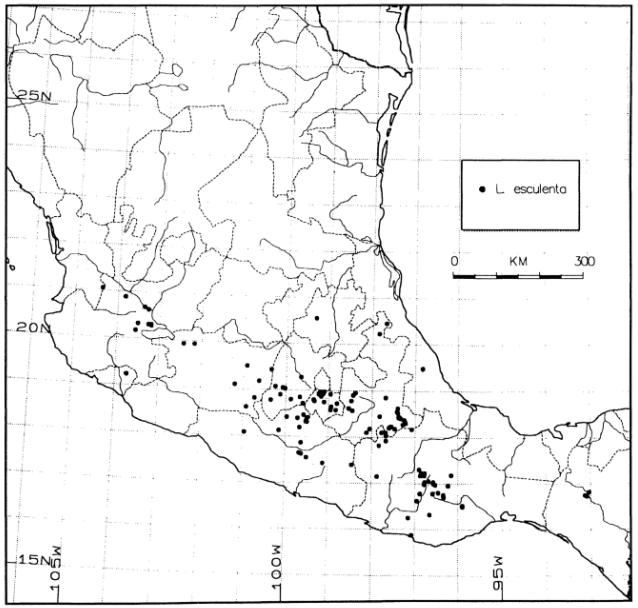
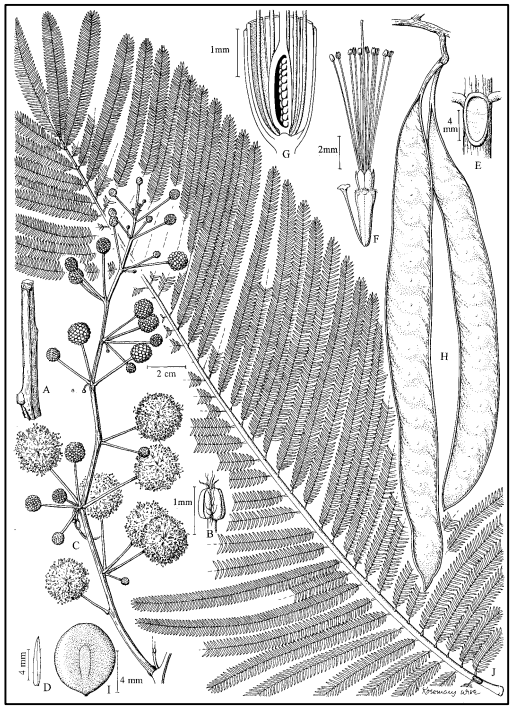
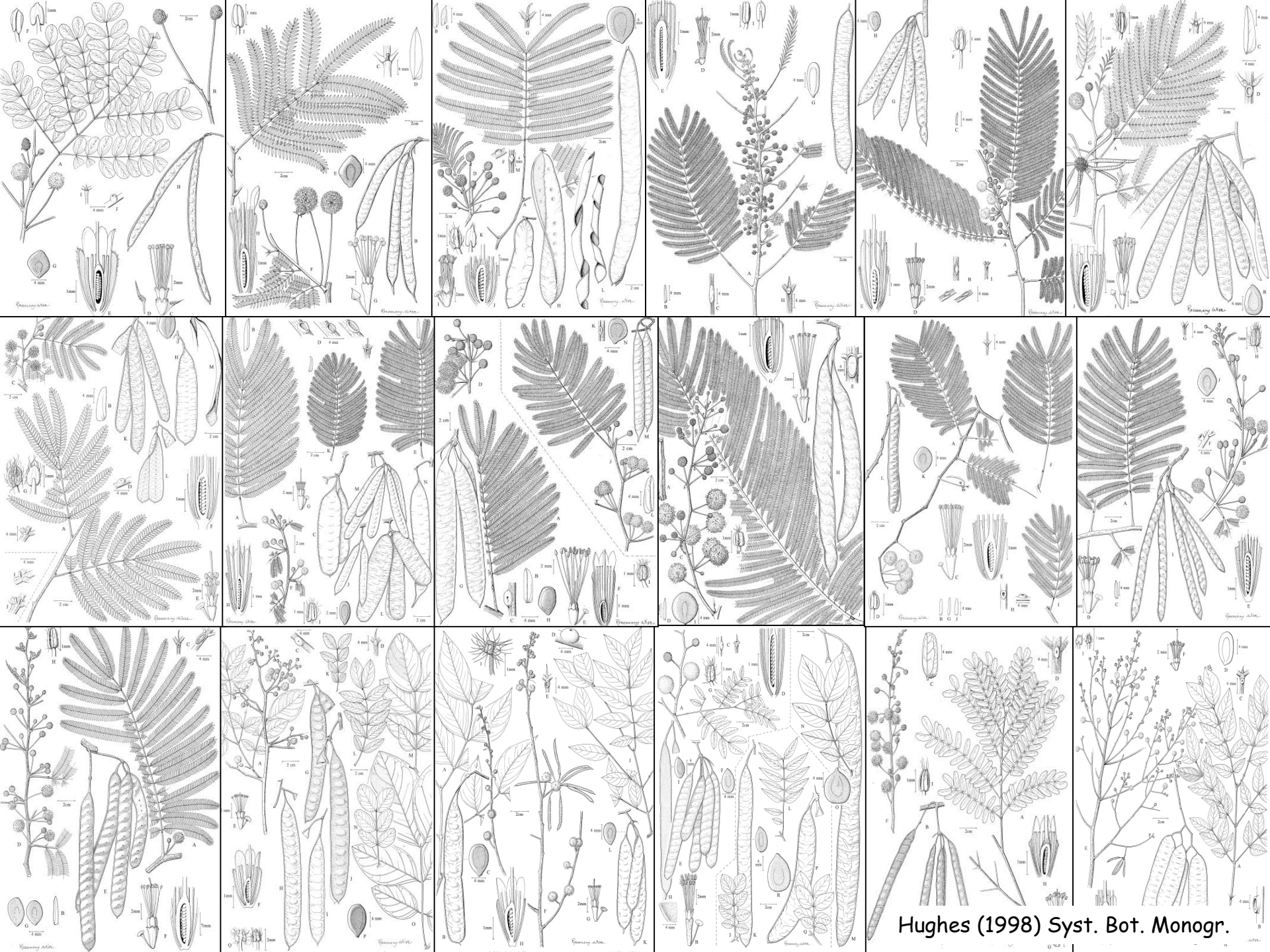
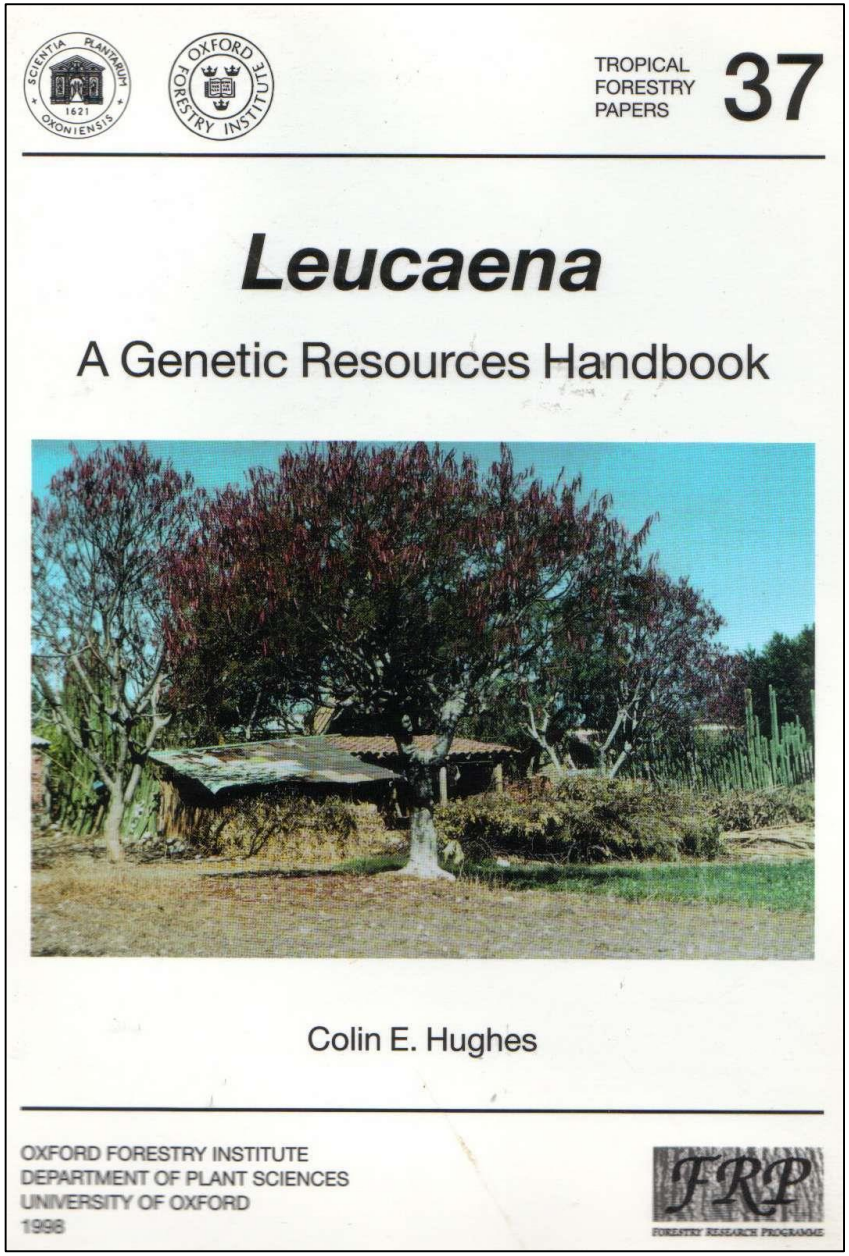


Figure 33 Map of south central Mexico showing the present day distribution of *L. esculenta*





Hughes (1998) Syst. Bot. Monogr.



- Taxonomy
- Species characteristics: tree size & form, ecogeography, psyllid resistance, phenology, wood quality, leaf quality, growth rates, weediness
- Ethnobotany & indigenous domestication as a food plant
- Hybrids
- Germplasm collections
- Seed management
- Conservation
- Domestication
- Identification
- Species accounts

Leucaena Online Data Resources

• *Images, distribution maps and an online key* constructed by Patrick Alexander for the identification of Leucaena species are available at: http://polyploid.net/leucaena/

• *Monograph of Leucaena* –Systematic Botany Monographs - available online via JSTOR at: http://www.jstor.org/stable/25027876

• *Leucaena Genetic Resources Handbook* – a .pdf [in English (TFP37) or in Spanish (TFP37S)] can be downloaded from the Bodleian Library in Oxford: http://www.bodley.ox.ac.uk/users/millsr/isbes/ODLF/TFP37.pdf

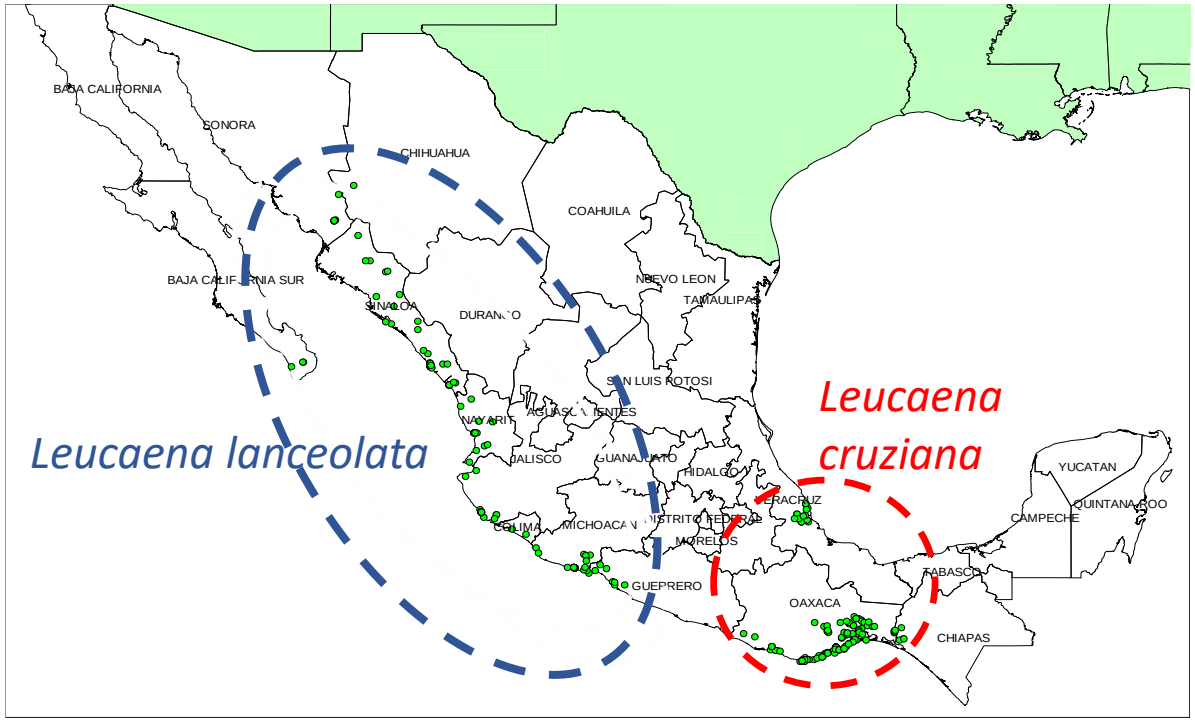
• *An online taxonomic and specimen database for Leucaena* is available, including data on more than 2800 specimens in 26 herbaria. Detailed field notes, common names, phenology and duplicate records are included, and the majority of specimens (2393) are georeferenced, at: http://herbaria.plants.ox.ac.uk/bol/leucaena

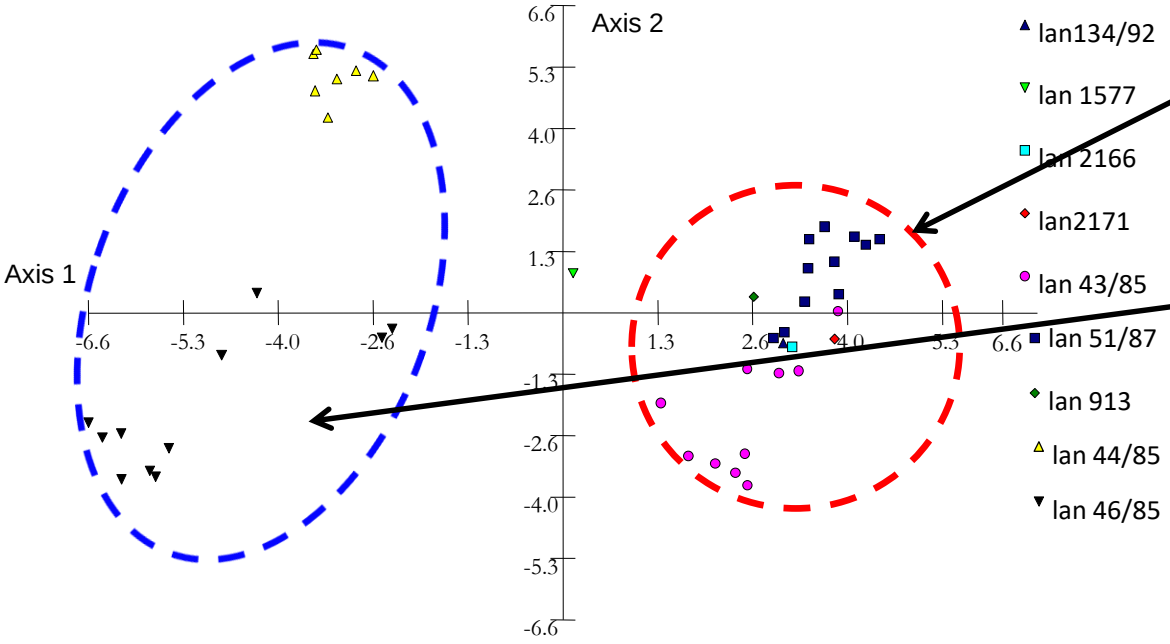
Species Limits

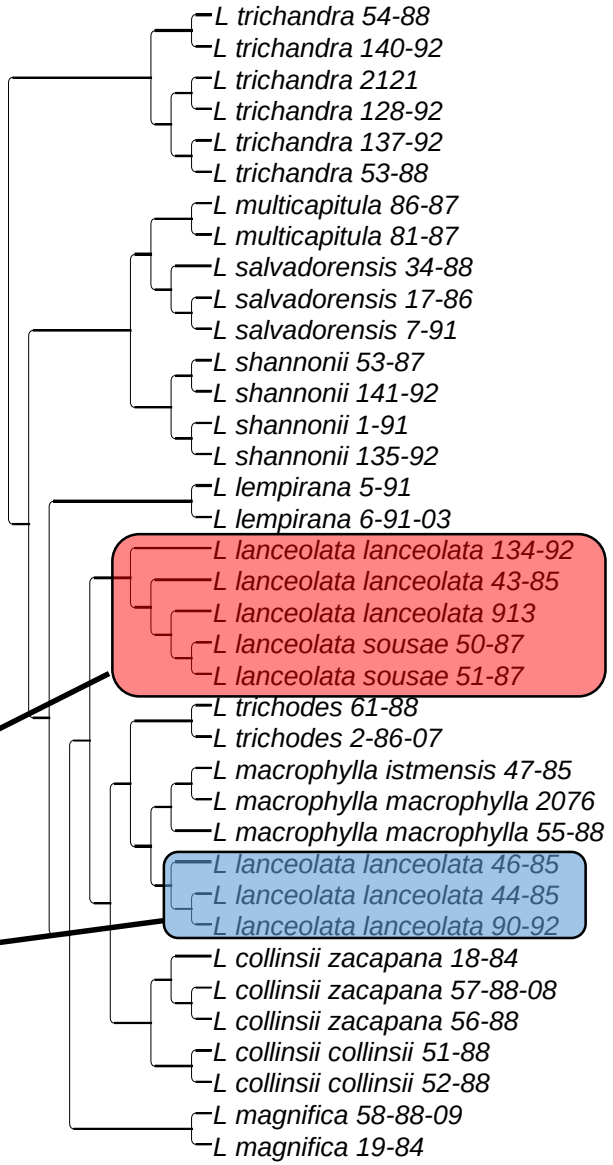
- Potential problems in the circumscription of some species, particularly for *L. lanceolata*, motivated re-assessments of species limits
  - 424 accessions representing two or more populations of each diploid species
  - 3 selective AFLP primer combinations
  - 1315 loci scored for diploids
  - Principle coordinates (MVSP) and STRUCTURE vers. 2.3.1

Govindarajulu et al. (2011)

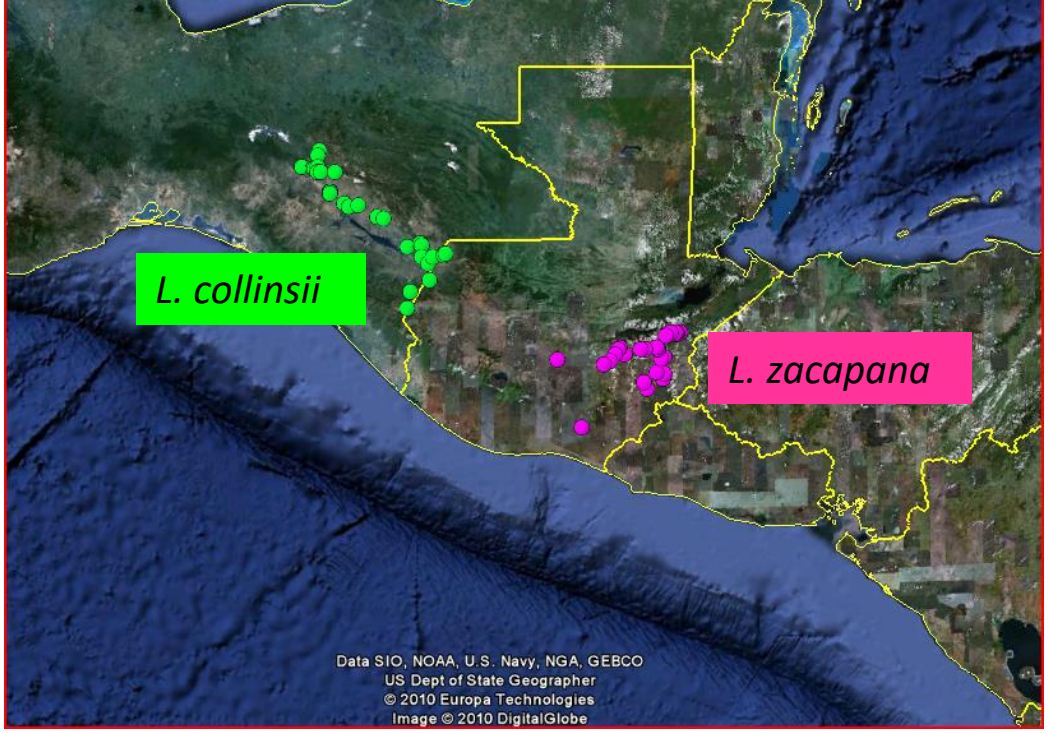
L. lanceolata





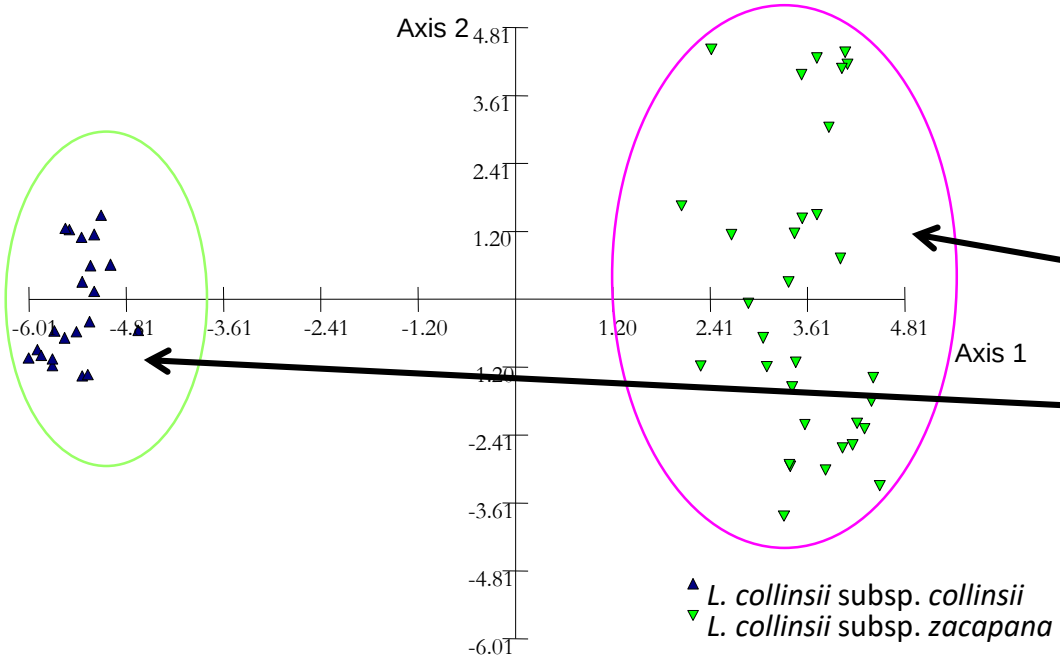


Govindarajulu et al. (2011)



L. collinsii

L trichandra 54-88
L trichandra 140-92
L trichandra 2121
L trichandra 128-92
L trichandra 137-92
L trichandra 53-88
L multicapitula 86-87
L multicapitula 81-87
L salvadorensis 34-88
L salvadorensis 17-86
L salvadorensis 7-91
L shannonii 53-87
L shannonii 141-92
L shannonii 1-91
L shannonii 135-92
L lempirana 5-91
L lempirana 6-91-03
L lanceolata lanceolata 134-92
L lanceolata lanceolata 43-85
L lanceolata lanceolata 913
L lanceolata sousae 50-87
L lanceolata sousae 51-87
L trichodes 61-88
L trichodes 2-86-07
L macrophylla istmensis 47-85
L macrophylla macrophylla 2076
L macrophylla macrophylla 55-88
L lanceolata lanceolata 46-85
L lanceolata lanceolata 44-85
L lanceolata lanceolata 90-92
L collinsii zacapana 18-84
L collinsii zacapana 57-88-08
L collinsii zacapana 56-88
L collinsii collinsii 51-88
L collinsii collinsii 52-88
L magnifica 58-88-09
L magnifica 19-84



Govindarajulu et al. (2011)

American Journal of Botany

American Journal of Botany 98(12): 2049–2063. 2011.

PHYLOGENETIC AND POPULATION GENETIC ANALYSES OF DIPLOID *LEUCAENA* (LEGUMINOSAE; MIMOSOIDEAE) REVEAL CRYPTIC SPECIES DIVERSITY AND PATTERNS OF DIVERGENT ALLOPATRIC SPECIATION[1]

RAJANIKANTH GOVINDARAJULU[2,5], COLIN E. HUGHES[3,4], AND C. DONOVAN BAILEY[2,4]

Two species added in 2011:

Leucaena cruziana

- Newly recognized lineage separate from *L. lanceolata*
- One of the diploid progenitors of tetraploid *L. leucocepahala*

Leucaena zacapana

- Sister to *L. collinsii,* but deeply divergent and geographically isolated
- Upranked from subspecies


collinsii


cruziana


diversifolia


esculenta


zacapana


lanceolata


retusa


confertiflora


cuspidata


trichodes


greggii


trichandra


salvadorensis


pallida


shannonii


leucocephala


involucrata

24 species


lempirana


macrophylla


magnifica


matudae


multicapitula


pueblana


pulverulenta


collinsii


cruziana


diversifolia


esculenta


zacapana


lanceolata


retusa


confertiflora


cuspidata


trichodes


greggii

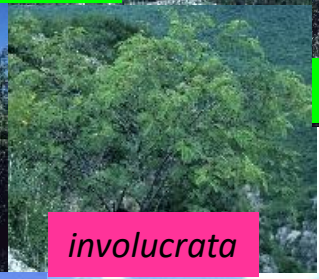

trichandra


salvadorensis


pallida


shannonii


leucocephala


involucrata

19 diploid species

5 tetraploid species

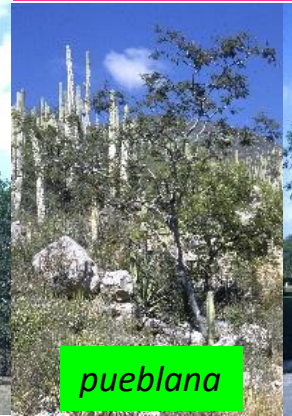

lempirana


macrophylla

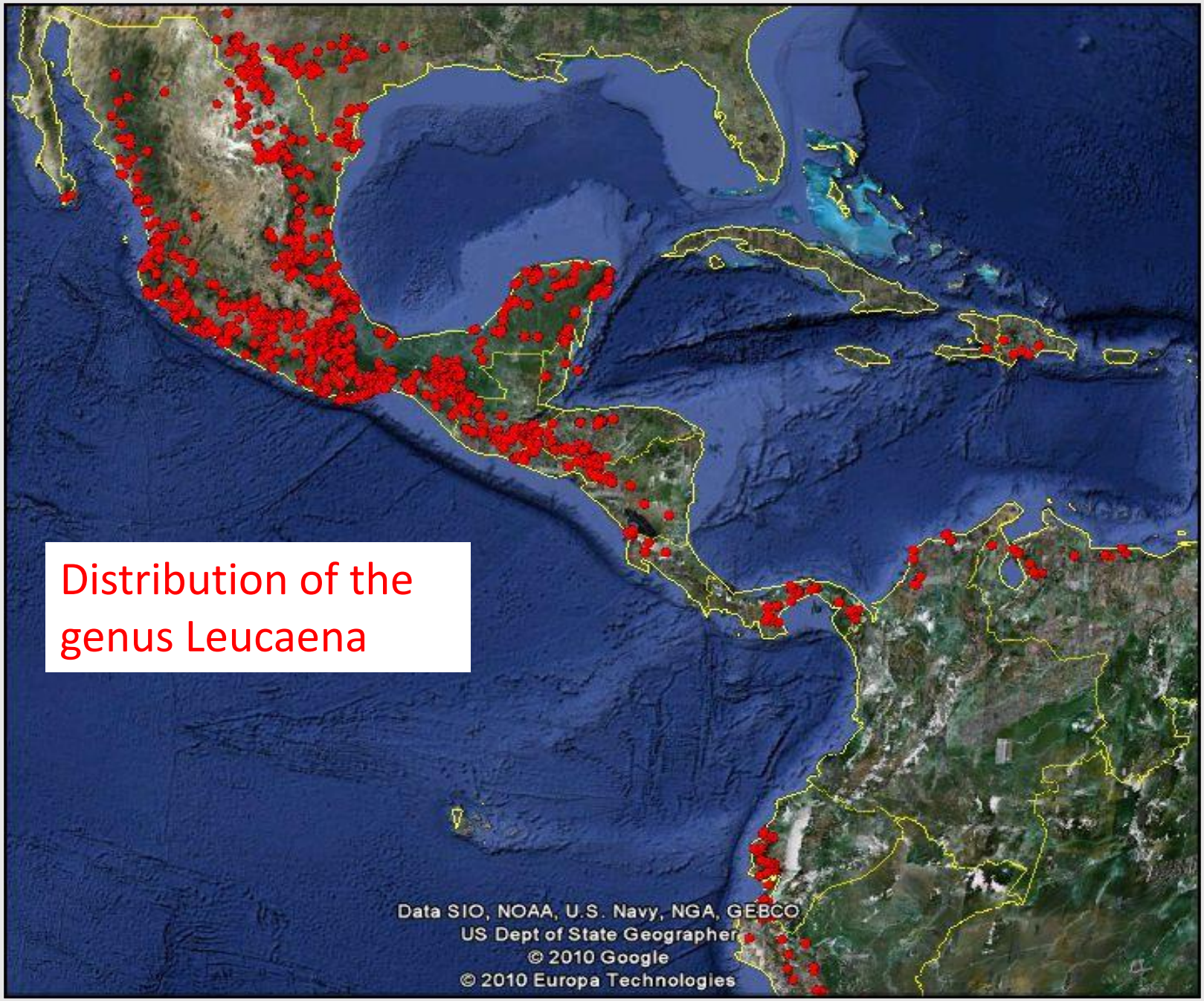

magnifica


matudae


multicapitula


pueblana


pulverulenta


Distribution of the genus Leucaena
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
US Dept of State Geographer
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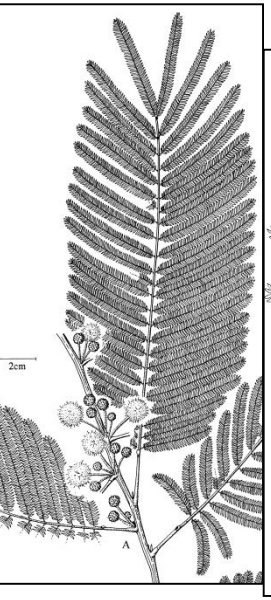
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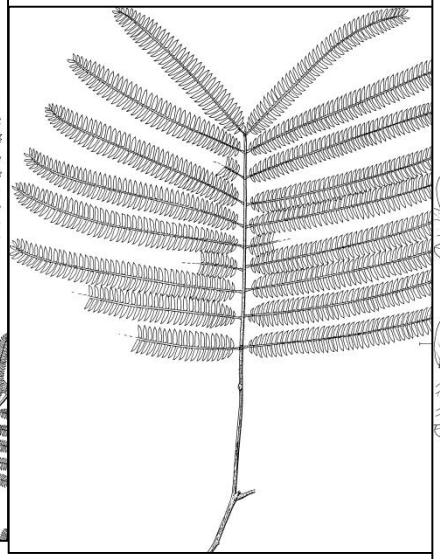

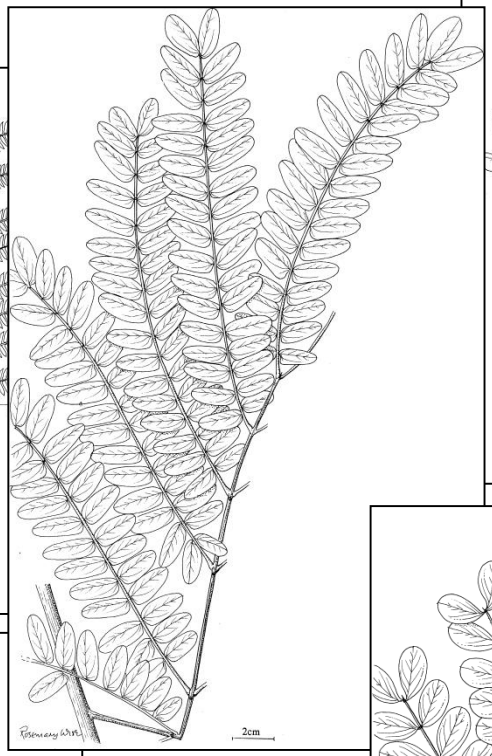
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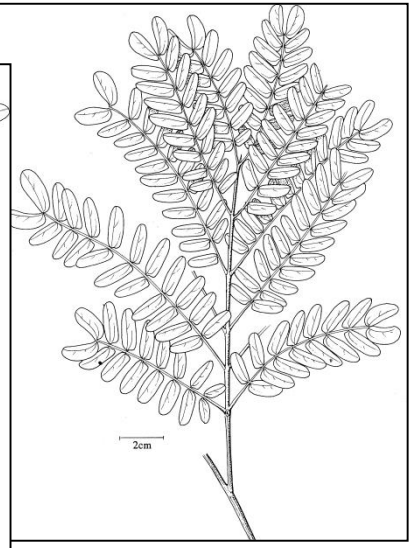
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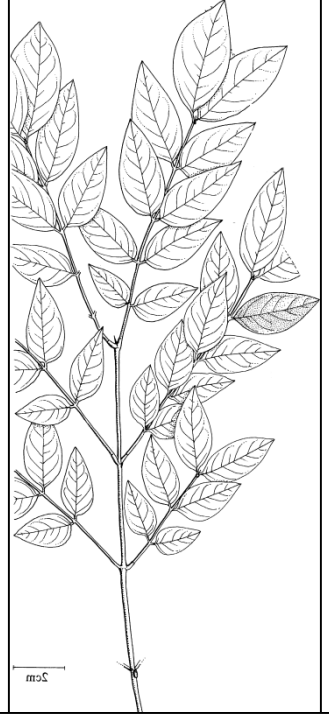
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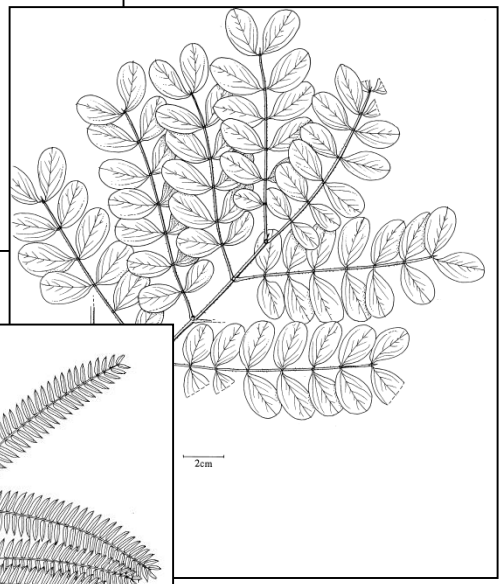
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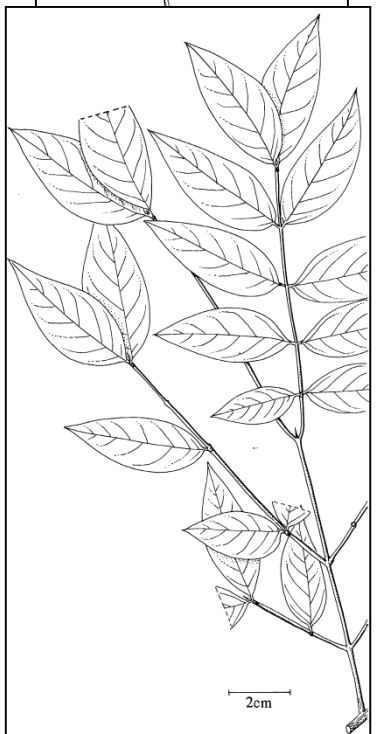
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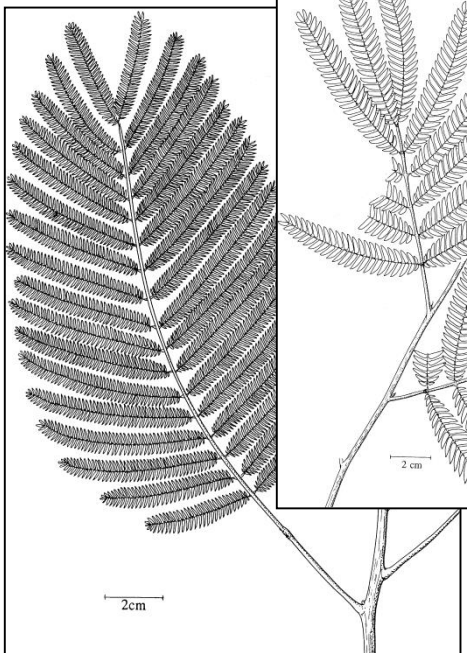
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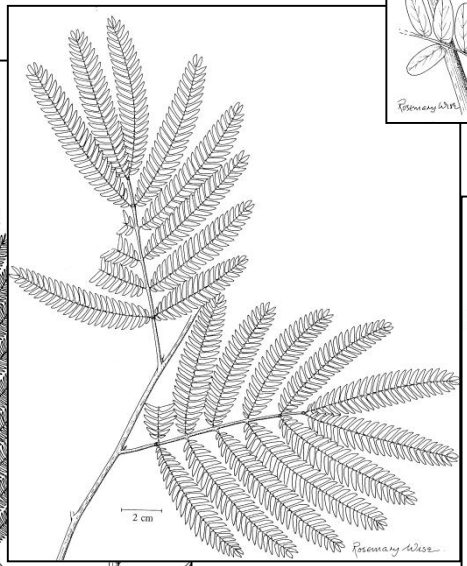
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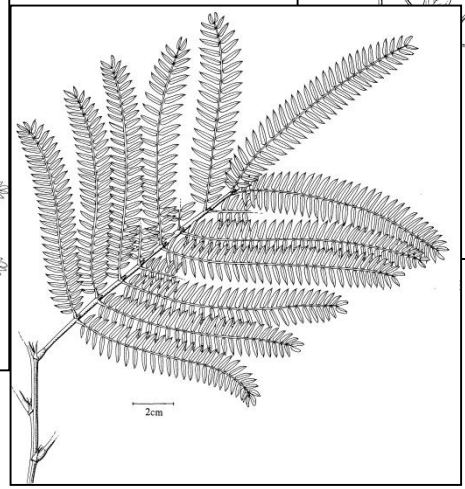
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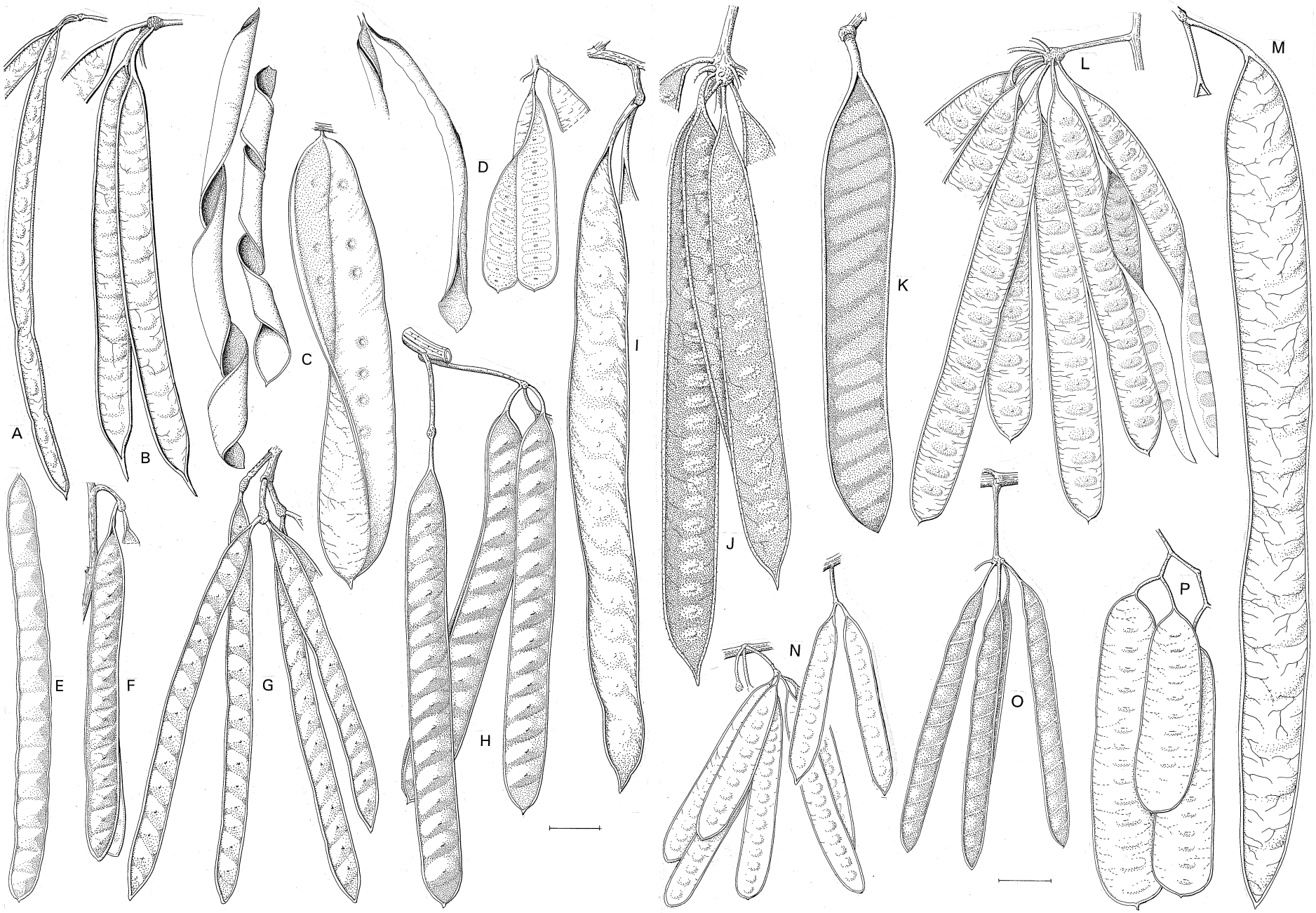
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Leucaena leucocephala

Tetraploid – L. cruziana x L. pulverulenta

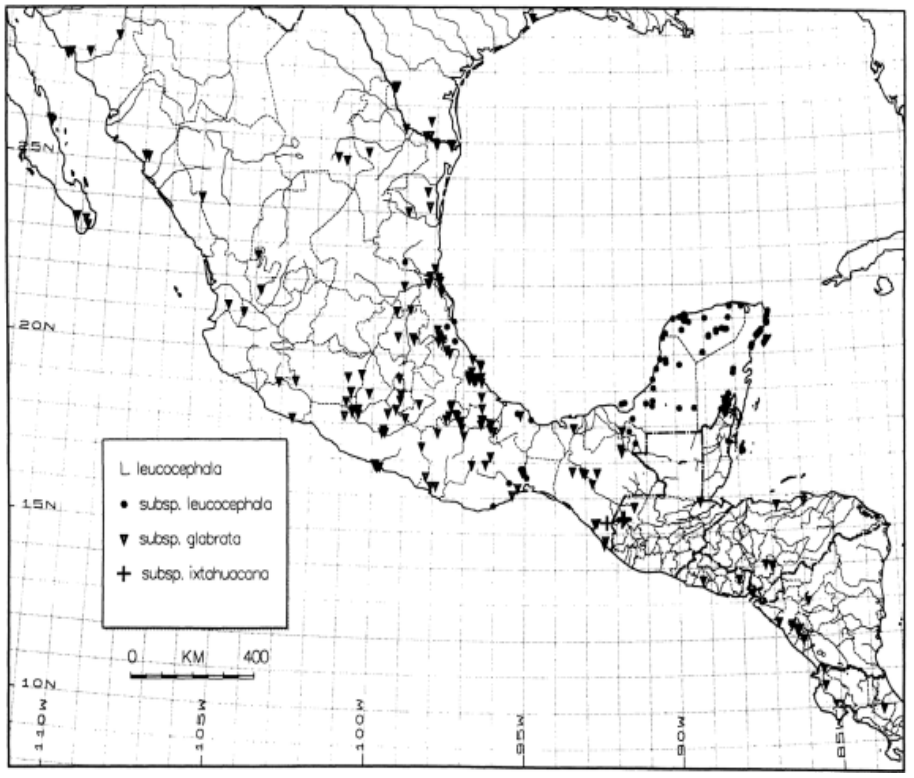
Fast-growing, easily managed

Psyllid susceptible

Excellent forage quality – the alfalfa of the tropics

One of the most common trees in the tropics

Invasive & weedy



Leucaena diversifolia

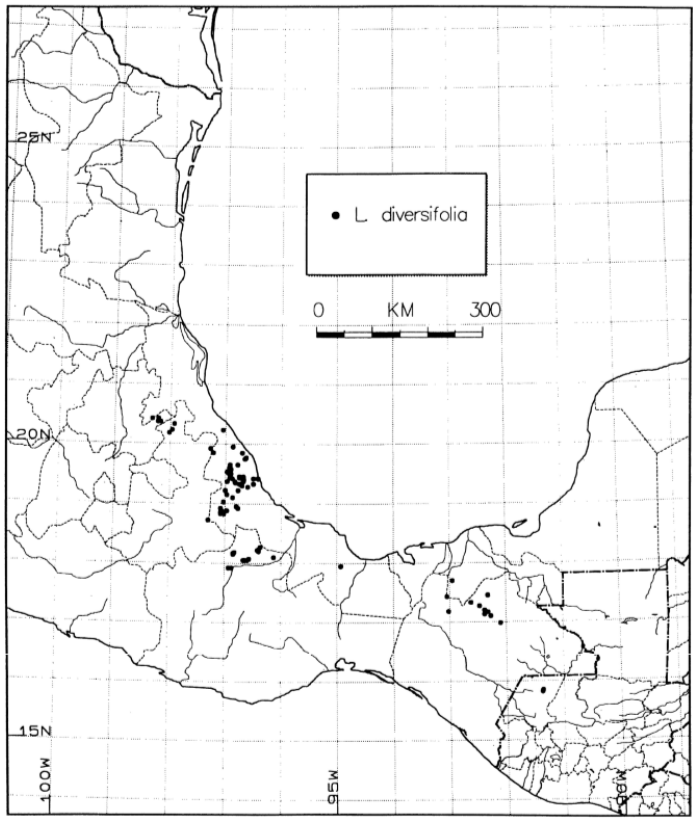
Tetraploid – L. pulverulenta x L. trichandra

Out-yields L. leucocephala under mid-elevation, cool but frost-free tropical highland conditions

Moderately psyllid resistant

Lower palatability and digestibility and higher condensed tannin levels than L. leucocephala

Spontaneous and artificial hybrids with L. leucocephala – L. x spontanea and KX3



Leucaena pallida

Tetraploid – L. pueblana x L. trichandra

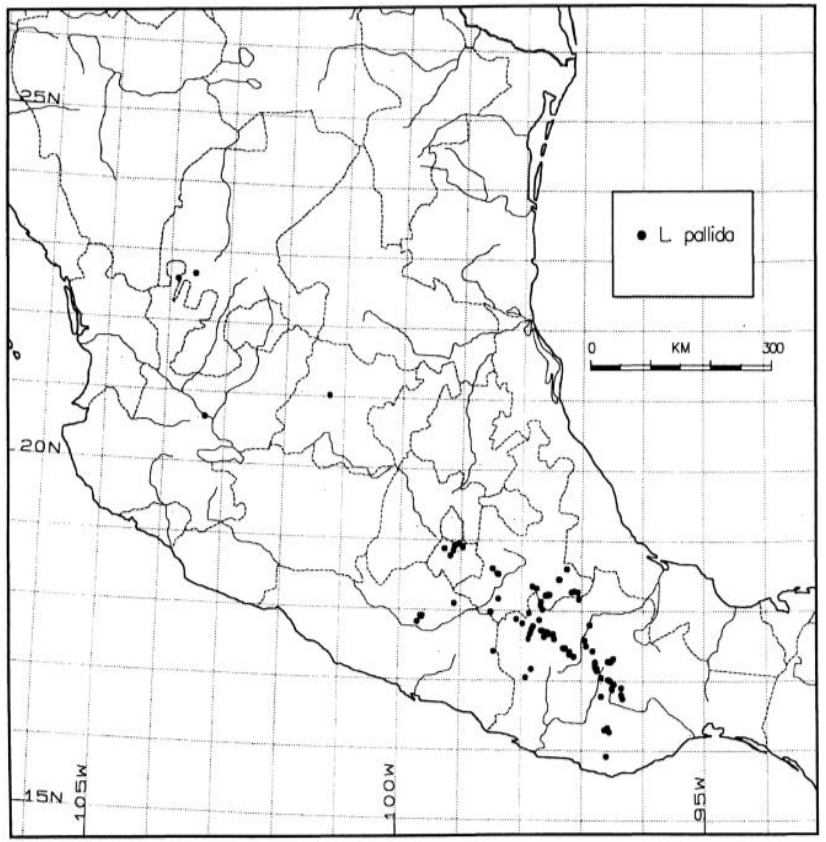
Branchy habit, fast growing & high yielding

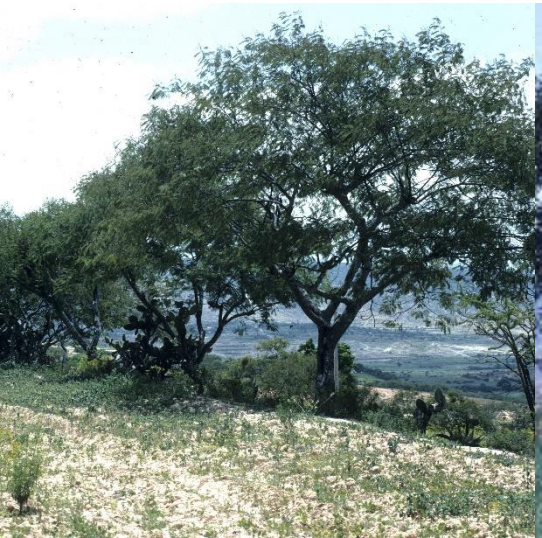
Cool tolerance

Excellent psyllid resistance

Lower edible fraction, higher condensed tannins and lower digestibility than L. leucocephala

Hybrids with L. leucocephala – KX2





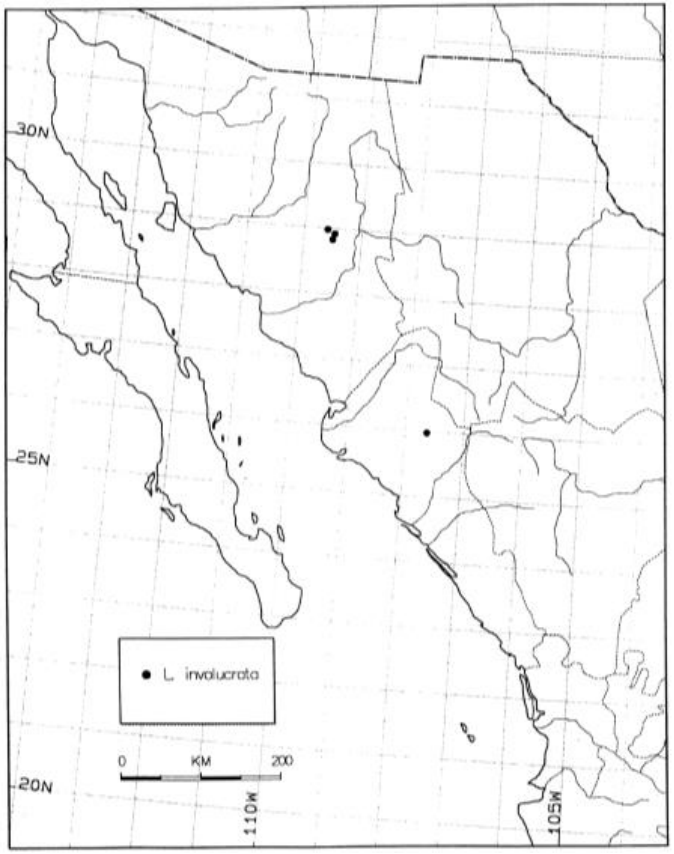
Leucaena involucrata

Tetraploid – likely an outlying species derived from tetraploid L. pallida, with which it shares the L. pueblana and L. trichandra diploid parentage

Similar in many ways to L. pallida, but poorly known

Known from just a handful of collections from Sonora in NW Mexico.

Potential and characteristics largely unknown



Leucaena confertiflora

Tetraploid – L. trichandra x L. cuspidata

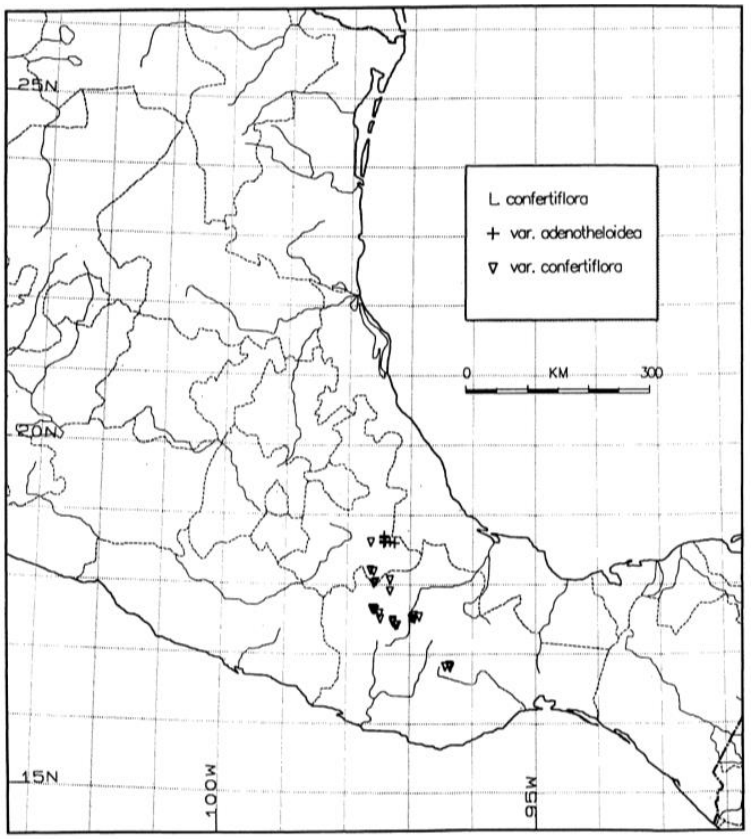
Small multi-stemmed tree; probably slow growing.
Cultivated and incipiently domesticated in S-C Mexico

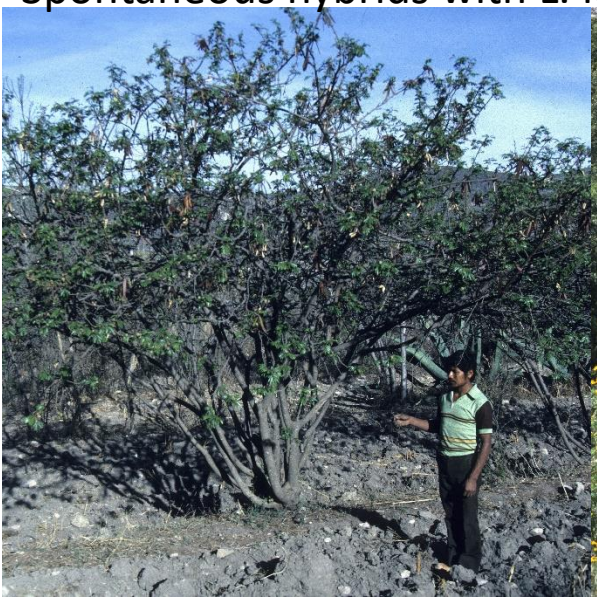
High elevation – 2500 m – cold tolerant

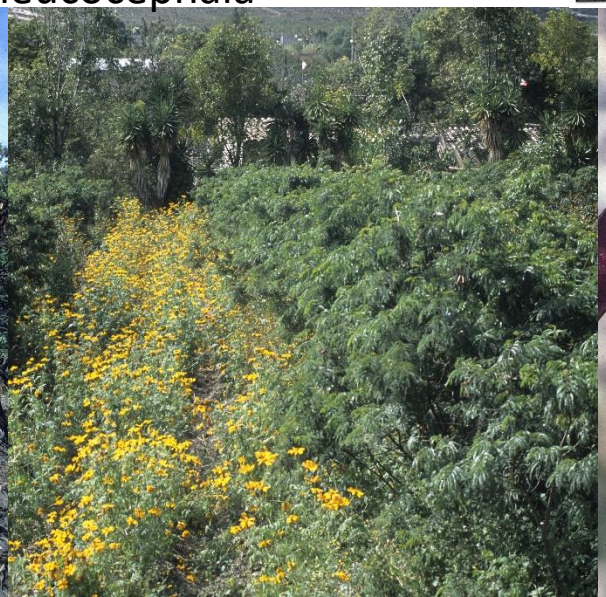
Highly psyllid resistant

Leaves: low digestibility and high condensed tannin

Spontaneous hybrids with L. leucocephala

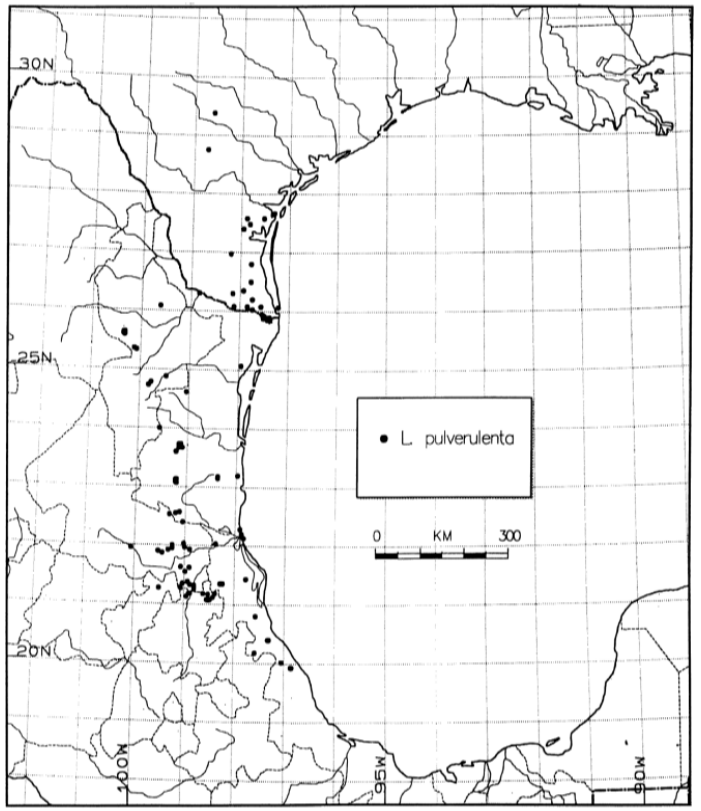






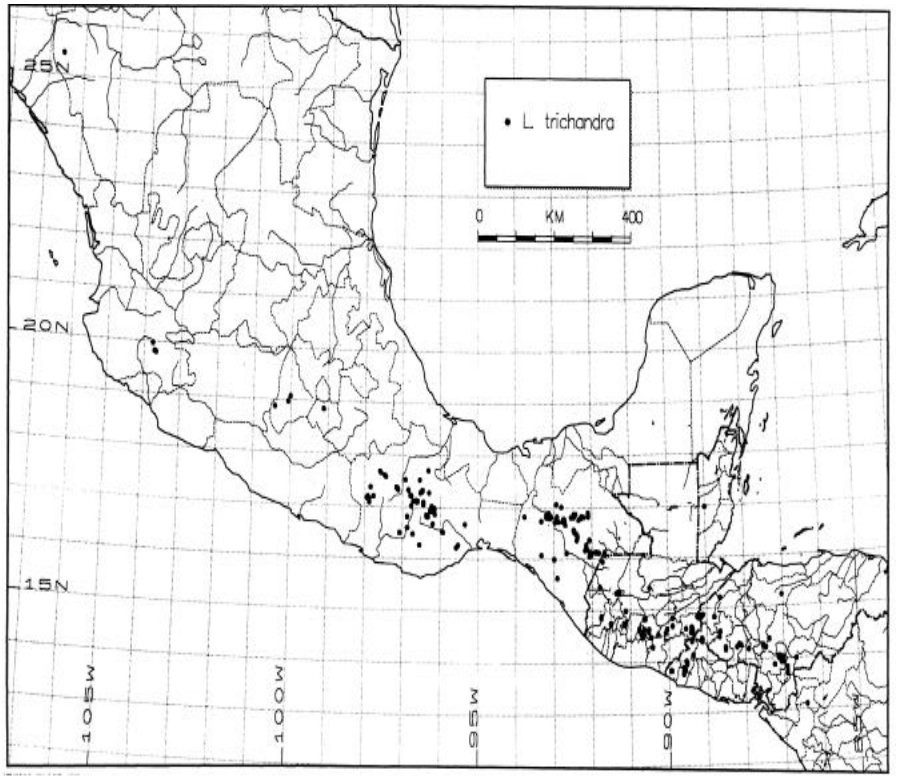
Leucaena pulverulenta

- One of the better known species; fast growing
- Moderate cold and limited frost tolerance, 19-29°N
- Moderately to highly susceptible to psyllids
- Leaves: low mimosine, but lower in vitro digestibility, crude protein & and higher condensed tannin than L. leucocephala
- One of the diploid progenitors of L. leucocephala.
- L. pulverulenta x L. leucocephala triploids



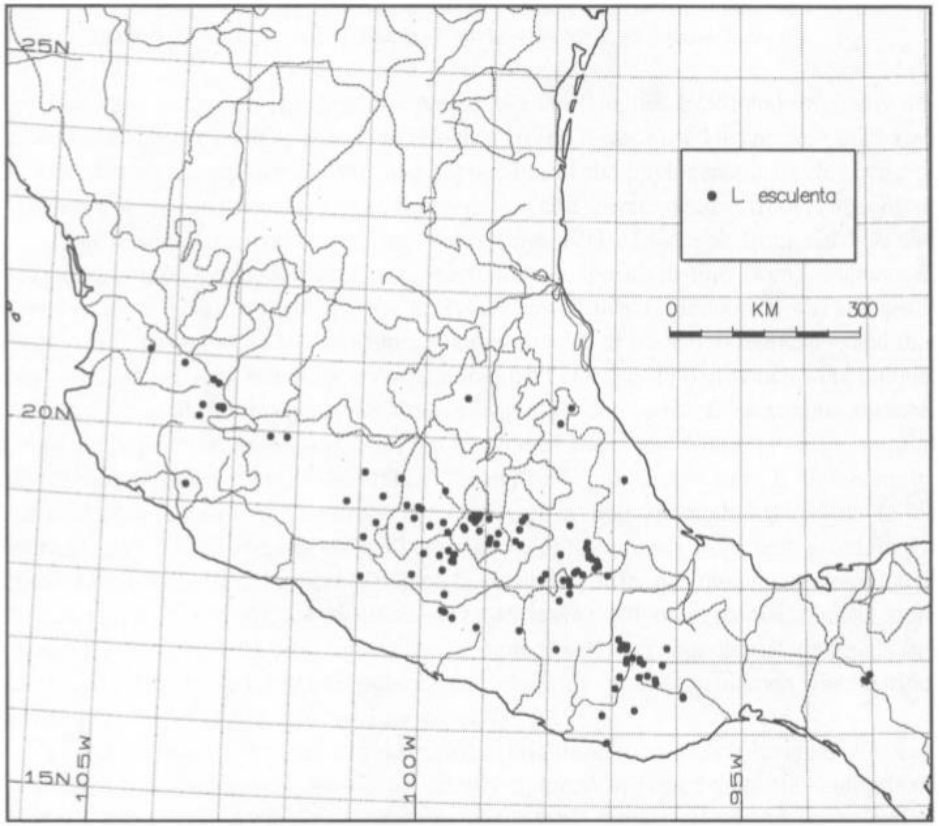
Leucaena trichandra

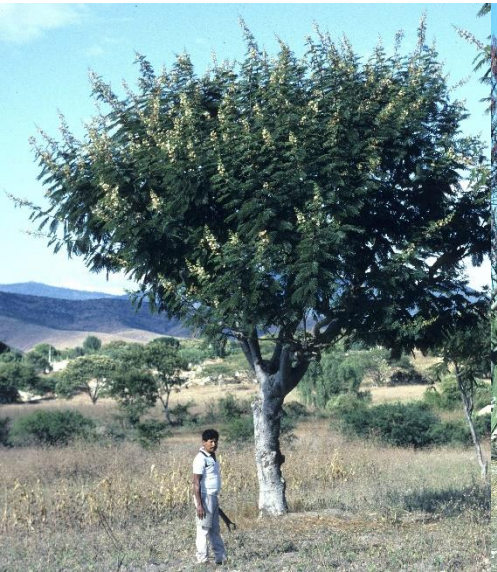
- Extremely variable: very wide geographic range. Seed source critically important.
- Sources from SE Guatemala especially promising
- Variable in morphology, leaves, growth rates, psyllid resistance, condensed tannin
- Tolerates nutrient-poor acidic soils
- Triploid hybrids with L. leucocephala



Leucaena esculenta

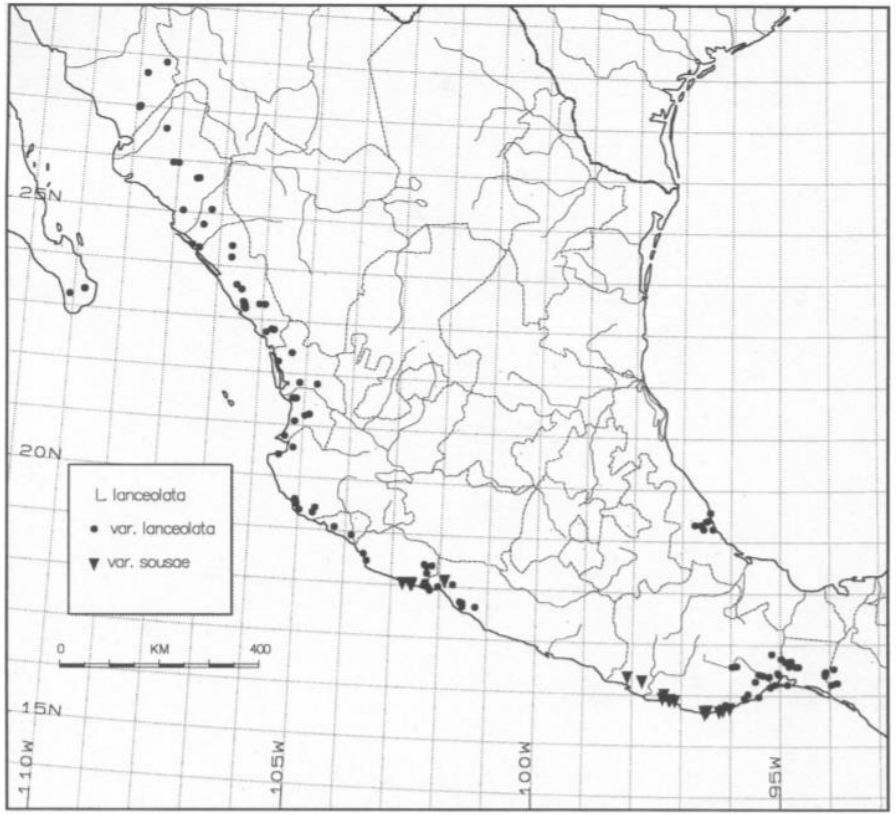
- Large tree; fast growing; high yield
- Moderately drought tolerant – 7 month dry season
- High psyllid resistance
- Leaves: low edible fraction; low in vitro dry matter digestibility; high condensed tannin
- Frequent sterile triploid spontaneous hybrids with *L. leucocephala* = KX4





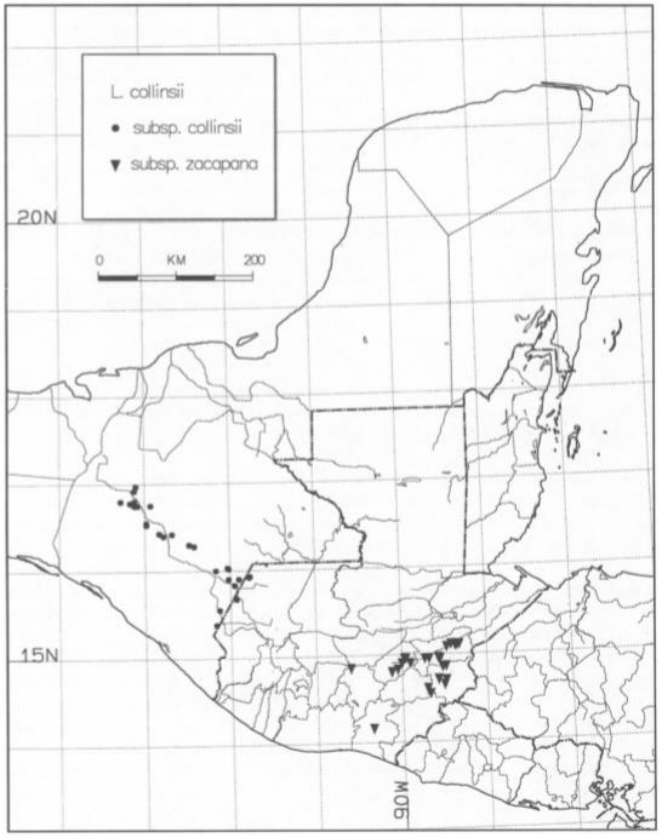
Leucaena cruziana & L. lanceolata

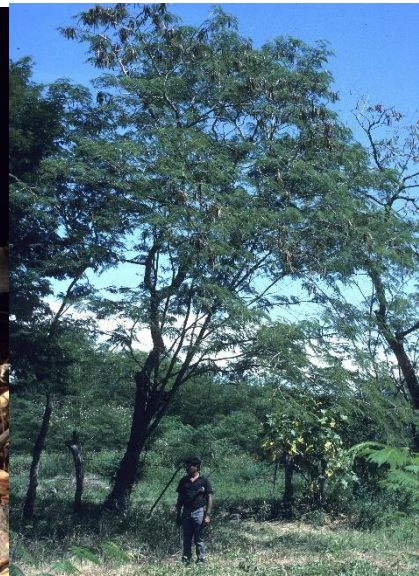
- Truly tropical – coastal – mainly < 400m elevation
- Low psyllid resistance
- Leaves: high in vitro digestibility, low condensed tannin content – forage quality similar to *L. leucocephala*
- *L. cruziana* = diploid progenitor of tetraploid *L. leucocephala*



Leucaena collinsii & L. zacapana

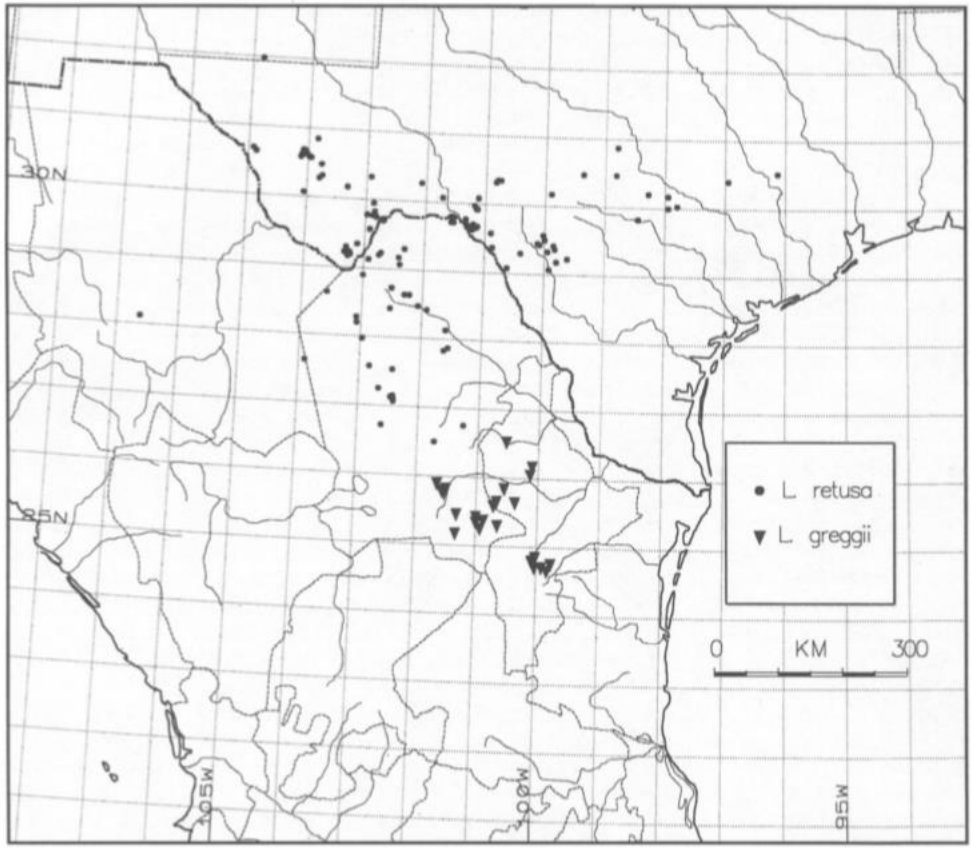
- Notable for dense durable wood & high wood biomass production
- Drought tolerant – 500-700 mm rainfall; 7 month dry season
- Highly psyllid resistant
- Leaves: high digestibility and low to zero tannin content





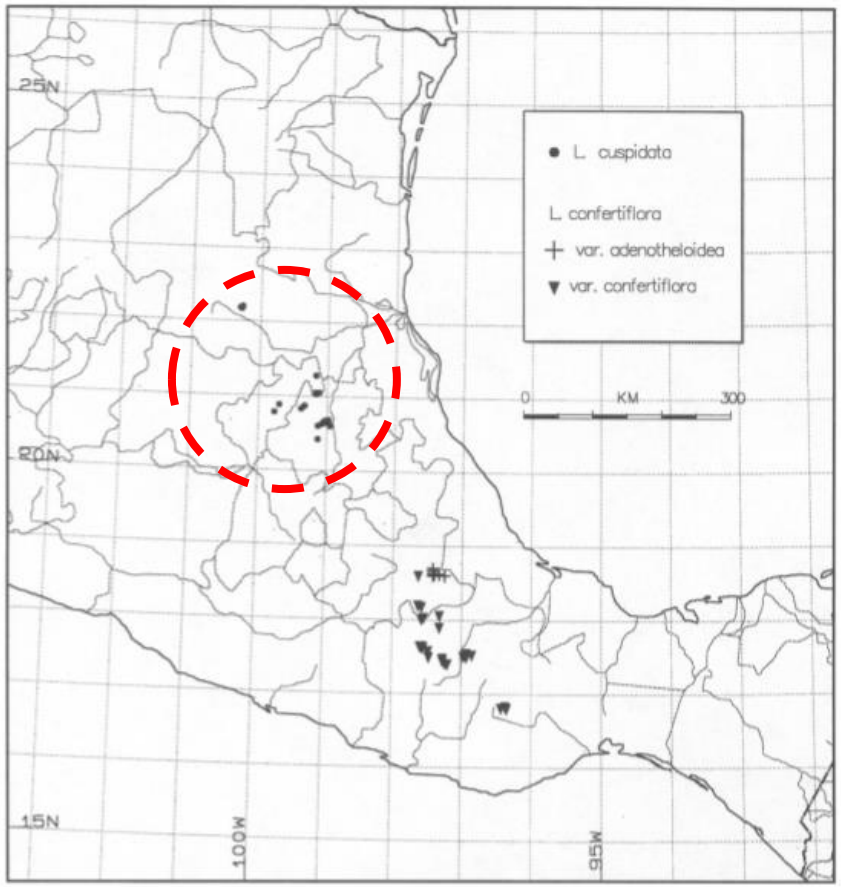
Leucaena retusa
Leucaena greggii

- Slow growing
- The two most northerly species 25-30°N
- Frost tolerant
- Psyllid resistant
- Leaves – low digestibility and high condensed tannin



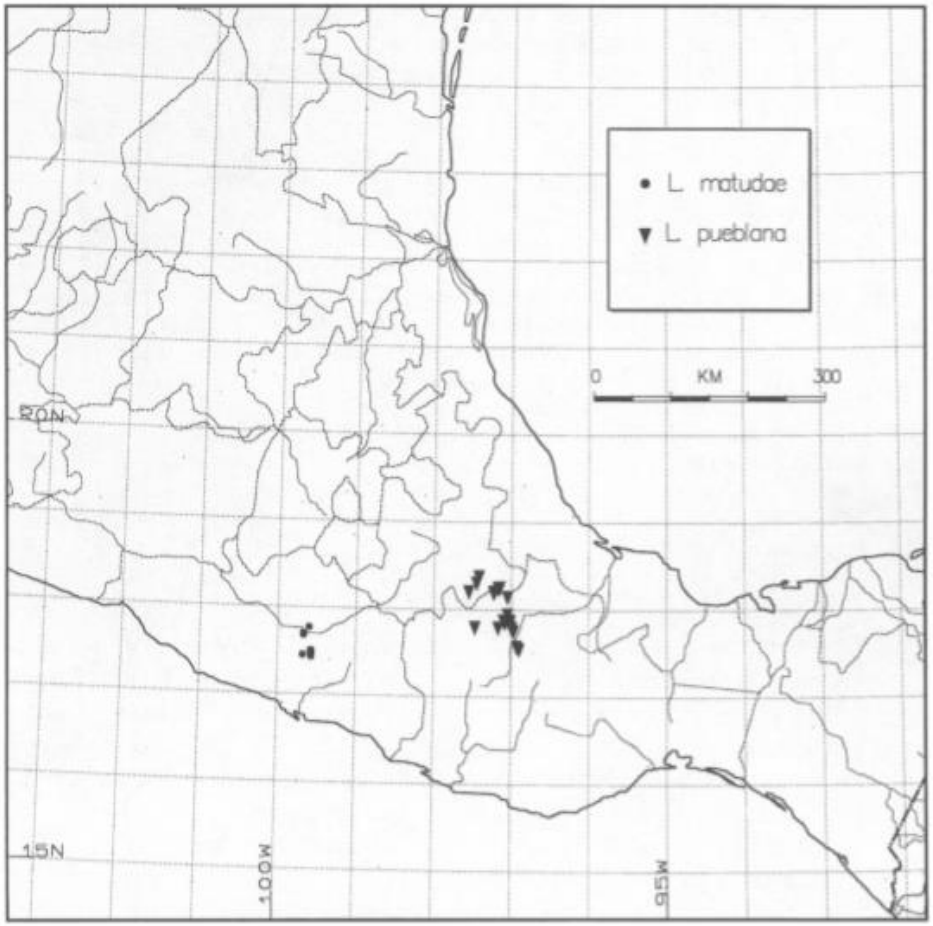
Leucaena cuspidata

- Poorly known and unusual species
- Rarely cultivated so far
- Growth potential unknown, but probably slow growing
- Multi-stemmed from base
- Cold tolerant – 1400-2400 m elevation
- Leaves – little data – but probably low digestibility and high condensed tannins



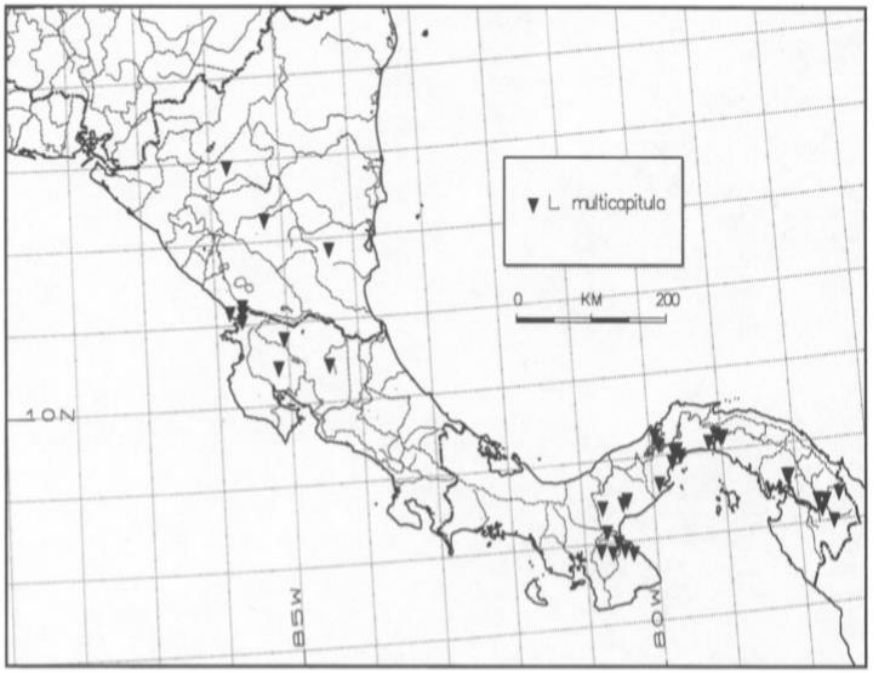
Leucaena matudae & L. pueblana

- Poorly known
- Rarely cultivated, but probably slow growing
- Drought tolerance – 500 – 800 mm mean annual rainfall, 7-8 month dry season
- Highly psyllid resistant
- Leaves – low crude protein content & high condensed tannin levels



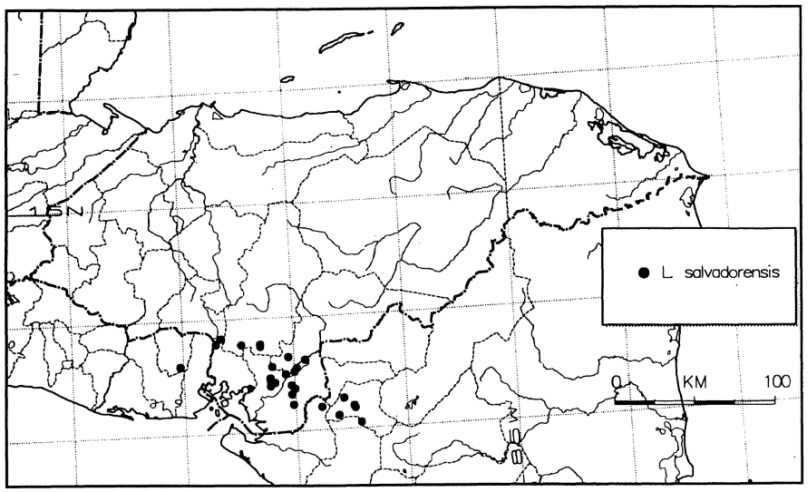
L. multicapitula

- Poorly known
- The largest Leucaena forming a large tree to 25m height. Fast growing
- Tropical lowland forest, including rain forests with rainfall up to 2500 mm
- Leaves: highly susceptible to psyllid; high in vitro digestibility, low condensed tannin; high forage quality

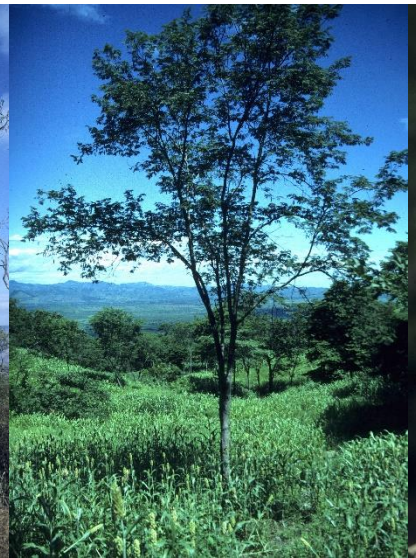


Leucaena salvadorensis

- Overlooked species until recently
- Highly esteemed species for wood production – fast growing, dense wood & high wood biomass producer
- Moderately susceptible to psyllid
- Forage quality poorly known, but probably high in vitro digestibility & low condensed tannin, but lower palatability than leucocephala

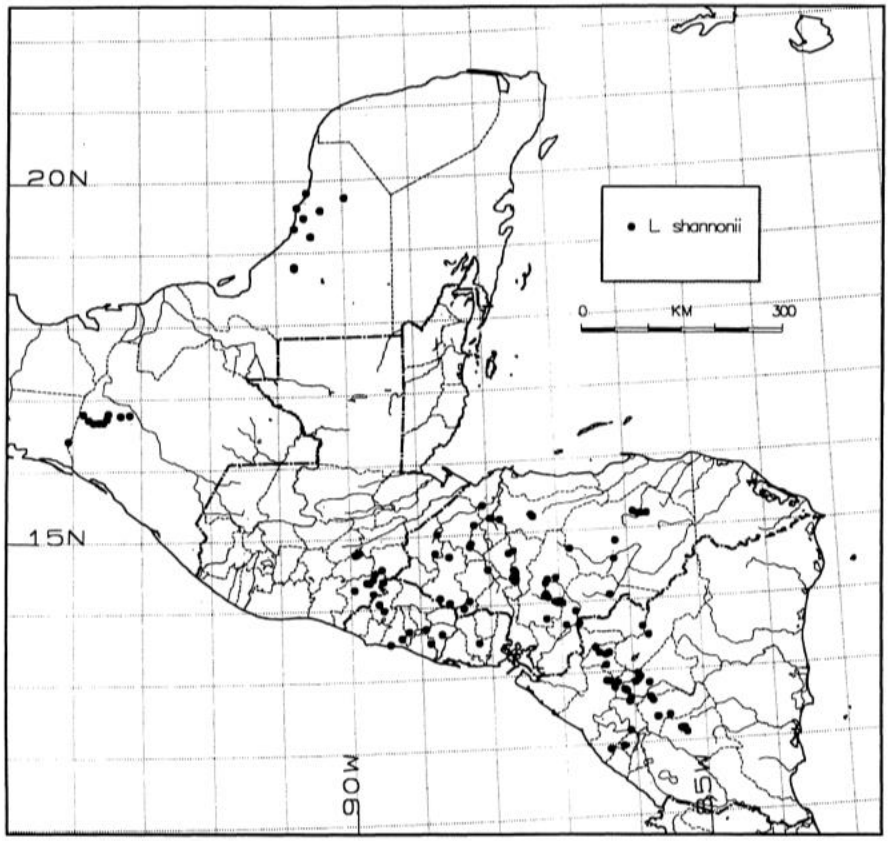






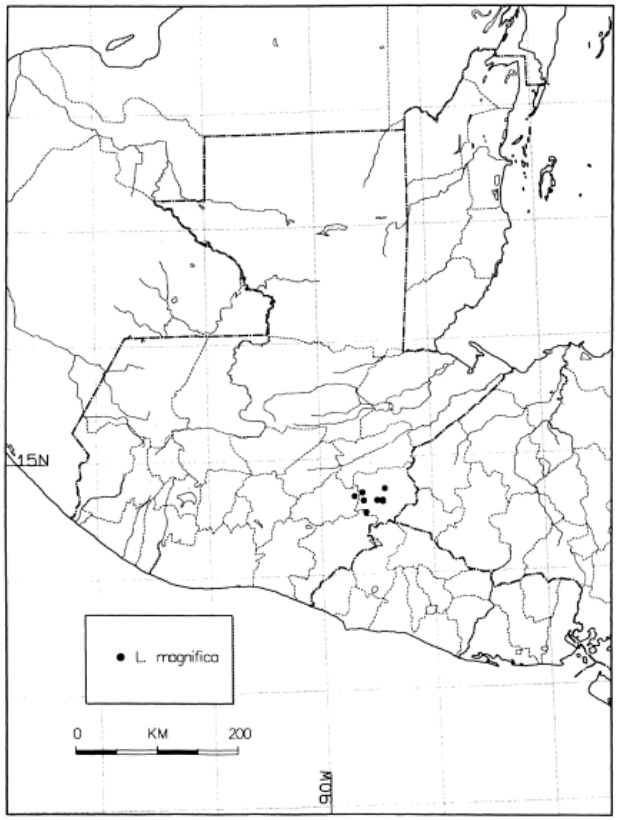
Leucaena shannonii

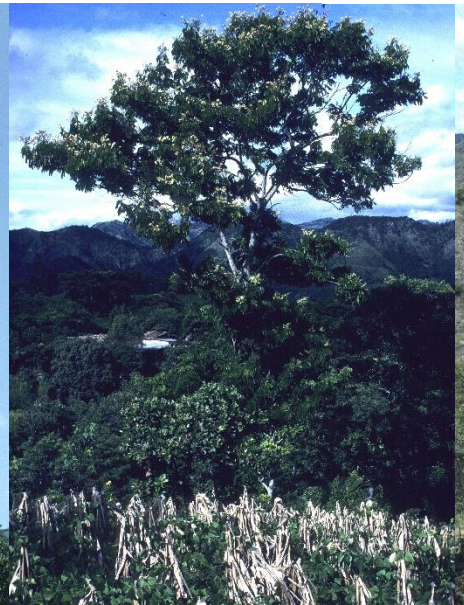
- Limited potential
- Slow growing
- Moderately susceptible to psyllids
- Good forage quality – very high crude protein content, high in vitro digestibility, low condensed tannin content



Leucaena magnifica

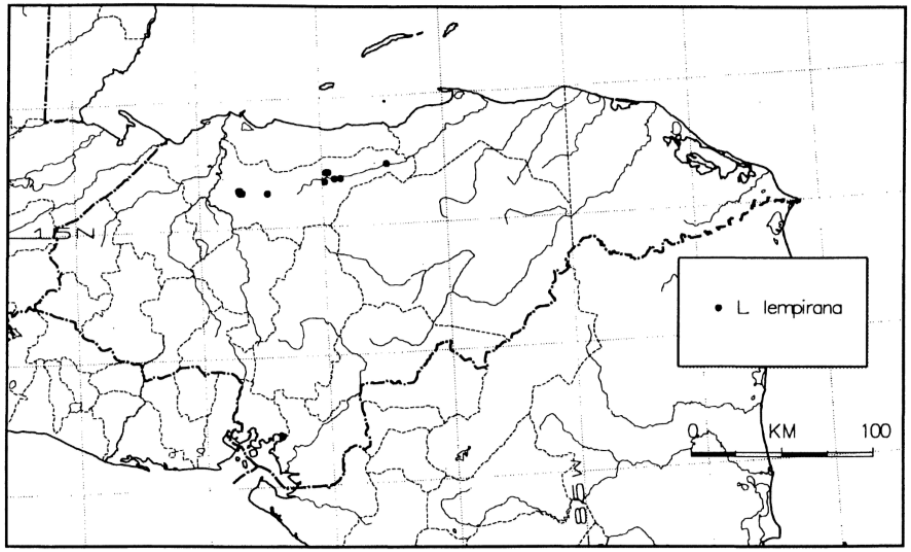
- Species discovered in 1984; only known from a few populations in SE Guatemala, <400km^2 natural range – critically endangered species
- Large tree, fast growing
- Moderately psyllid susceptible
- Leaves: high in vitro digestibility, very low condensed tannin





Leucaena lempirana

- Discovered in 1990 and first described in 1997
- Tree to 15 m ht
- Poorly known and little tested in trials
- Highly susceptible to psyllid
- Forage potential unknown

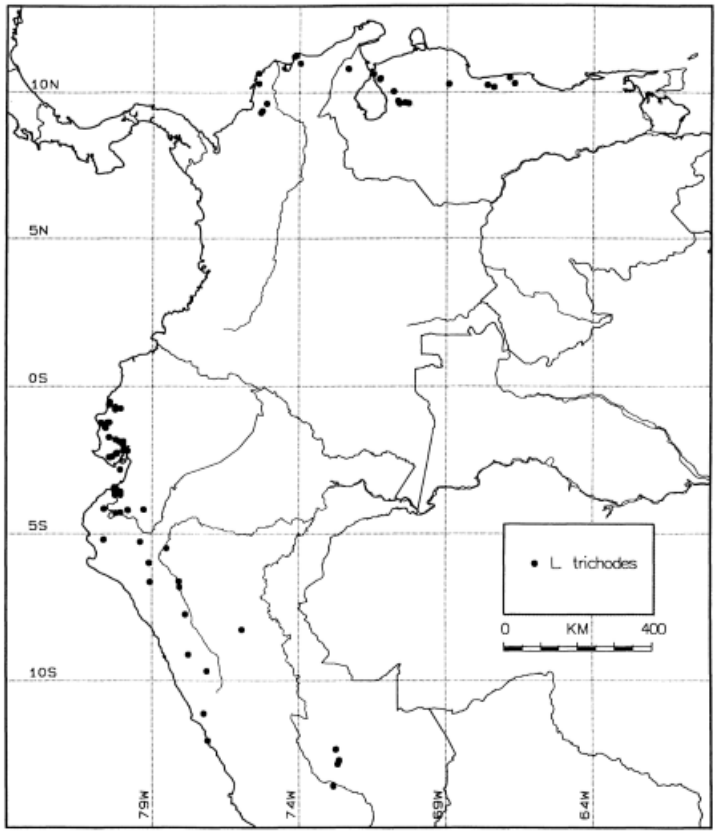






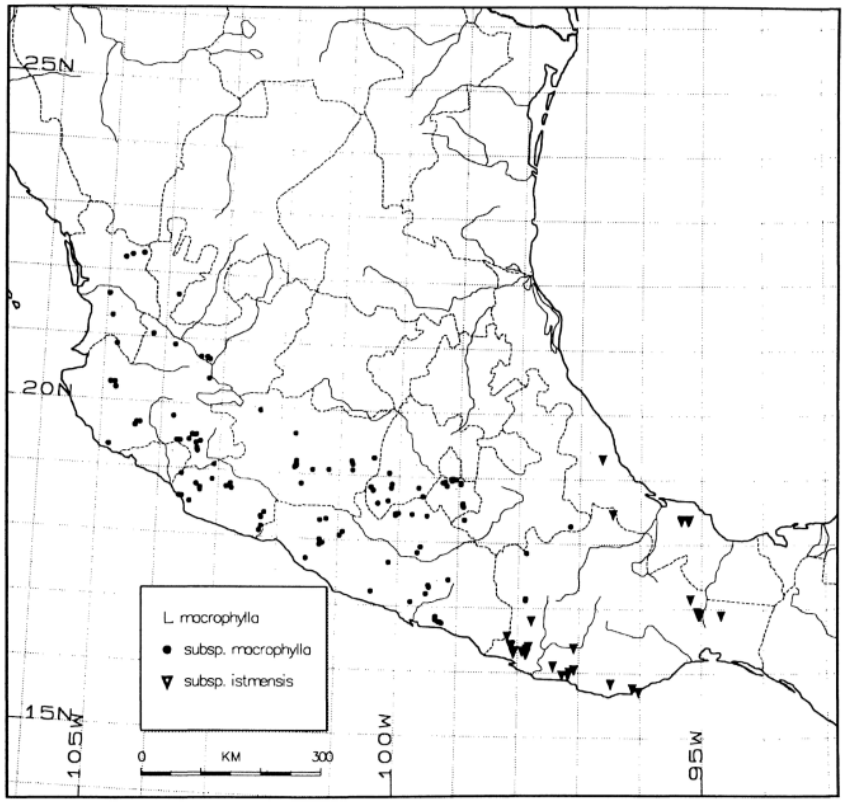
Leucaena trichodes

- Only species native to South America
- Poorly known and rarely cultivated; potential little investigated
- Leaves: high in vitro digestibility, very low (almost zero) condensed tannin



Leucaena macrophylla

- Very large leaflets (3-7 cm long)
- Two subspecies – the coastal subspecies istmensis very fast growing in trials
- Moderately susceptible to psyllids
- Leaves: little used for forage so far. High in vitro digestibility, low condensed tannins



Triploid Hybrids

L. pulverulenta x L. leucocephala

- First spontaneous hybrid noticed in the genus in west Java, where 2 parents cultivated since 1900
- First artificial hybrid to be used commercially – propagated by grafting as a shade tree over tea plantations in Indonesia.
- Fast-growing, outperforms L. leucocephala, but highly susceptible to psyllids
- Completely sterile or weakly fertile

L. trichandra x L. leucocephala

- Spontaneous hybrids in Indonesia
- Artificially recreated in Hawaii
- Largely sterile

L. esculenta x L. leucocephala

- Very frequent and widespread spontaneous hybrid in S-C Mexico – named Leucaena xmixtec, also in Colombia & Senegal
- Completely sterile
- Artificially generated in Hawaii
- Fast growing

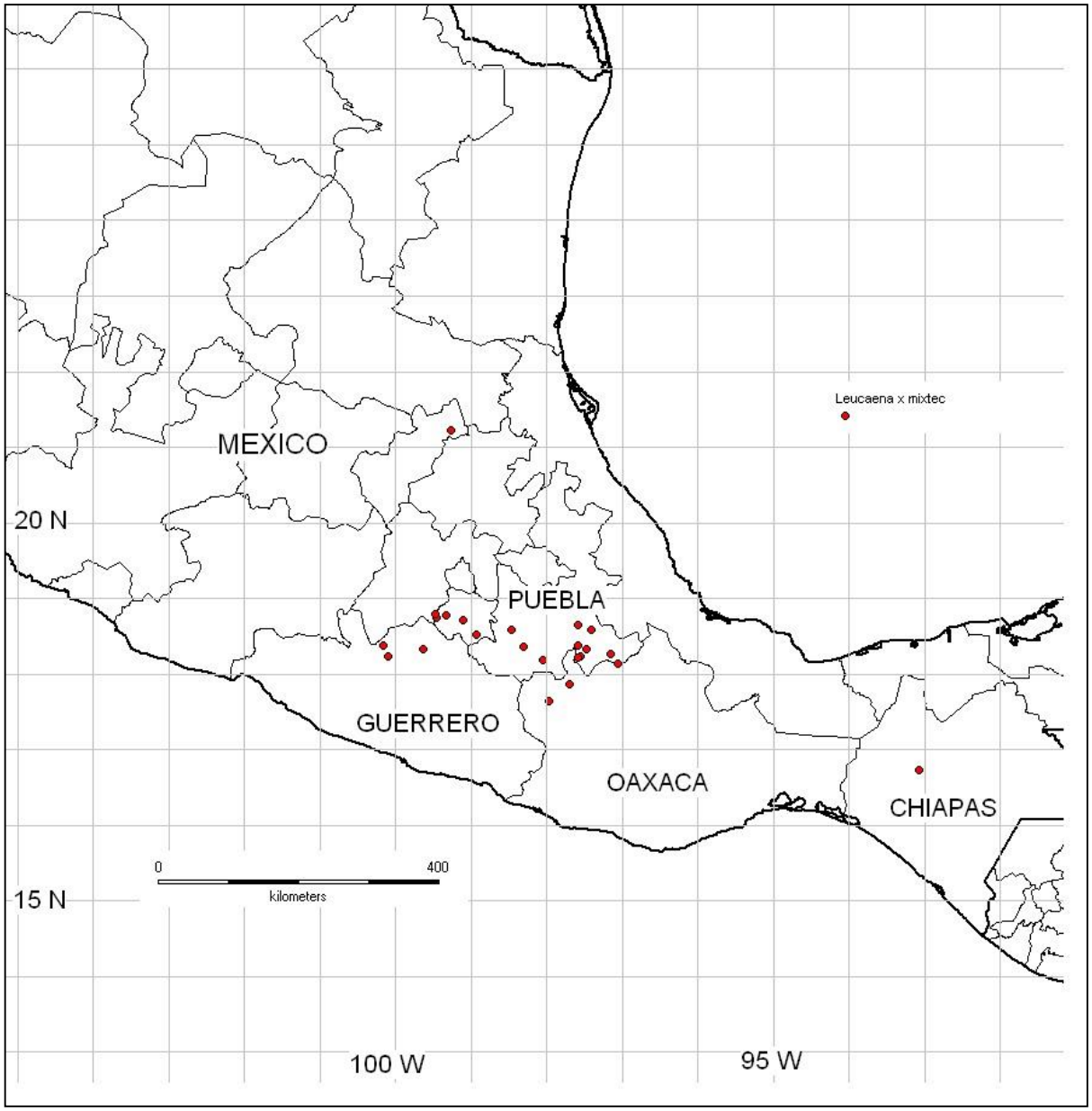
Leucaena x mixtec

Sterile triploid hybrids

= *L. Leucocephala* (tetraploid) x *L. esculenta* (diploid)

= KX4

Guaje macho - Leucaena x mixtec – sterile triploid hybrids

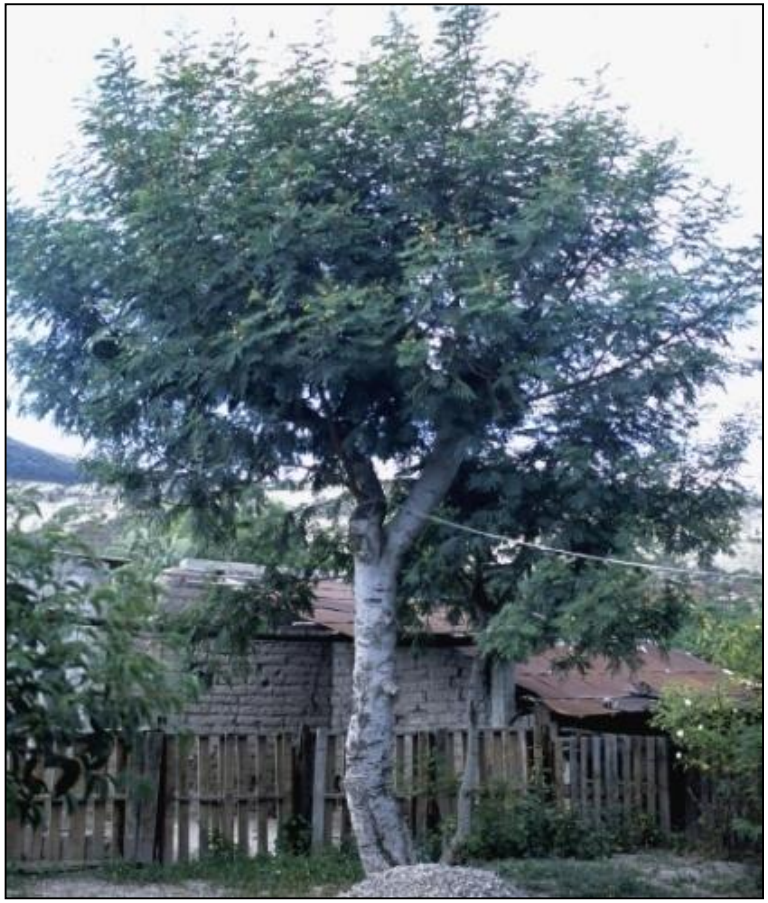


> 50 individual trees

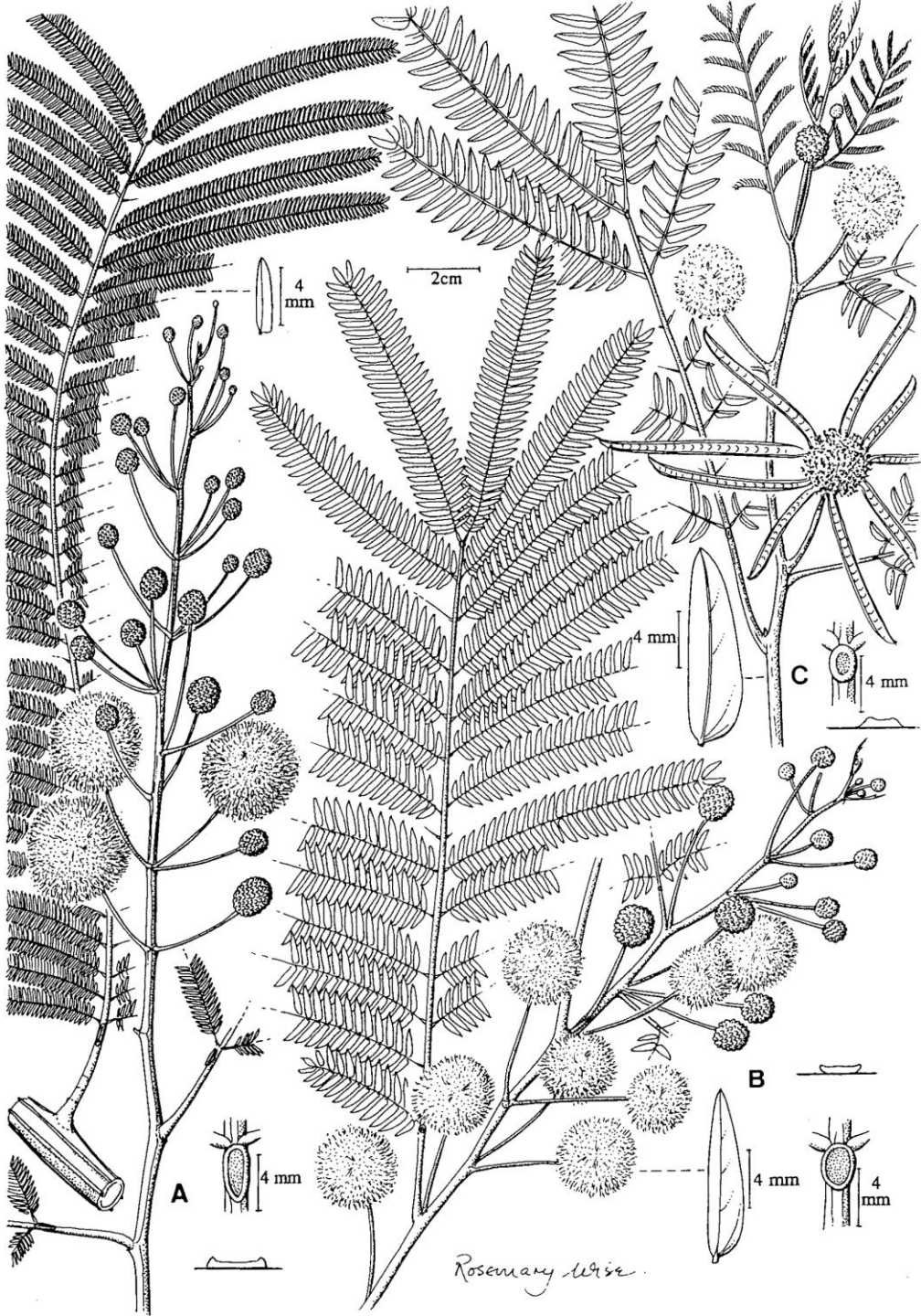
Puebla, Morelos, Oaxaca, Chiapas, Guerrero

Independent F1 hybrids

Leucaena x mixtec
= *L. Leucocephala* (tetraploid) x
L. esculenta (diploid)



Triploid leaf formula
$3\ln F_1 = 2\ln P_1 + \ln P_2$



Hughes & Harris (1994) Pl. Syst & Evol.

Spontaneous Hybridization

When species are brought together in artificial sympatry – spontaneous hybrids are highly likely to occur. These can be cryptic and hard to identify.

Likely that this accounts for the origins of some of the tetraploids, including L. leucocephala

We have documented a significant number of such spontaneous hybrids:

- L. xmixtec (KX4) widespread in Mexico; also documented in Senegal, west Africa
- L. xspontanea – L. leucocephala x L. diversifolia – common in Veracruz, Mexico and individuals also found in northern Guatemala
- Probable L. leucocephala x L. confertiflora tetraploid hybrid in Puebla, Mexico
- L. leucocephala x L. pulverulenta in Indonesia
- L. leucocephala x L. trichandra

What can happen, probably will happen, given time.

For example, with widespread deployment of triploids one should expect at some point a hexaploid to appear

Conclusions

Tremendous diversity in the genus

Wide range of environmental tolerances – cold, drought etc –

Species bioclimatic niche modelling using comprehensive species occurrence data – predict where species will grow

Very wide range of forage quality traits, growth rates, psyllid tolerances

Hard to rank diploids in a simplistic way – lack of adequate data on forage quality for many species. Several species remain very poorly known.

L. pulverulenta – diploid progenitor of L. leucocephala
L. trichandra – critical importance of seed source – provenance

The history of Leucaena breeding is a history of (i) chasing a moving target as new challenges come along – first mimosine, then psyllid tolerance, now sterility; (ii) over-reliance on a very narrow genetic base, e.g. single self-fertile lines of L. leucocephala.