For this week:

A small snack of a few dozen wild almonds contain enough cyanide to kill humans. How did humans turn the almond into an important nut crop?




BIO 235
Plants & People
Evolution &
Domestication
of Crops





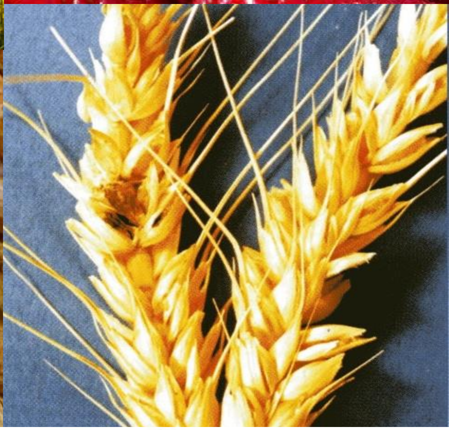


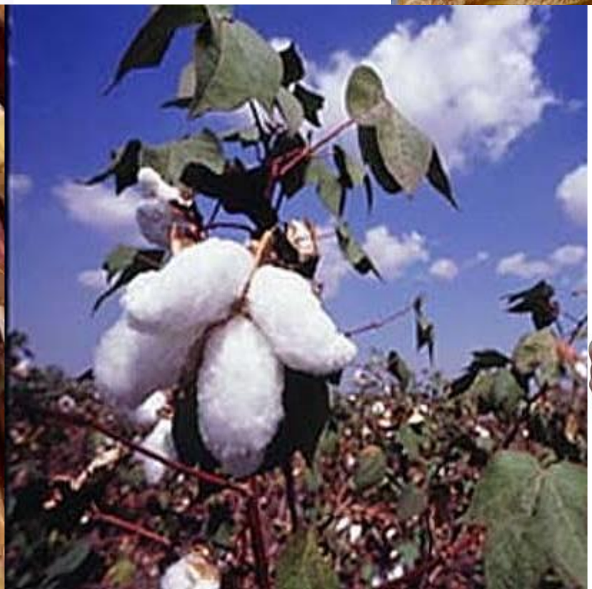
Lecture 5
Hybridization, Polyploidy & Crop Domestication I – Guajes, nopales & maguey

- Polyploidy preceding domestication – Cotton
- Hybrids and polyploids as triggers for domestication – wheat, strawberry
- Edgar Anderson
- Guajes, nopales & maguey
- Serendipitous backyard hybridization & the origin of crops

Colin Hughes
Institute of Systematic Botany
colin.hughes@systbot.uzh.ch

Polyploidy & Crops





Polyploidy

x = base chromosome number of a lineage; 2n = chromosome number in somatic tissue regardless of whether an individual is diploid 2n = 2x, triploid 2n = 3x, tetraploid 2n = 4x, etc.

- haploid (= x) (say 6)
- diploid, 2n = 2x = 12
- tetraploid, 2n = 4x = 24
- hexaploid, 2n = 6x = 36
- octoploid, 2n = 8x = 48
- decaploid, 2n = 10x = 60 etc etc

- Polyploidy is normal in ferns (95%), common in Angiosperms (30-70%), rare in Gymnosperms, infrequent in Animals

- Ploidy changes may represent 2-4% of speciation events in flowering plants and 7% in ferns

Polyploids

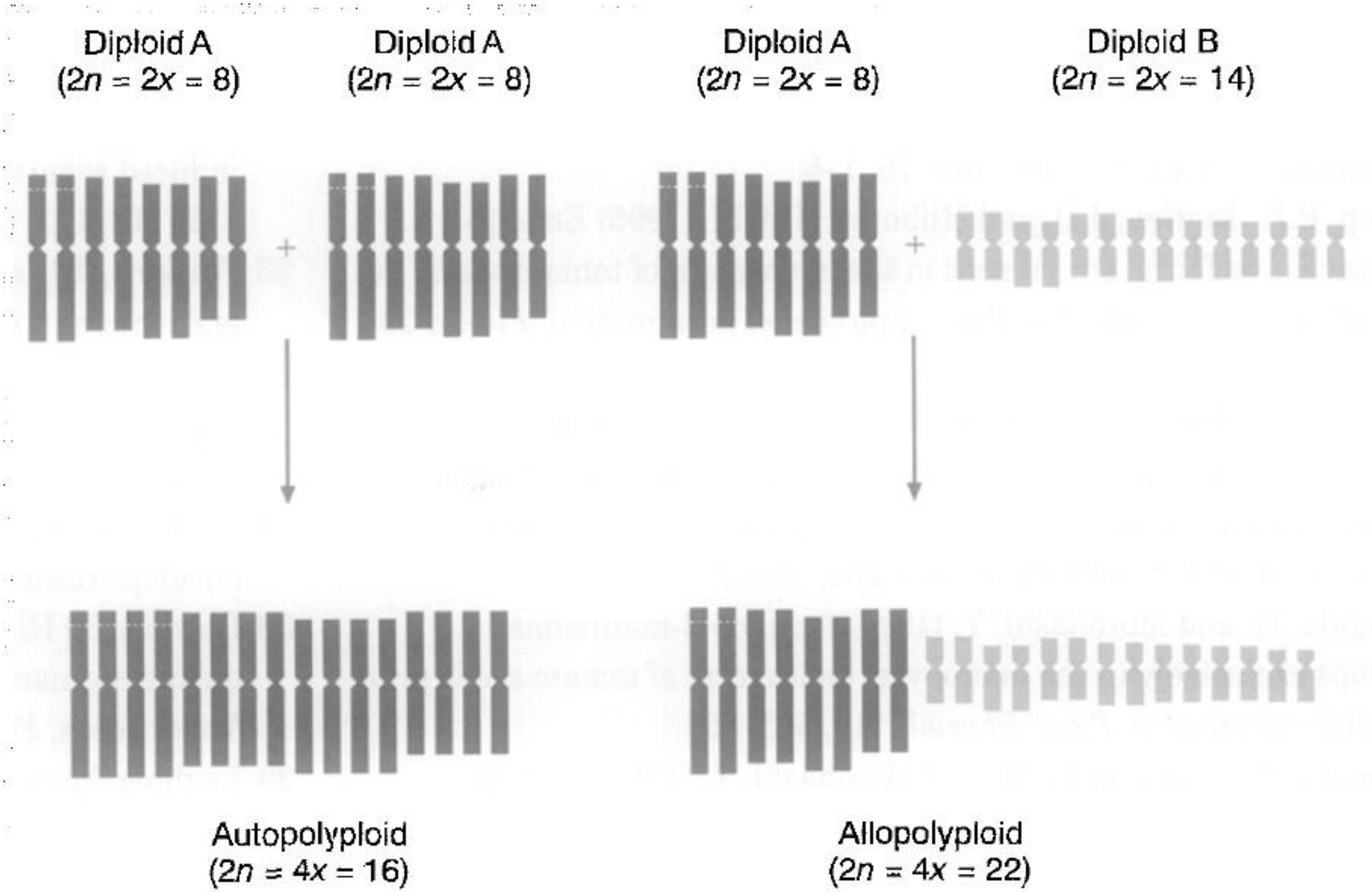
<u>Autopolyploids</u> (*AAAA*)

- between genetically very similar plants
- parents the same species
- chromosomes homologous
- at meiosis quadrivalents

<u>Allopolyploids</u> (*AABB*)

- between genetically dissimilar plants
- parents different species
- chromosomes not homologous
- at meiosis bivalents

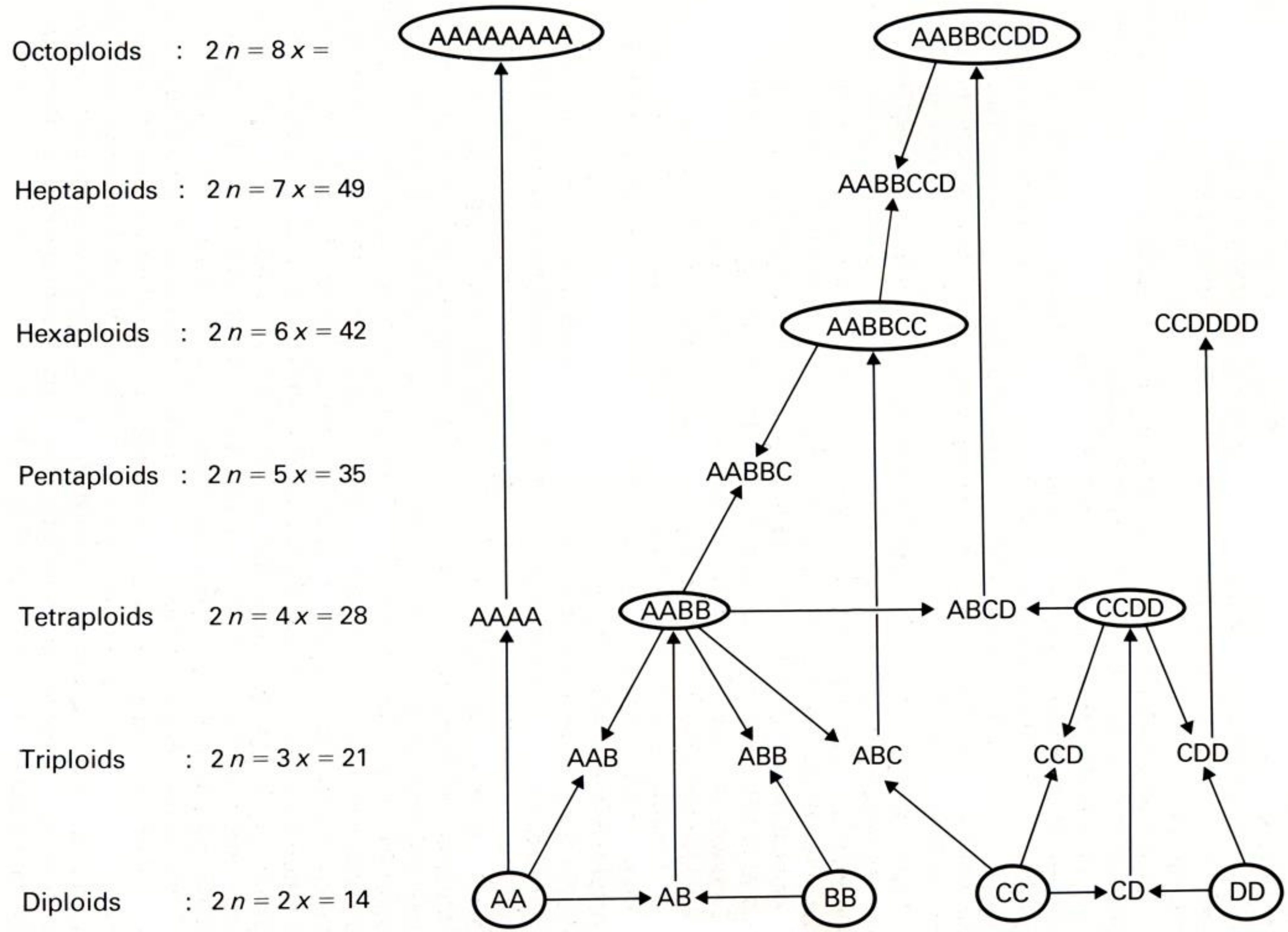
Otto & Whitton 2000. Ann. Rev Genet. 34: 401



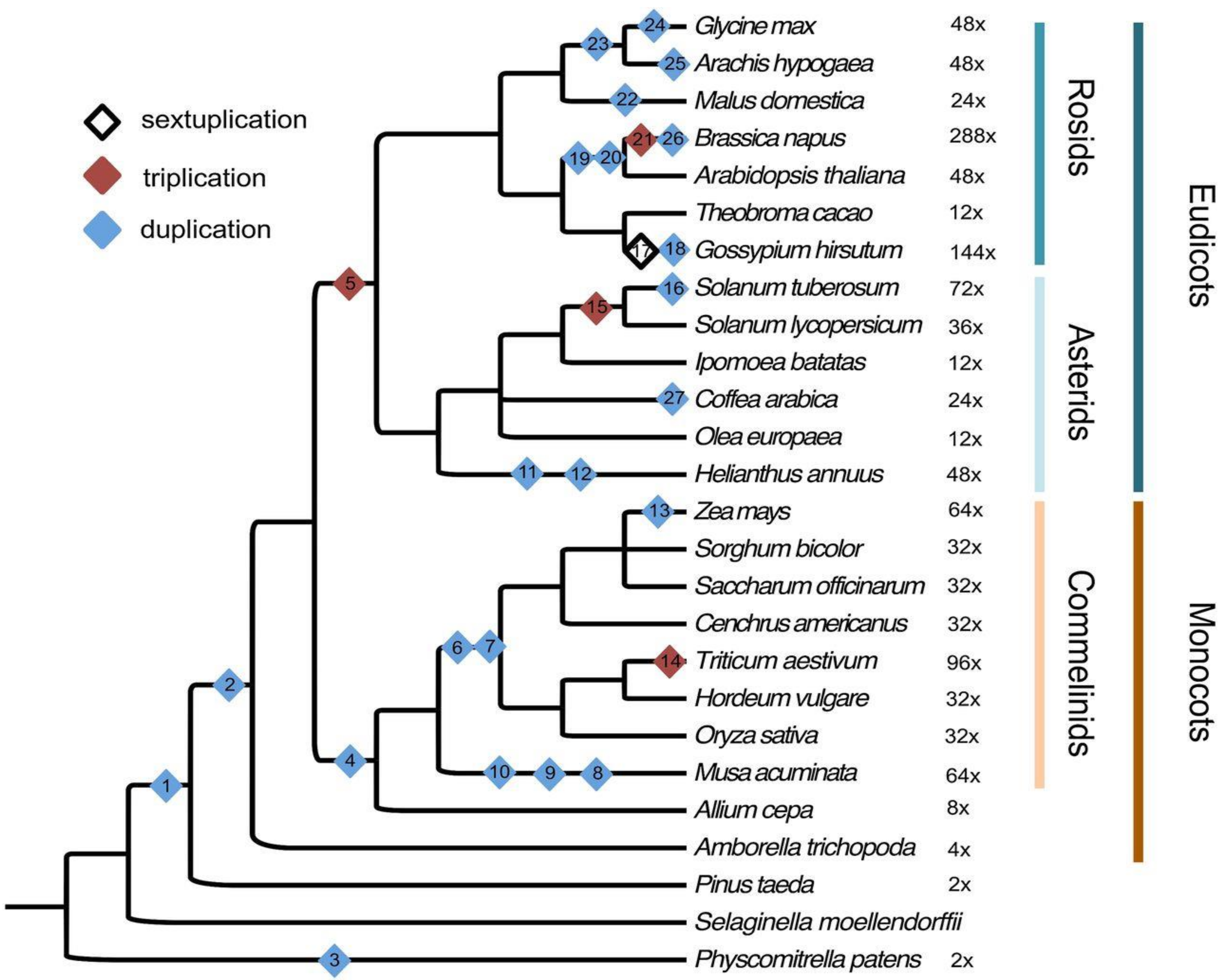
Leitch & Bennett 1997. Trends in Pl. Sci. 2: 470

Polyploid complex

Stace, Plant taxonomy



Whole genome duplications & land plant phylogeny



Renny-Byfield & Wendel (2014)

Polyploidy & Crops

Whole Genome Duplication, WGD

- Genomic plasticity and rapid genome evolution
- Neofunctionalization of genes
- Diploidization
- Addition of novel genetic material
- Opening up of vast new terrains of gene expression space

Hybrid vigour / Heterosis – hybrids and allopolyploids tend to be bigger and faster growing

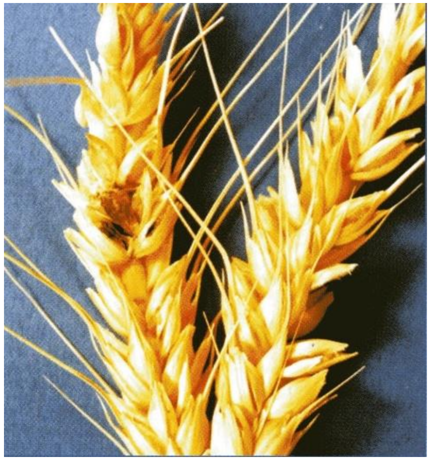
Recombination and emergence of transgressive phenotypes providing novel traits

Hybridization, Polyploidy & Crop Domestication

Polyploidy preceding domestication
Tetraploid Cotton

Spontaneous hybrids in cultivation

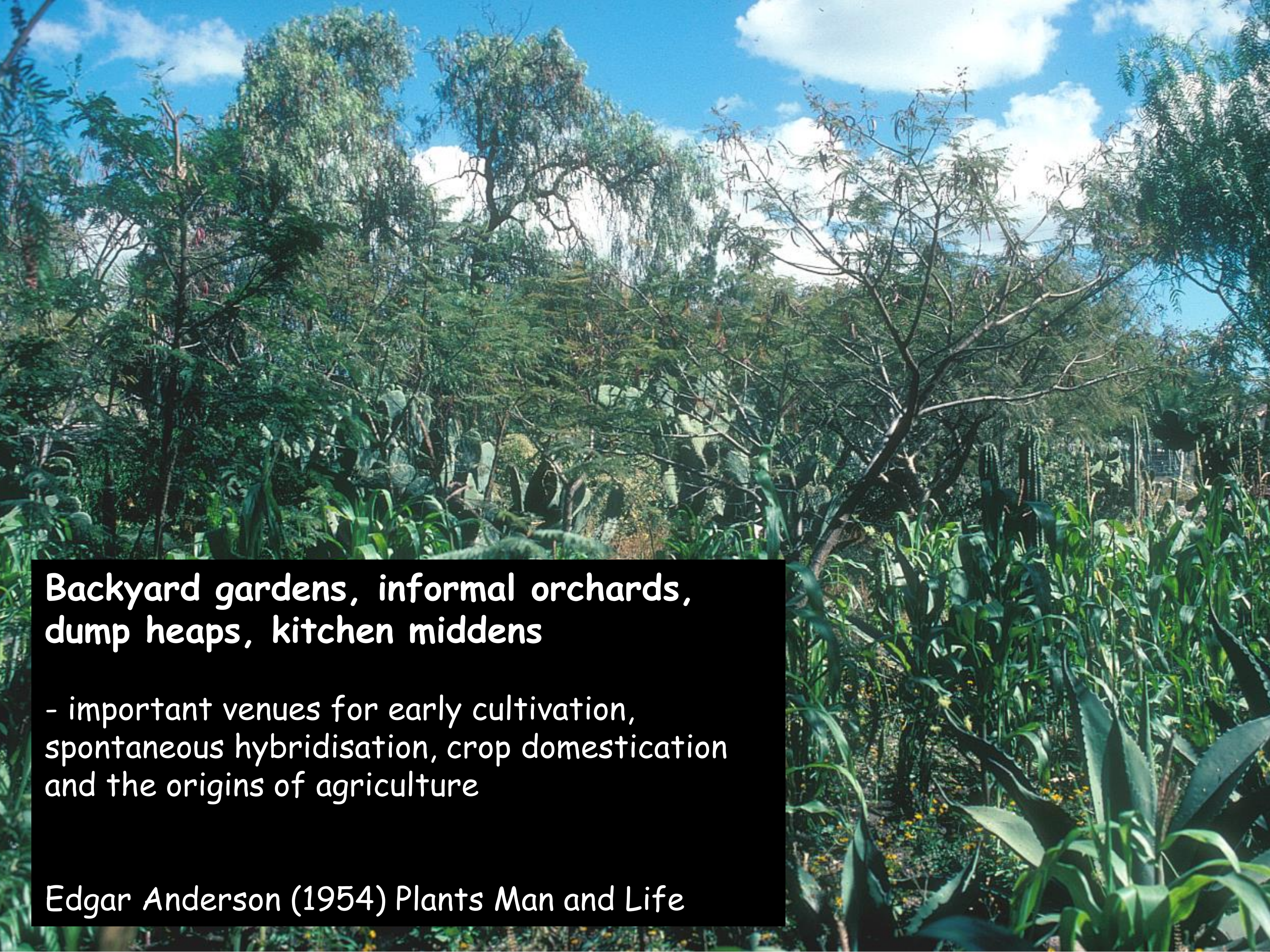
Hexaploid breadwheat

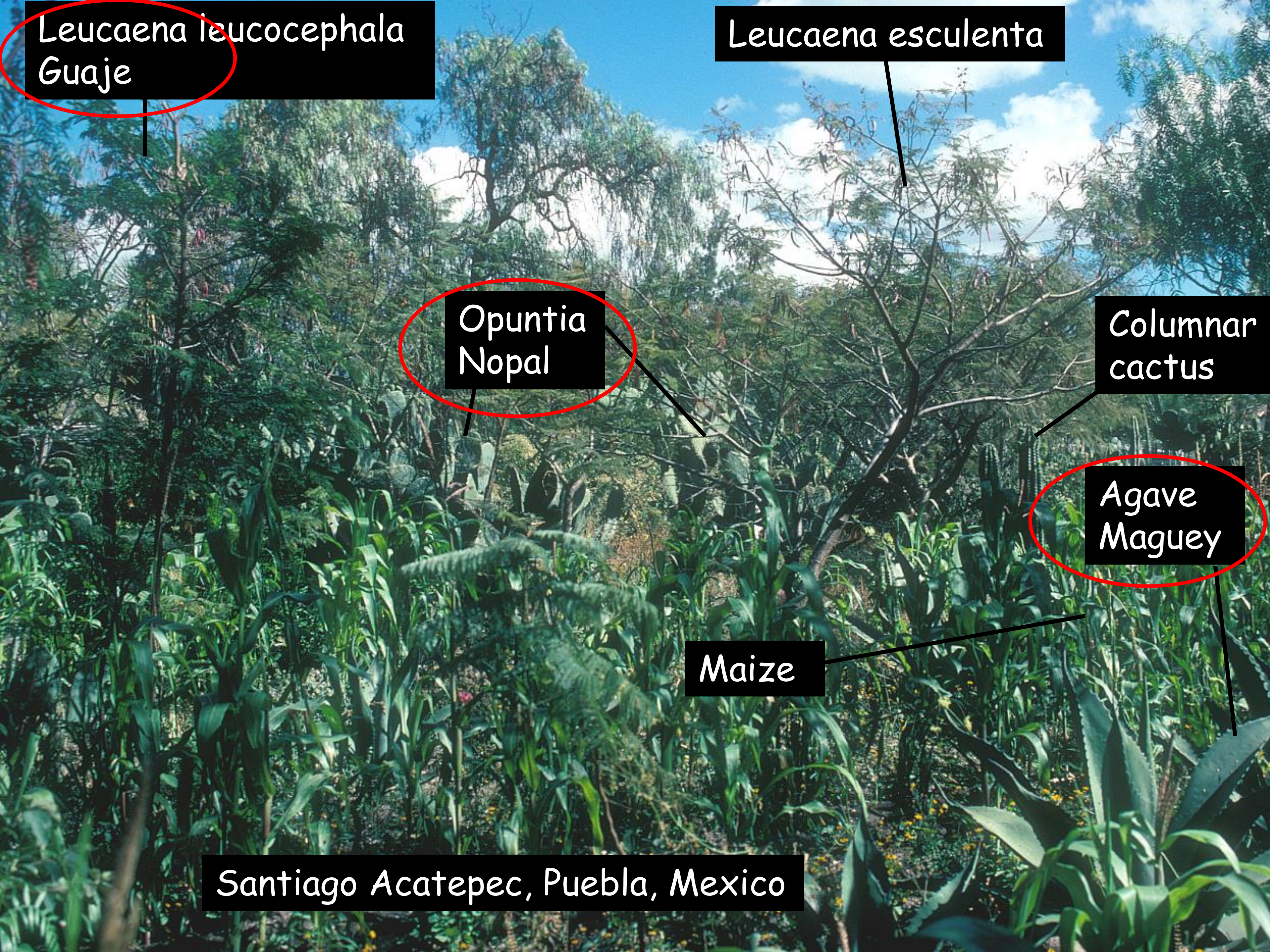


Octaploid Strawberry

?? Unclear to what extent hybridization and polyploidization preceded domestication or were precipitated by human activities

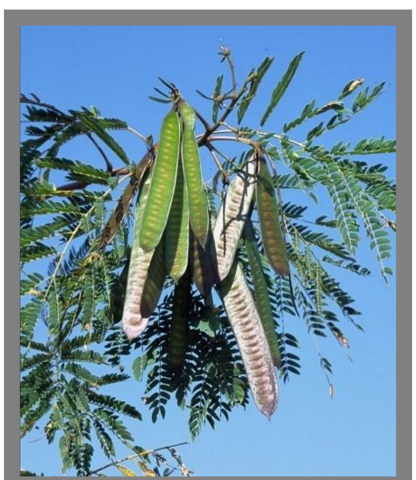
Bananas, Citrus, Potatoes, Kiwi Fruit, Peanuts, Agave, Opuntia, etc, etc.......

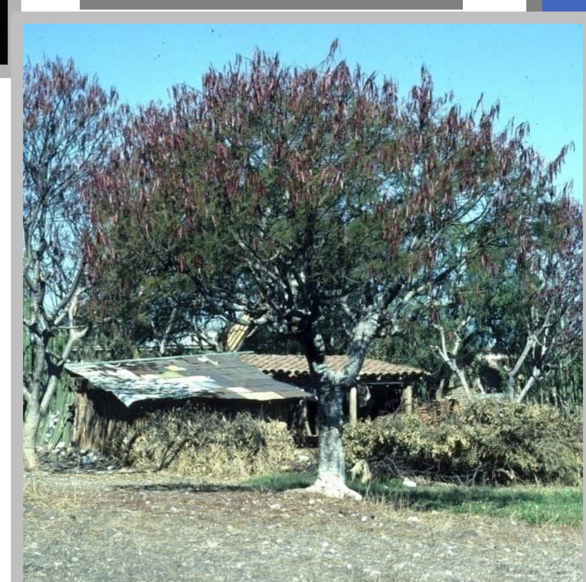

Backyard gardens, informal orchards, dump heaps, kitchen middens
- important venues for early cultivation, spontaneous hybridisation, crop domestication and the origins of agriculture
Edgar Anderson (1954) Plants Man and Life


Leucaena leucocephala
Guaje
Leucaena esculenta
Opuntia
Nopal
Columnar
cactus
Agave
Maguey
Maize
Santiago Acatepec, Puebla, Mexico

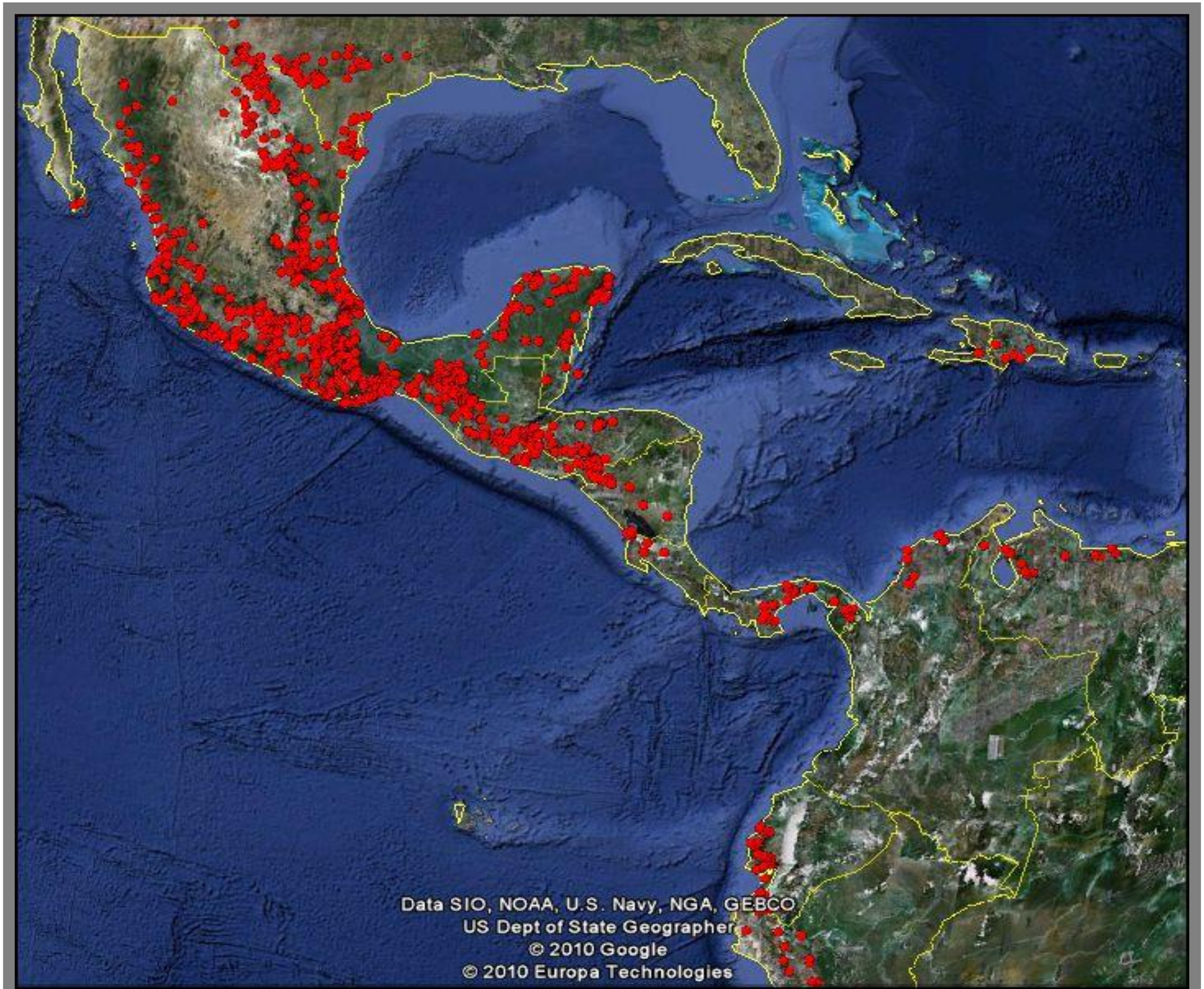
Guaje - *Leucaena* - Leguminosae

22 species
- **17 diploids**
- **5 tetraploids**
- **2 named hybrids**





Oaxaca, Mexico


Data SIO, NOAA, U.S. Navy, NGA, GEBCO
US Dept of State Geographer
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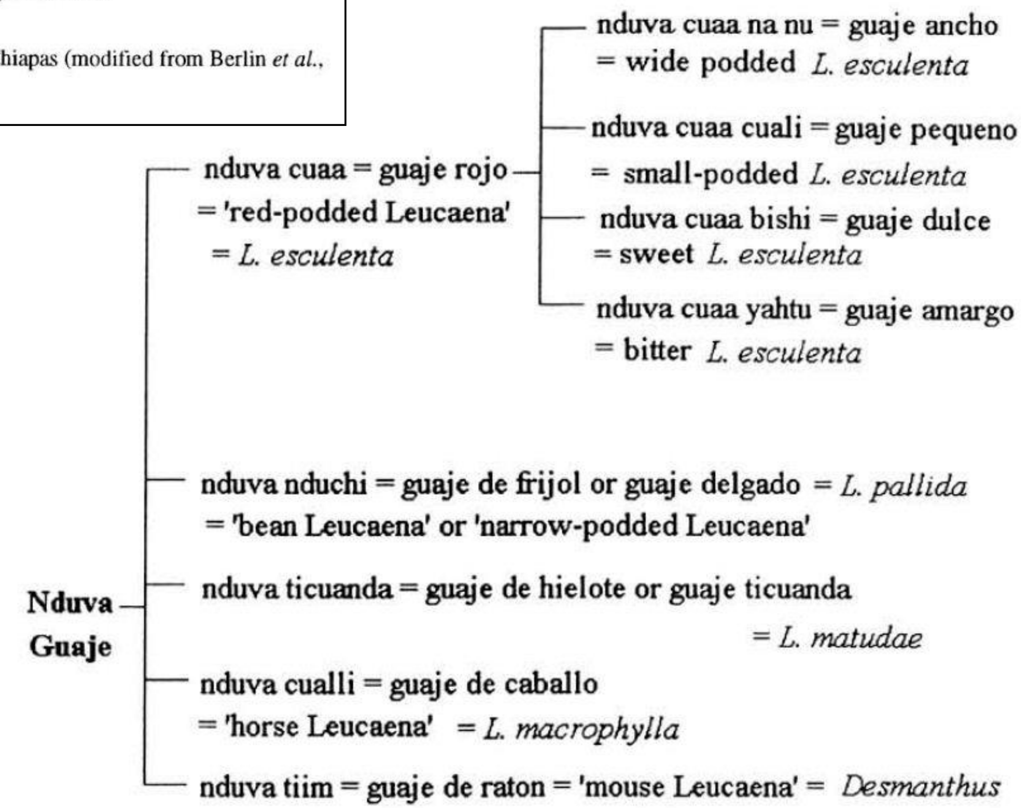
Leucaena – finely differentiated cognitive systems

Tzeltal classification of *Leucaena* species in the Municipality of Tenejapa, Chiapas (modified from Berlin *et al*., 1974)

Tzeltal, Chiapas



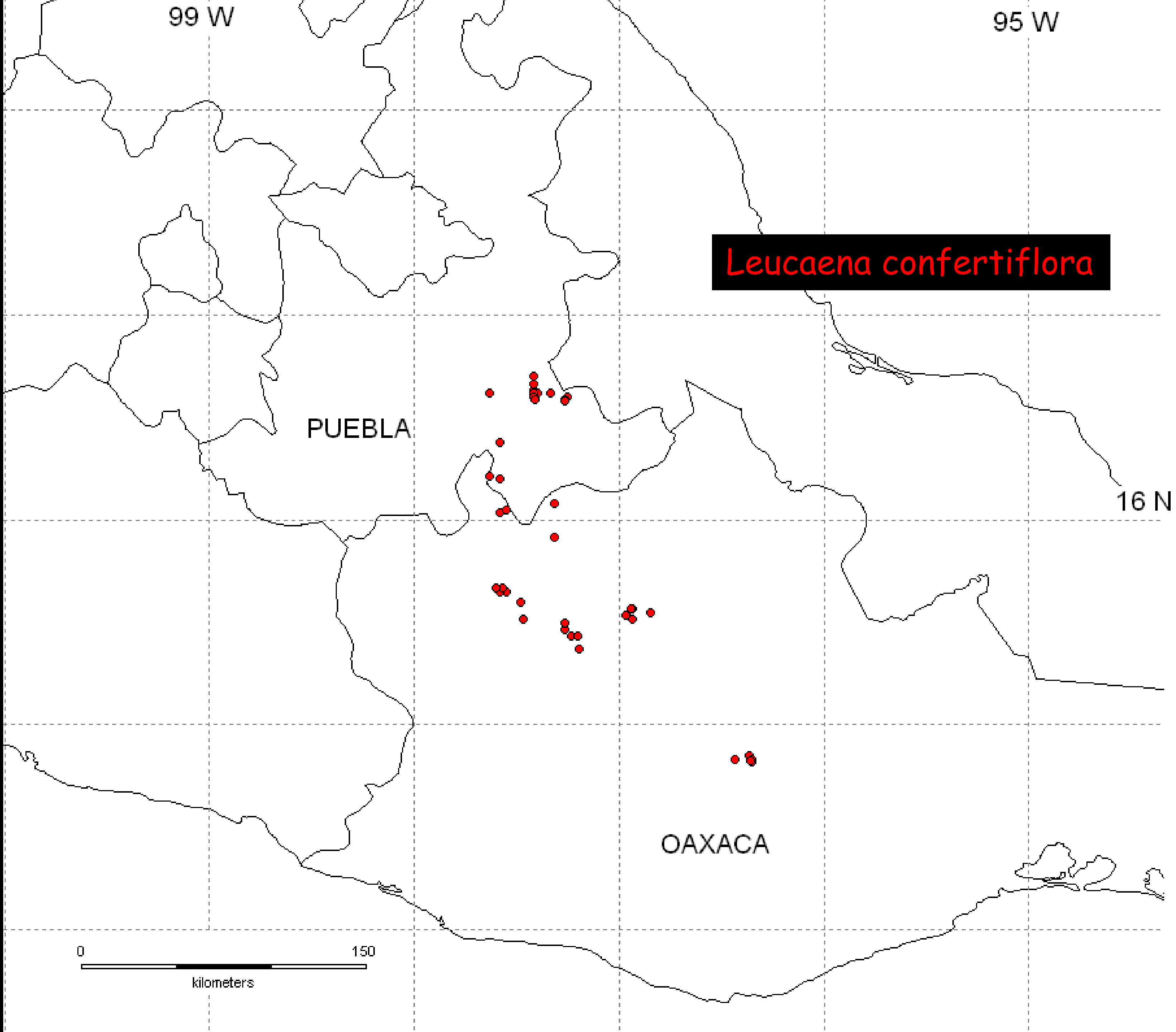
Mixtec classification of *Leucaena* species, La Montana, Alcozauca, Guerrero (modified from Casas and Caballero, 1996)

Mixtec, Guerrero

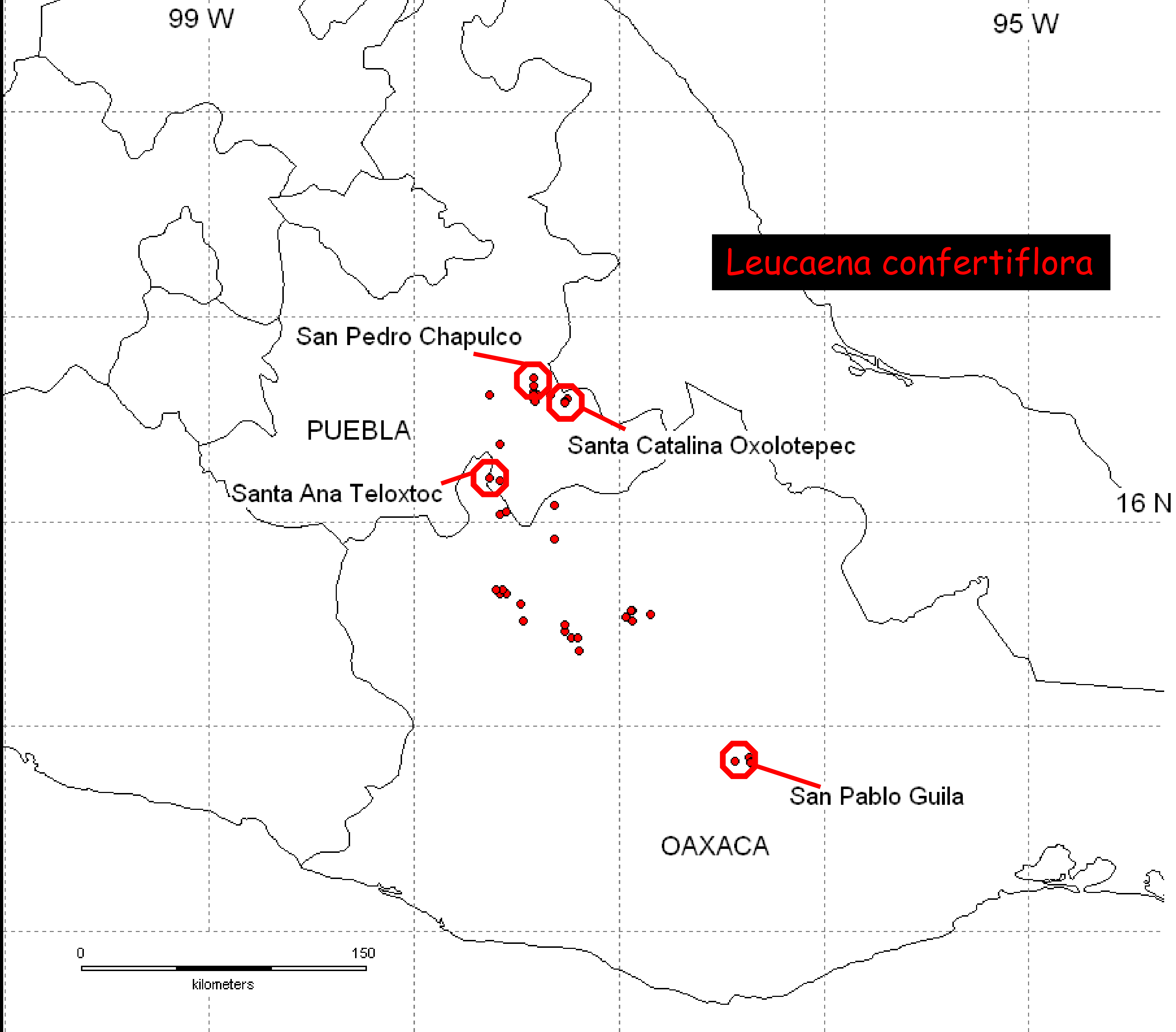

Guaje Zacaztin
Guaje rojo
Guaje macho
Guaje manso
Guaje chiquito
Guaje verde
Guaje delgado




Leucaena confertiflora



99 W
95 W
Leucaena confertiflora
16 N
PUEBLA
OAXACA
0
150
kilometers


99 W
95 W
Leucaena confertiflora
San Pedro Chapulco
PUEBLA
Santa Catalina Oxolotepec
Santa Ana Teloxtoc
16 N
San Pablo Guila
OAXACA
0
150
kilometers

Leucaena confertiflora in San Pedro Chapulco, Puebla

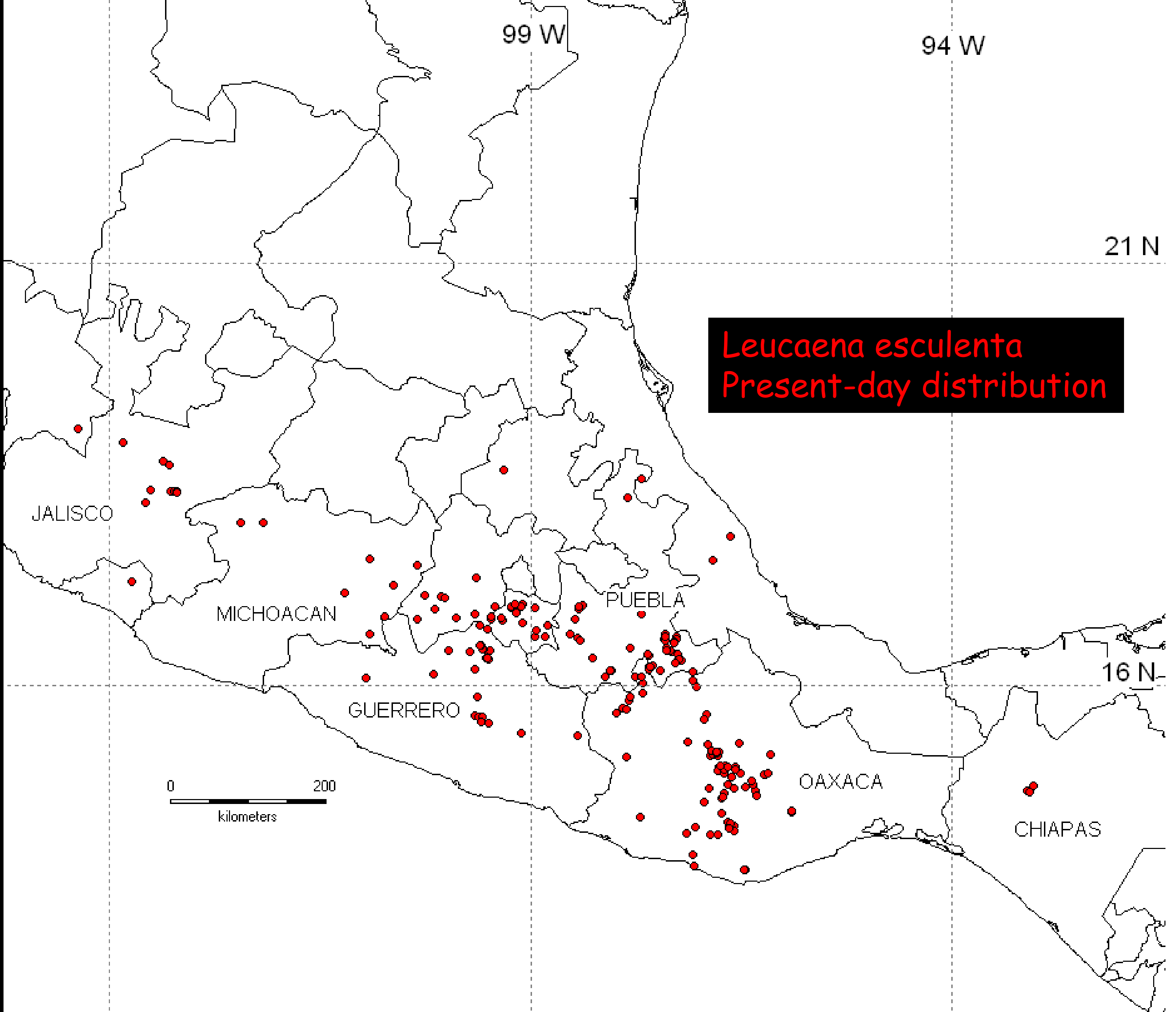
Zárate 1984. Domesticación incipiente del guaje zacatzín

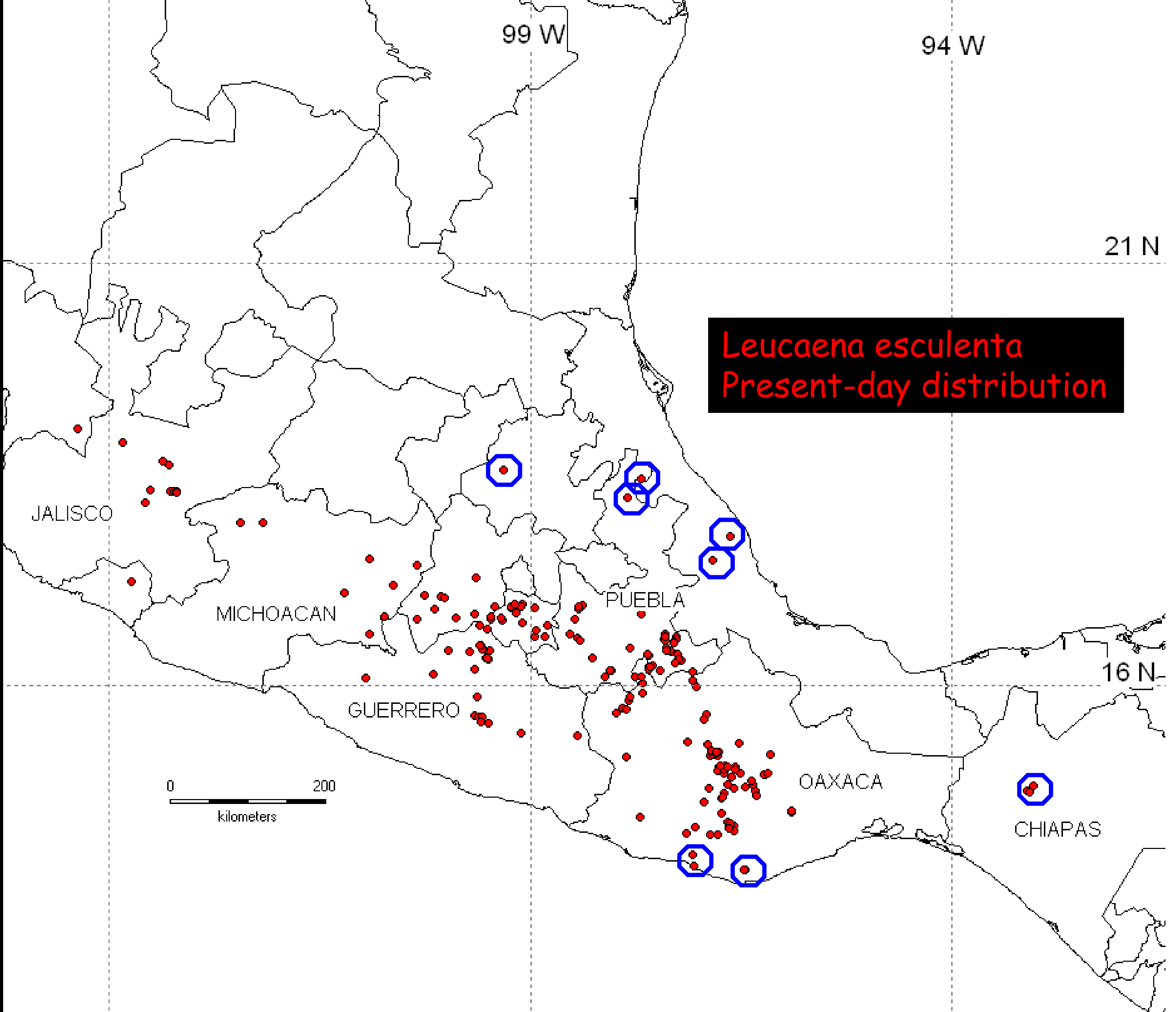
Leucaena esculenta

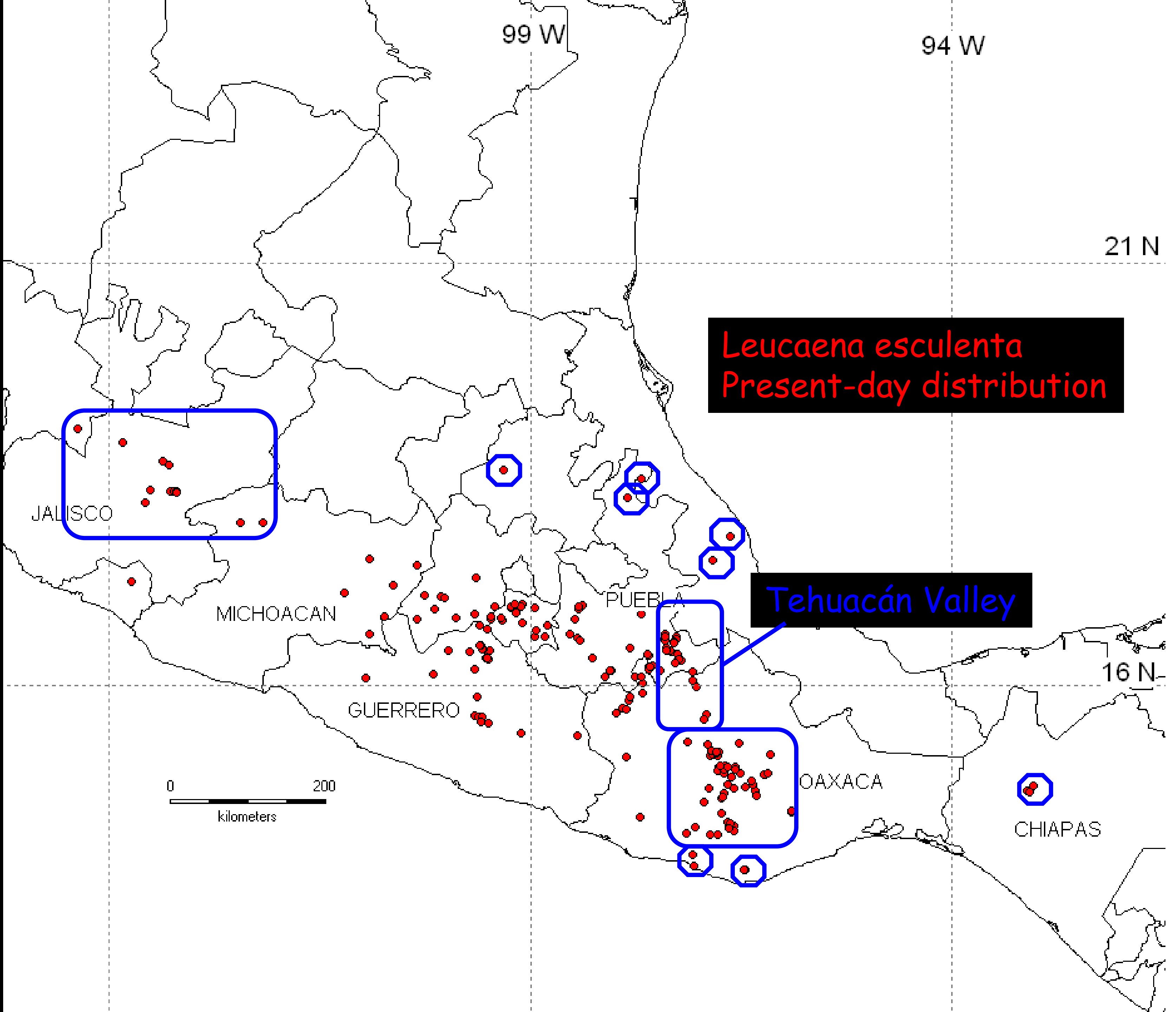
One of the most widely cultivated trees in south-central Mexico

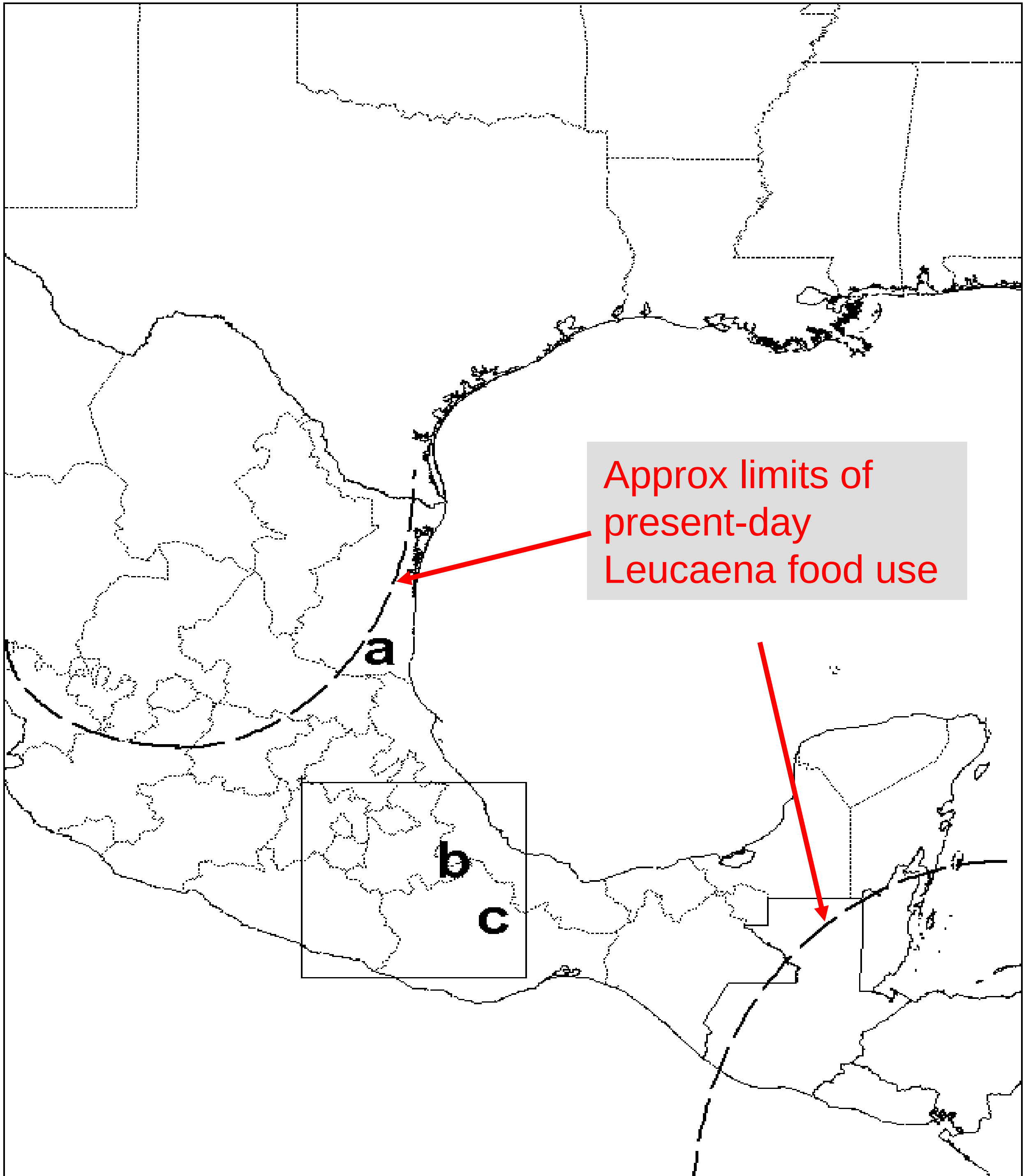
Quantitative differences in pod and seed traits between wild, managed and cultivated populations

Casas & Caballero (1996) Economic Botany


Leucaena esculenta
Present-day distribution
99 W
94 W
21 N
16 N
JALISCO
MICHOACAN
GUERRERO
PUEBLA
OAXACA
CHIAPAS
0
200
kilometers


Leucaena esculenta
Present-day distribution
99 W
94 W
21 N
16 N
JALISCO
MICHOACAN
GUERRERO
PUEBLA
OAXACA
CHIAPAS
0
200
kilometers


Leucaena esculenta
Present-day distribution
Tehuacán Valley
99 W
94 W
21 N
16 N
JALISCO
MICHOACAN
GUERRERO
PUEBLA
OAXACA
CHIAPAS
0
200
kilometers



Archaeobotanical record for Leucaena

a Ocampo, Tamaulipas

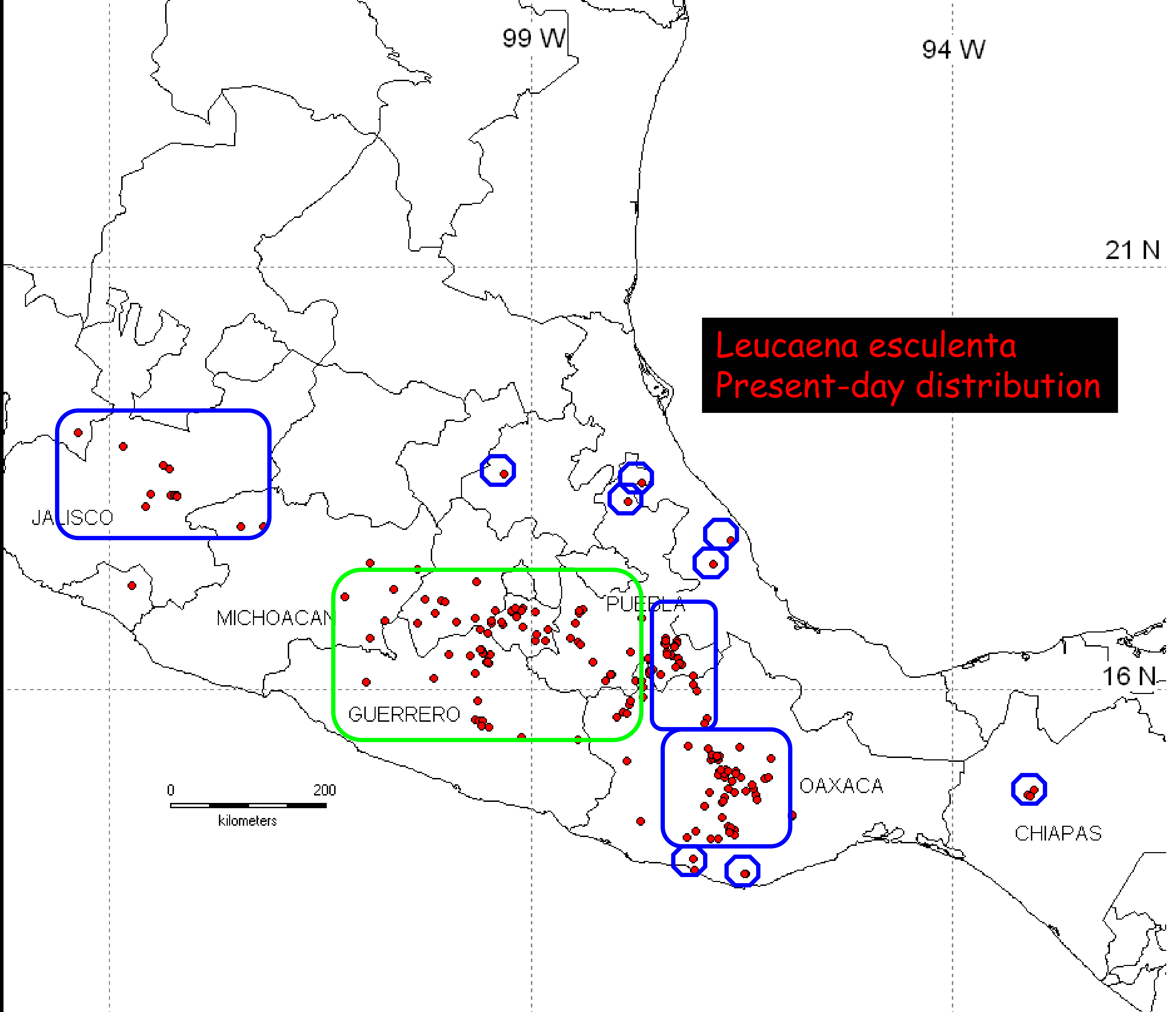
b Coxcatlán & Purrón, Tehuacán Valley

c Guilá Naquitz, Oaxaca

Minor but constant food source for last 6,000 yrs

Increased abundance and appearance of L. esculenta in Coxcatlán from 3,200 BP indicating cultivation in Tehuacán

Zárate 2000 *Economic Botany*


99 W
94 W
21 N
16 N
Leucaena esculenta
Present-day distribution
JALISCO
MICHOACAN
GUERRERO
PUEBLA
OAXACA
CHIAPAS
0
200
kilometers

Seeds of 13 species are used as food

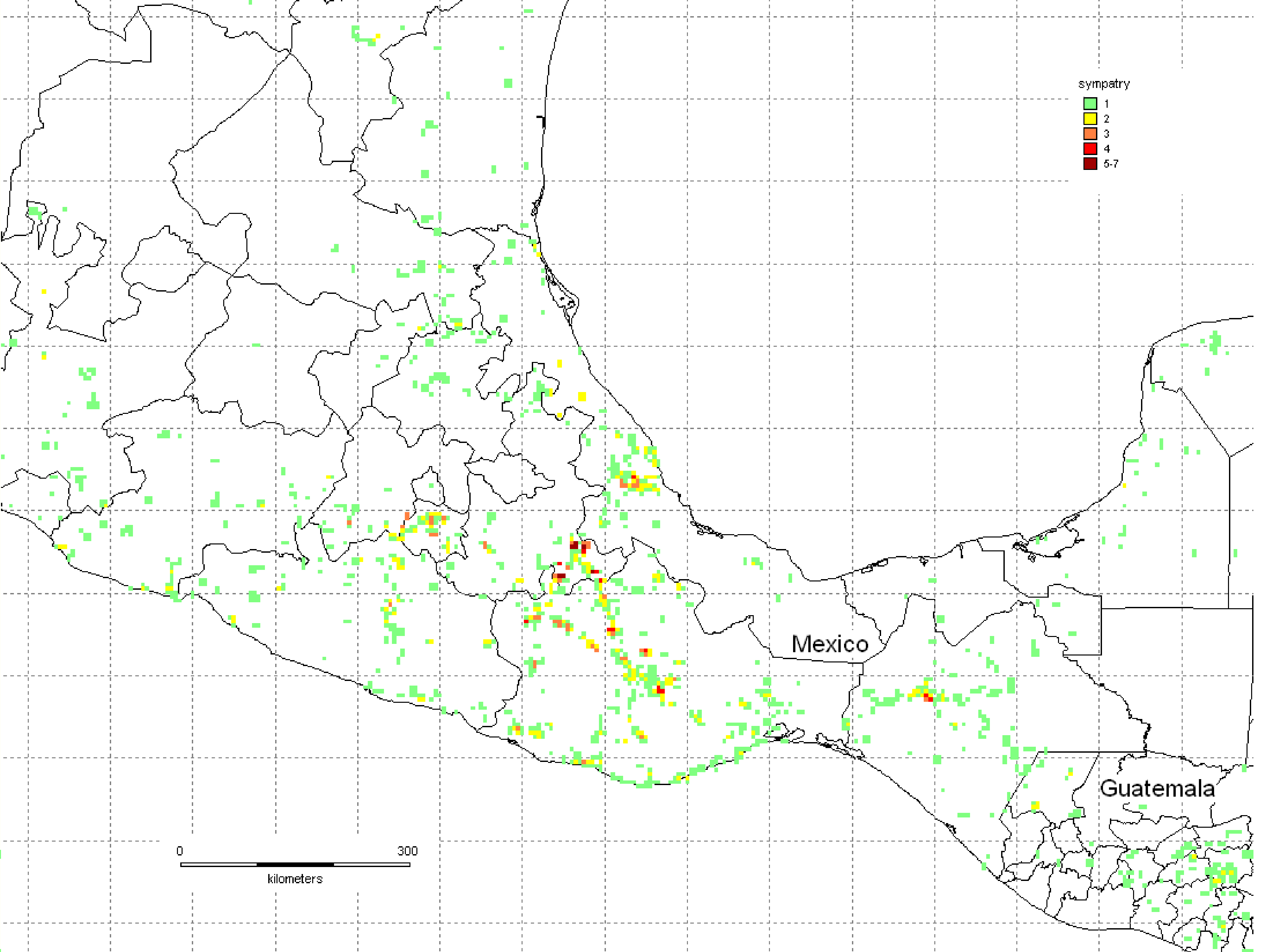
Prevalent throughout S-C Mexico and NW fringes of Guatemala

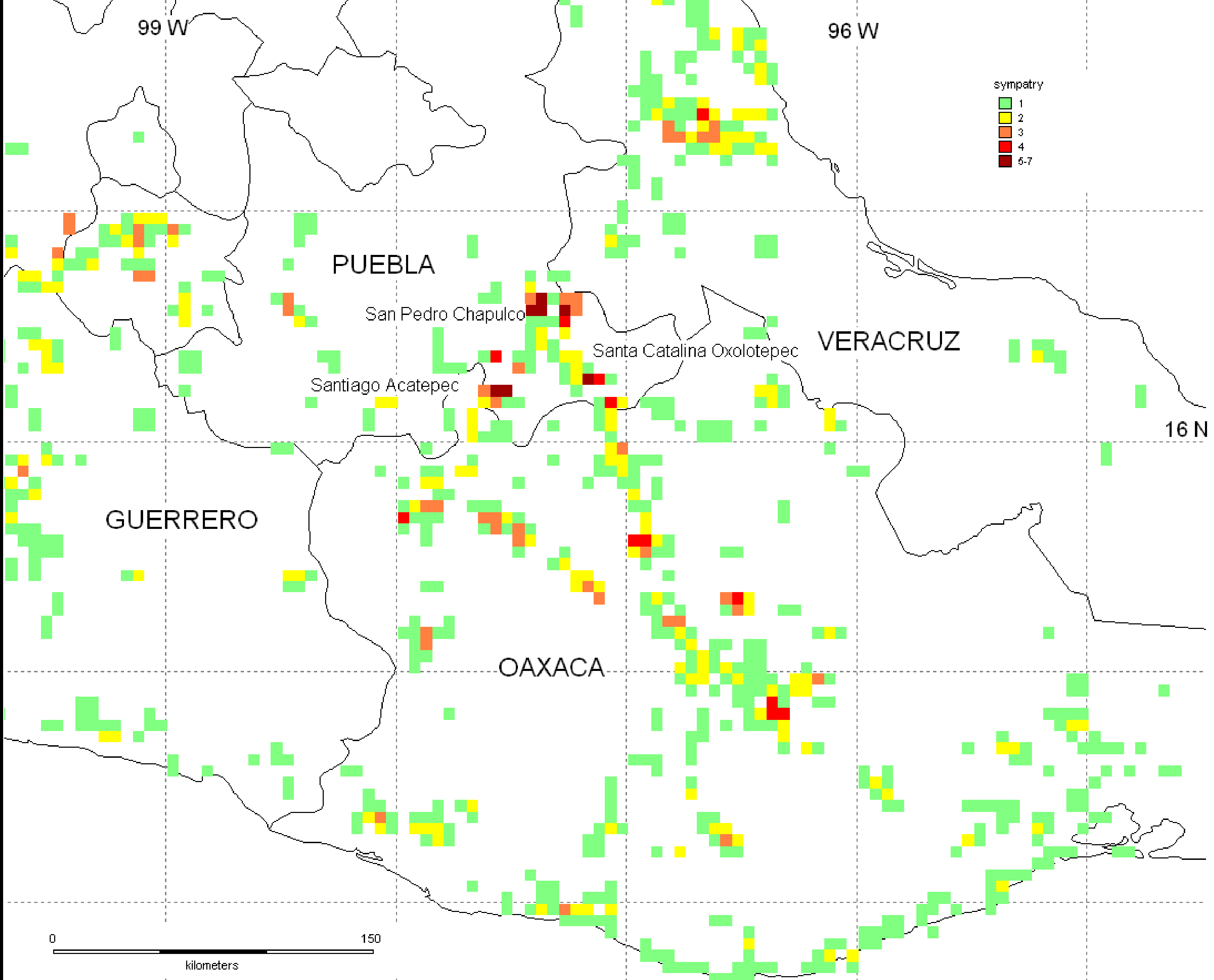
Wild – managed – cultivated (8 of the 13 species) – incipiently domesticated

Home consumption – local & regional marketing

Very local – regional – wider translocation

Numerous repeated and spatially and temporally independent wild to cultivated transitions

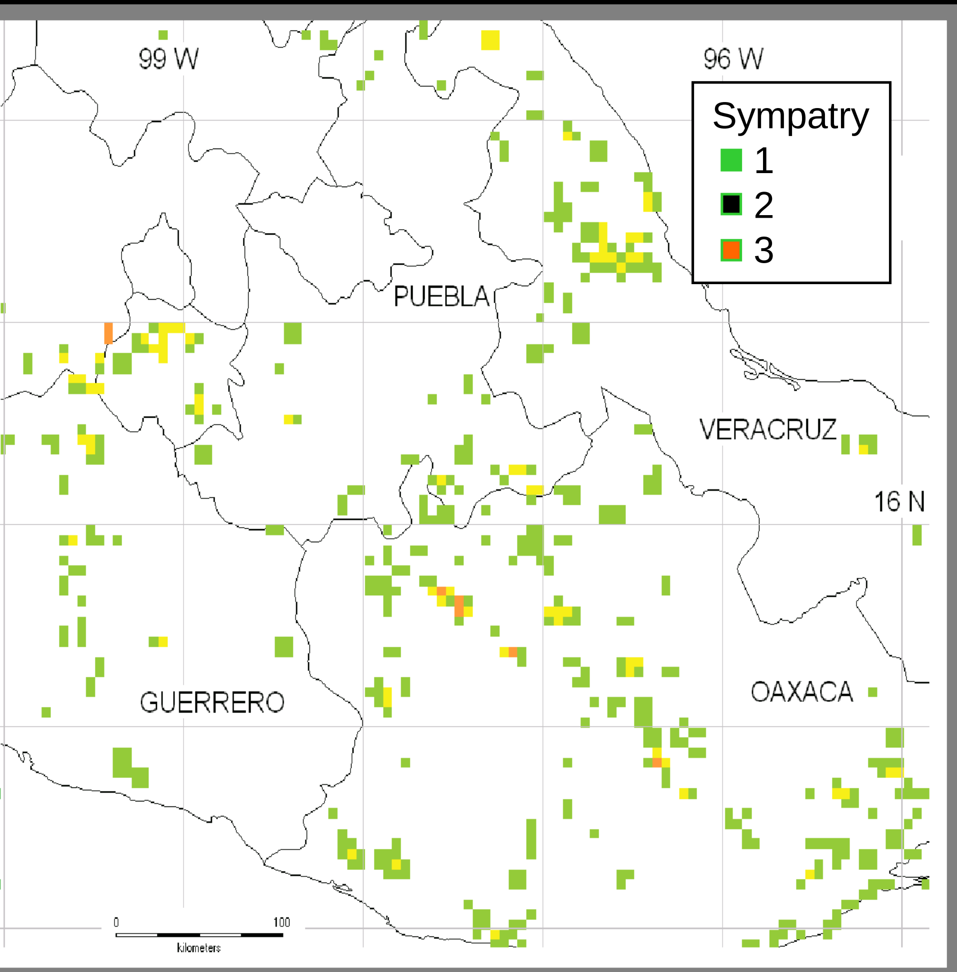

sympatry
1
2
3
4
5-7
Mexico
Guatemala
0
300
kilometers



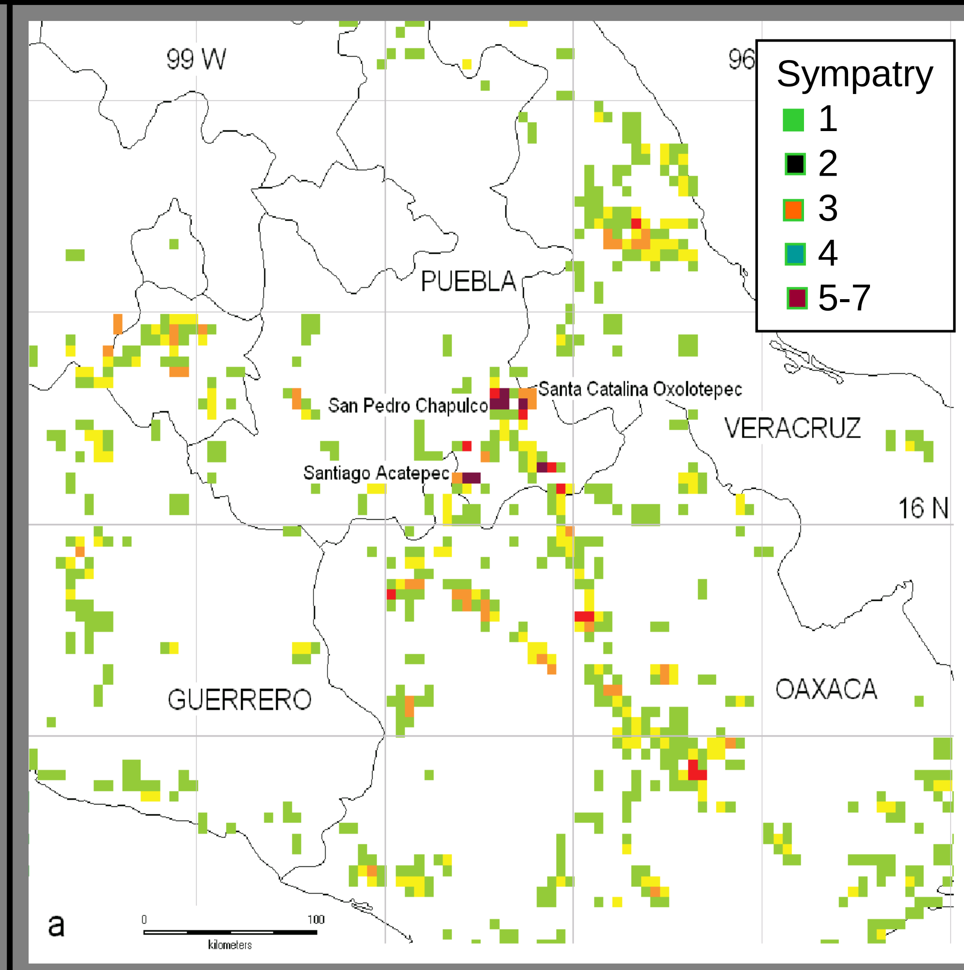
99 W
96 W
16 N
sympatry
1
2
3
4
5-7
PUEBLA
VERACRUZ
GUERRERO
OAXACA
San Pedro Chapulco
Santa Catalina Oxolotepec
Santiago Acatepec
0
150
kilometers

Geography

Hughes et al. 2007



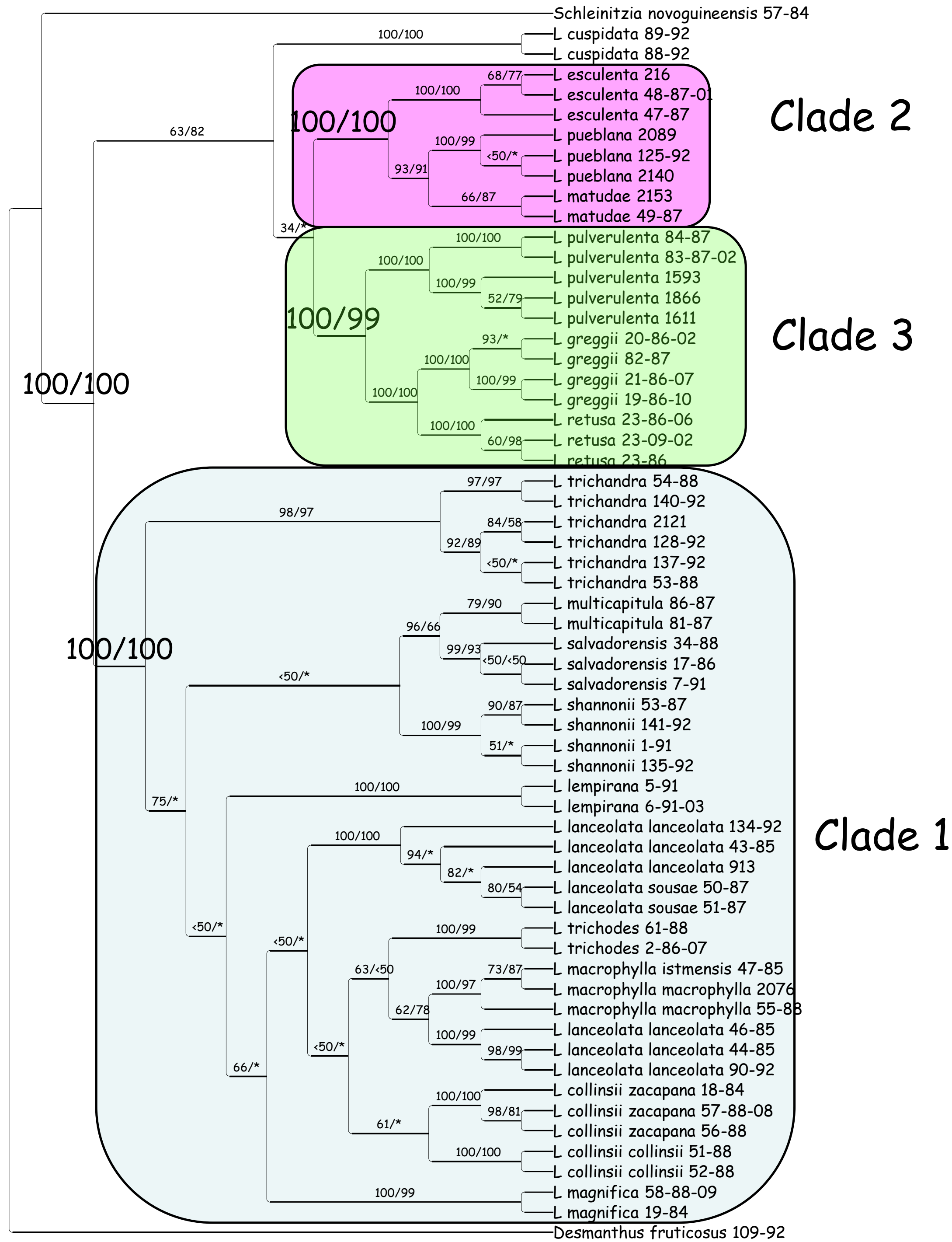
"Wild" Populations



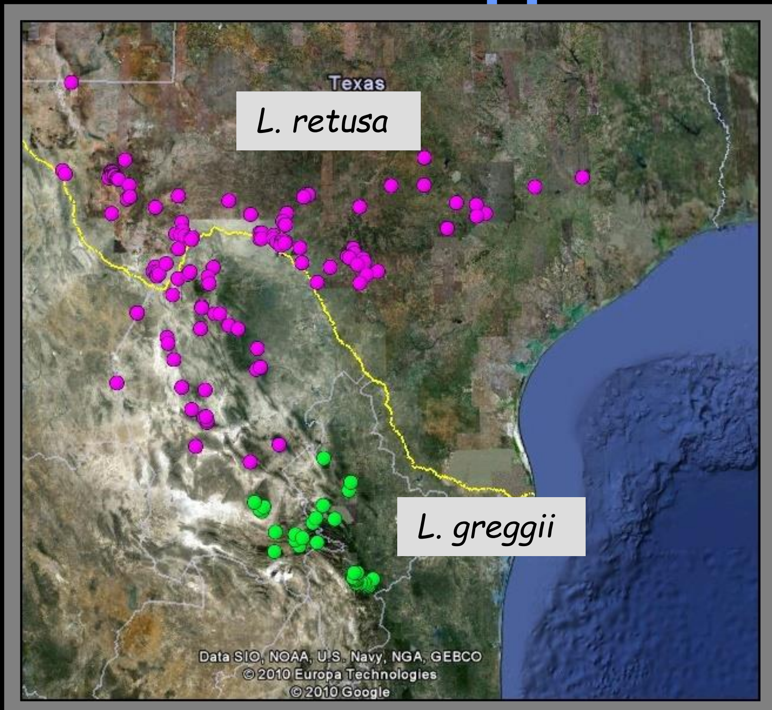
All Collections

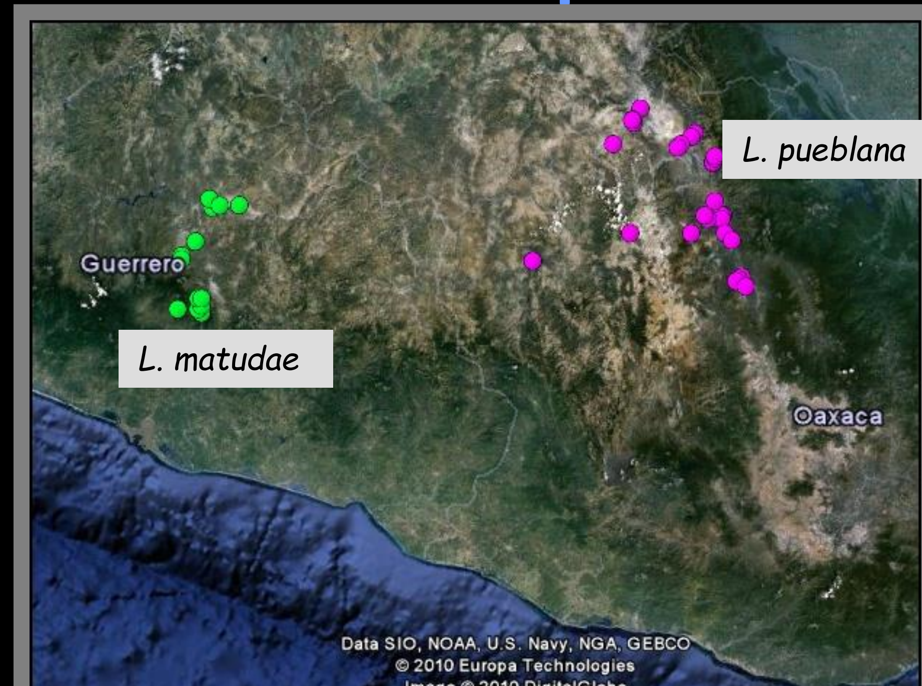
Combined Diploid Phylogeny

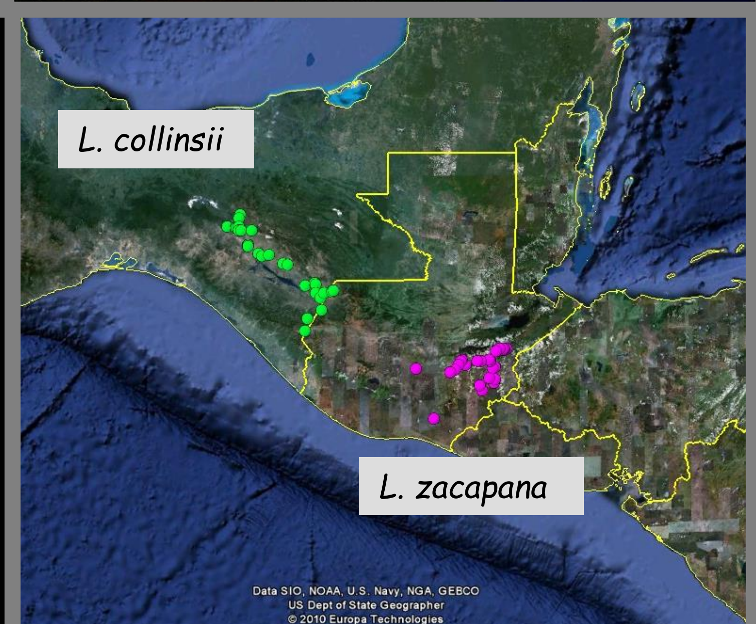
ML tree from RAxML
- 6960 aligned bases
- Support values 1) ML bootstrops from RAxML 2) jackknife values from NONA
- *- clades that collapse in the strict consensus parsimony result.

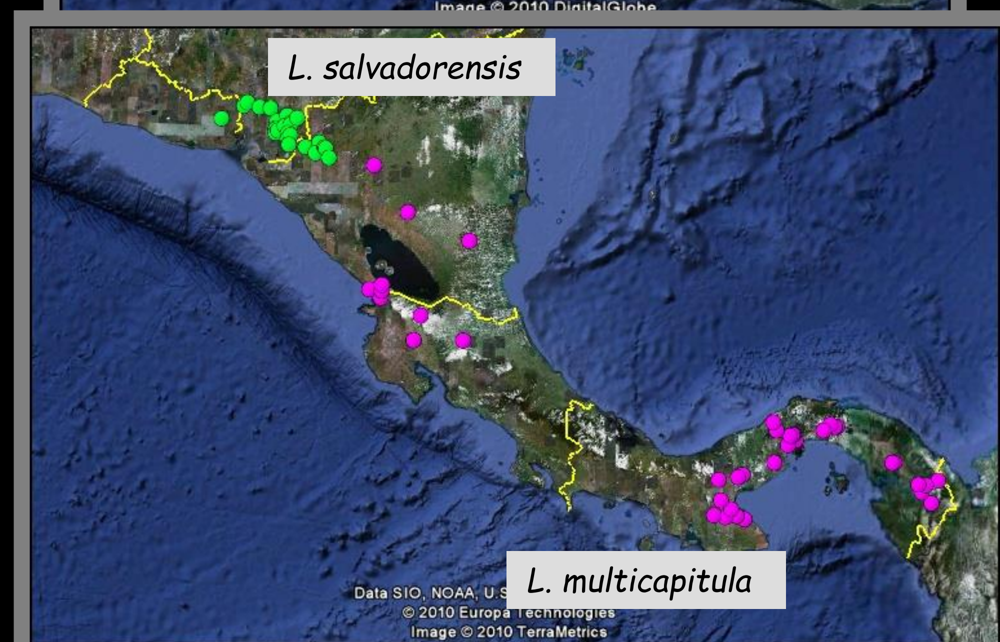


Well-Supported Pairs of Sister Species









Crossability

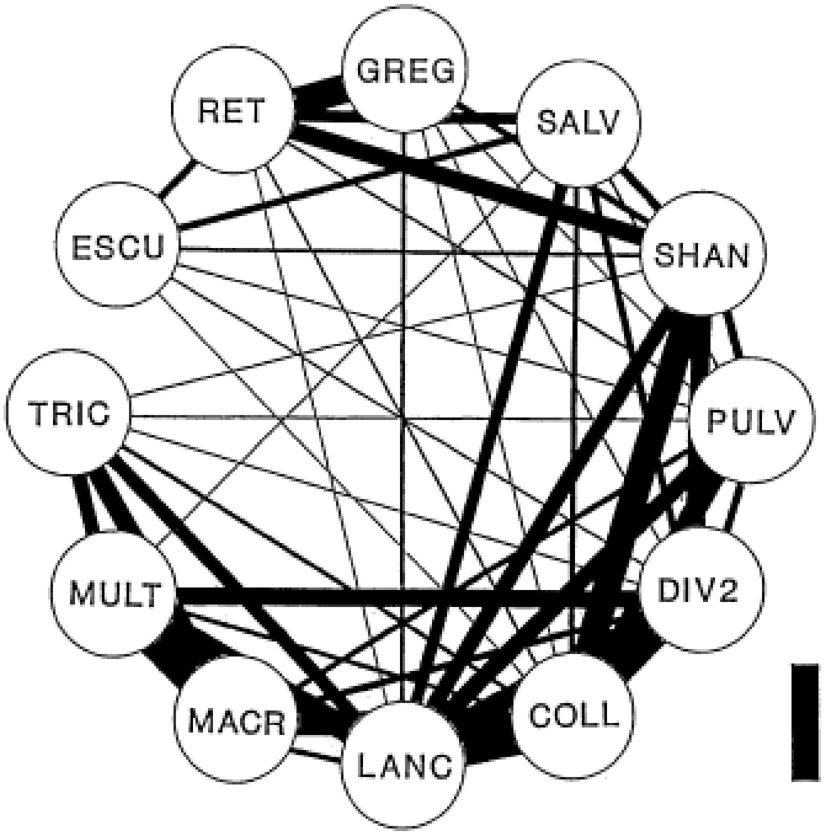
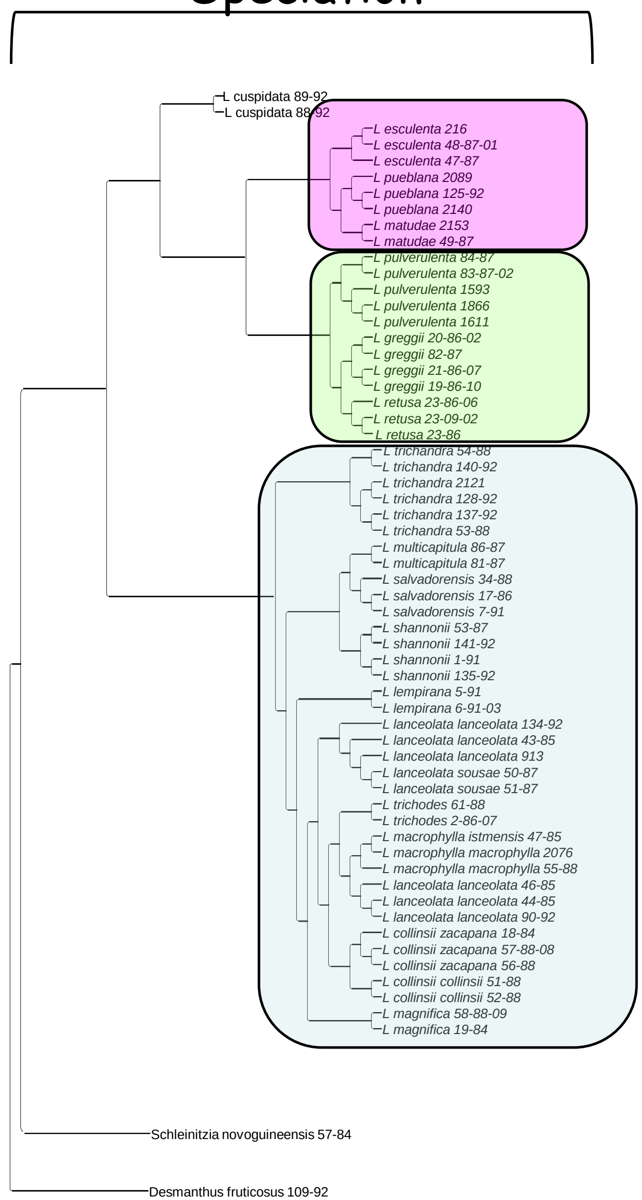


Fig. 6. Relative ease of interspecific hybrid seed production among 12 diploid *Leucaena* species, using maximal data from reciprocal crosses for each species × species mating. Bar thickness indicates a crossability index of 100%.

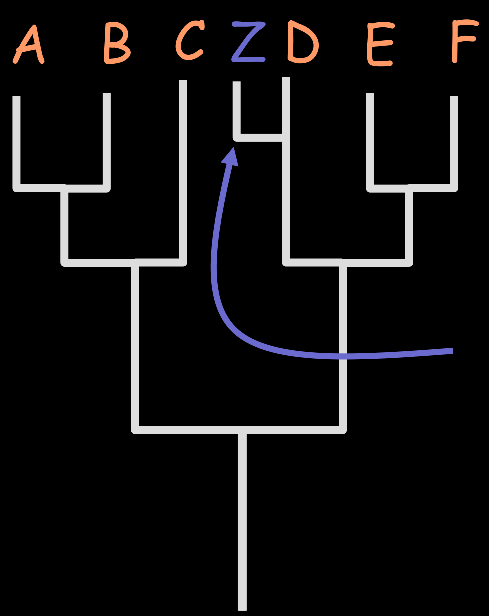
Sorensson & Brewbaker, 1994

Diploid Allopatric Speciation

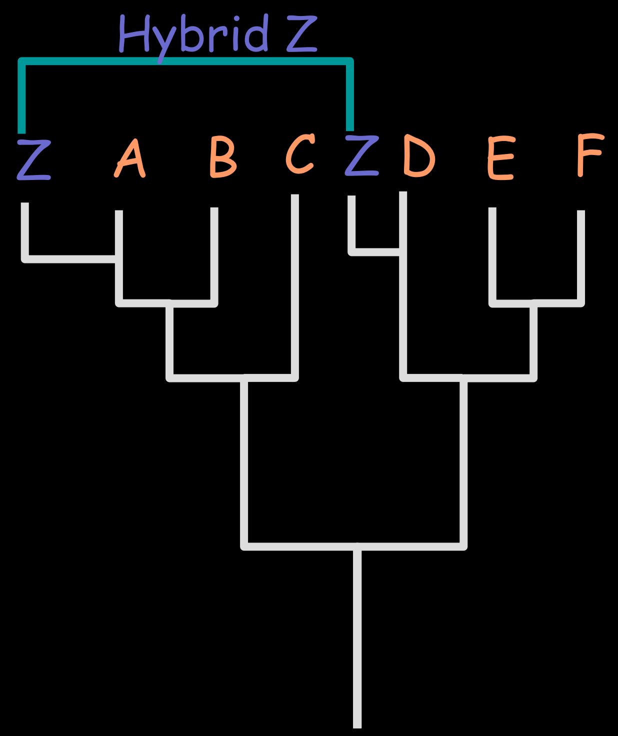


Results from biparentally inherited loci can provide information on allopolyploid origins

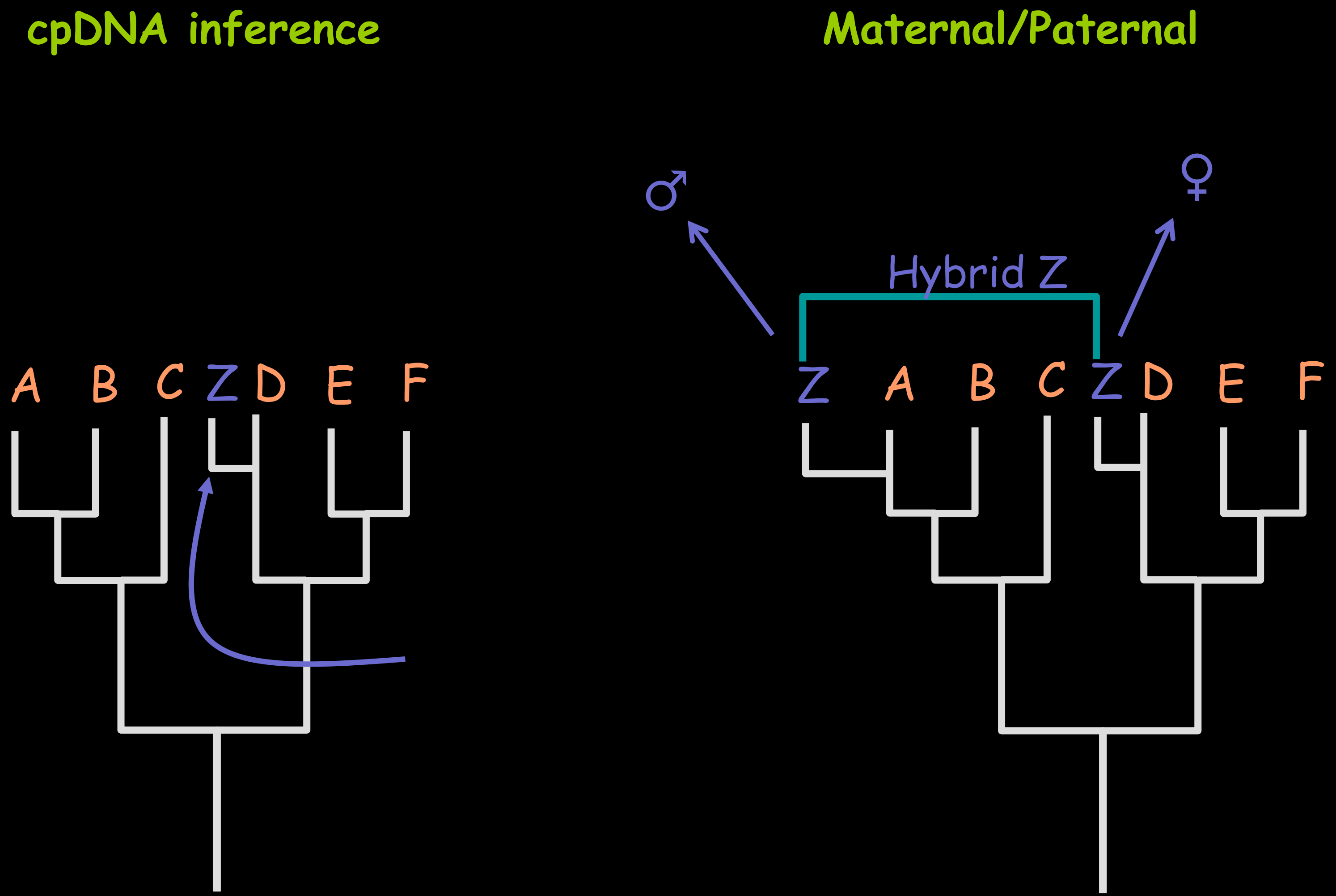
- Autopolyploids



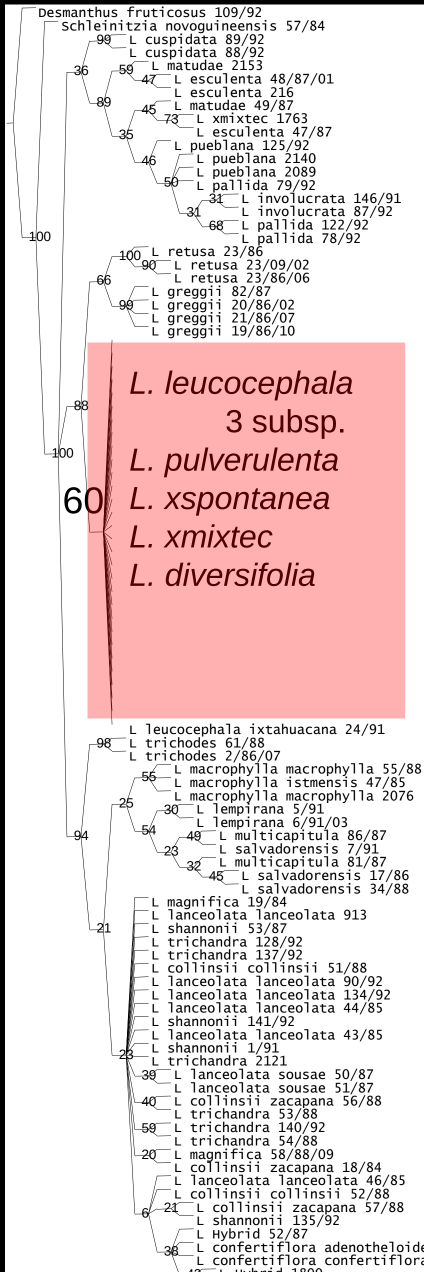
- Allopolyploids:
  - Hybridization
  - Polyploidy



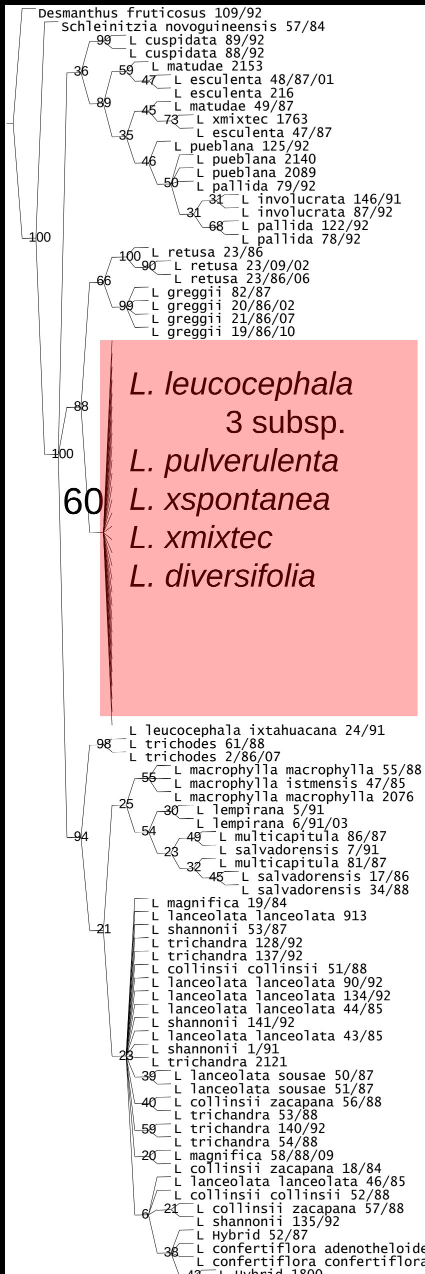
Chloroplast Loci and Maternal/Paternal Inheritance



cpDNA Tree ♀


Desmanthus fruticosus 109/92
Schleinitzia novoguineensis 57/84
L cuspidata 89/92
L cuspidata 88/92
L matudae 2153
L esculenta 48/87/01
L esculenta 216
L matudae 49/87
L xmixtec 1763
L esculenta 47/87
L pueblana 125/92
L pueblana 2140
L pueblana 2089
L pallida 79/92
L involucrata 146/91
L involucrata 87/92
L pallida 122/92
L pallida 78/92
L retusa 23/86
L retusa 23/09/02
L retusa 23/86/06
L greggii 82/87
L greggii 20/86/02
L greggii 21/86/07
L greggii 19/86/10
L. leucocephala
3 subsp.
L. pulverulenta
L. xspontanea
L. xmixtec
L. diversifolia
60
L leucocephala ixtahuacana 24/91
L trichodes 61/88
L trichodes 2/86/07
L macrophylla macrophylla 55/88
L macrophylla istmensis 47/85
L macrophylla macrophylla 2076
L lempirana 5/91
L lempirana 6/91/03
L multicapitula 86/87
L salvadorensis 7/91
L multicapitula 81/87
L salvadorensis 17/86
L salvadorensis 34/88
L magnifica 19/84
L lanceolata lanceolata 913
L shannonii 53/87
L trichandra 128/92
L trichandra 137/92
L collinsii collinsii 51/88
L lanceolata lanceolata 90/92
L lanceolata lanceolata 134/92
L lanceolata lanceolata 44/85
L shannonii 141/92
L lanceolata lanceolata 43/85
L shannonii 1/91
L trichandra 2121
L lanceolata sousae 50/87
L lanceolata sousae 51/87
L collinsii zacapana 56/88
L trichandra 53/88
L trichandra 140/92
L trichandra 54/88
L magnifica 58/88/09
L collinsii zacapana 18/84
L lanceolata lanceolata 46/85
L collinsii collinsii 52/88
L collinsii zacapana 57/88
L shannonii 135/92
L Hybrid 52/87
L Hybrid 1800

cpDNA Tree ♀



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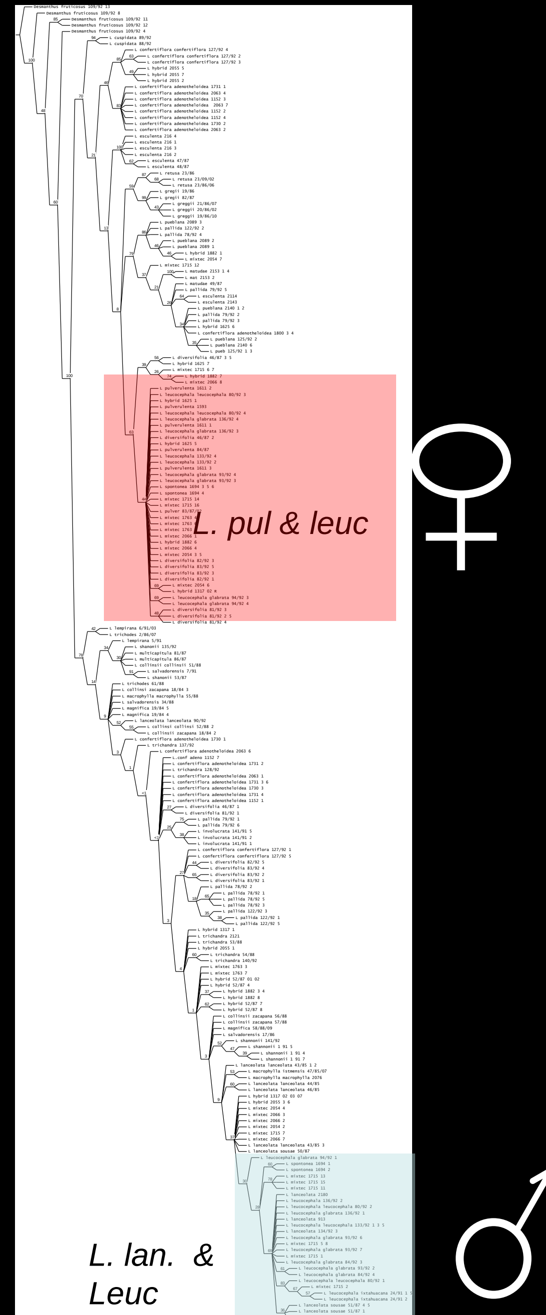
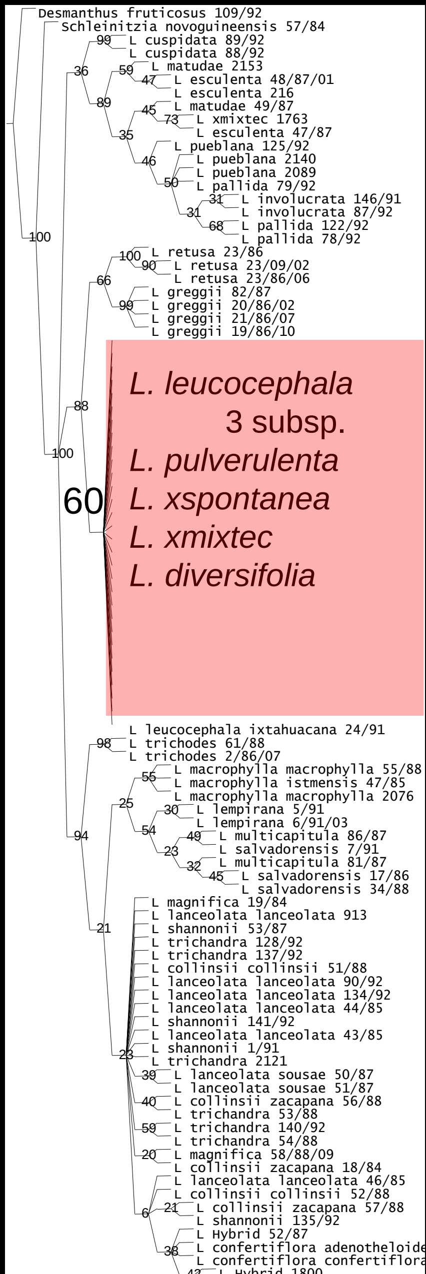


cpDNA Tree ♀



Desmanthus fruticosus 109/92
Schleinitzia novoguineensis 57/84
L cuspidata 89/92
L cuspidata 88/92
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L esculenta 48/87/01
L esculenta 216
L matudae 49/87
L xmixtec 1763
L esculenta 47/87
L pueblana 125/92
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L greggii 82/87
L greggii 20/86/02
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L. leucocephala
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L. xspontanea
L. xmixtec
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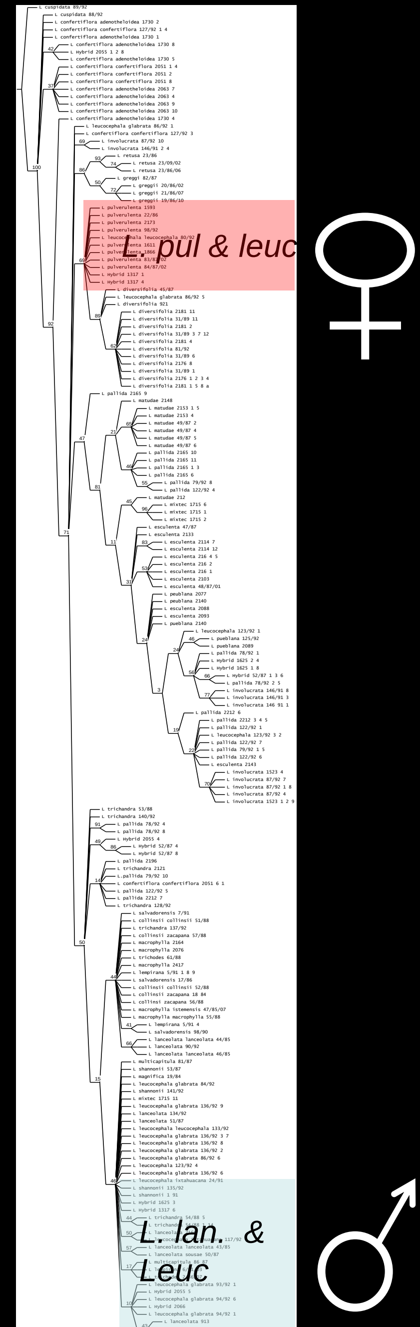
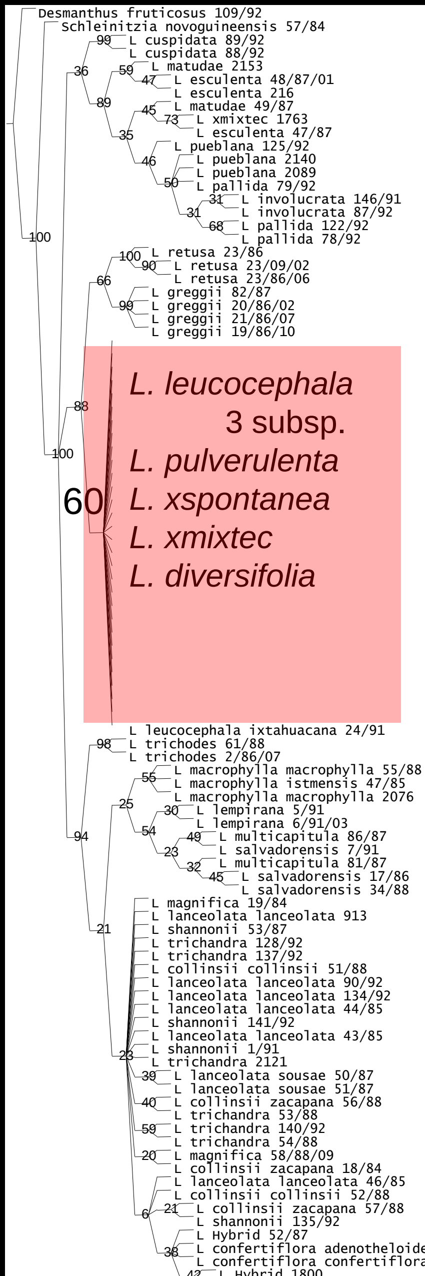
L macrophylla macrophylla 2076
L lempirana 5/91
L lempirana 6/91/03
L multicapitula 86/87
L salvadorensis 7/91
L multicapitula 81/87
L salvadorensis 17/86
L salvadorensis 34/88
L magnifica 19/84
L lanceolata lanceolata 913
L shannonii 53/87
L trichandra 128/92
L trichandra 137/92
L collinsii collinsii 51/88
L lanceolata lanceolata 90/92
L lanceolata lanceolata 134/92
L lanceolata lanceolata 44/85
L shannonii 141/92
L lanceolata lanceolata 43/85
L shannonii 1/91
L trichandra 2121
L lanceolata sousae 50/87
L lanceolata sousae 51/87
L collinsii zacapana 56/88
L trichandra 53/88
L trichandra 140/92
L trichandra 54/88
L magnifica 58/88/09
L collinsii zacapana 18/84
L lanceolata lanceolata 46/85
L collinsii collinsii 52/88
L collinsii zacapana 57/88
L shannonii 135/92
L Hybrid 52/87
L confertiflora adenotheloide
L confertiflora confertiflora
L Hybrid 1800

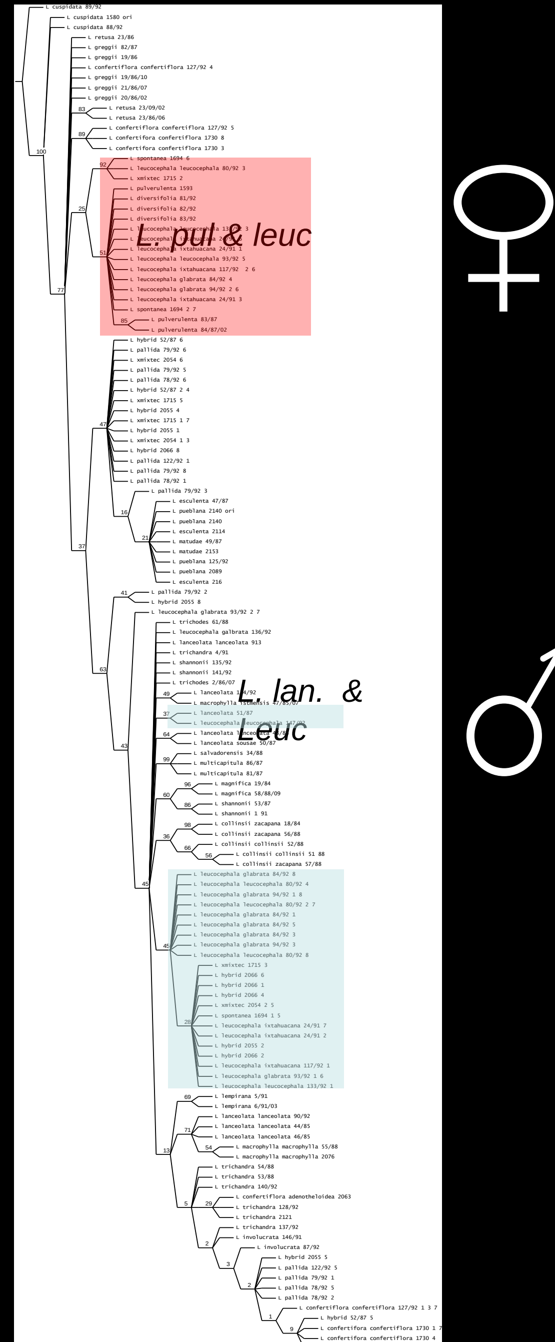


L. pul & leuc
♀
L. lan. &
Leuc
♂

cpDNA Tree ♀



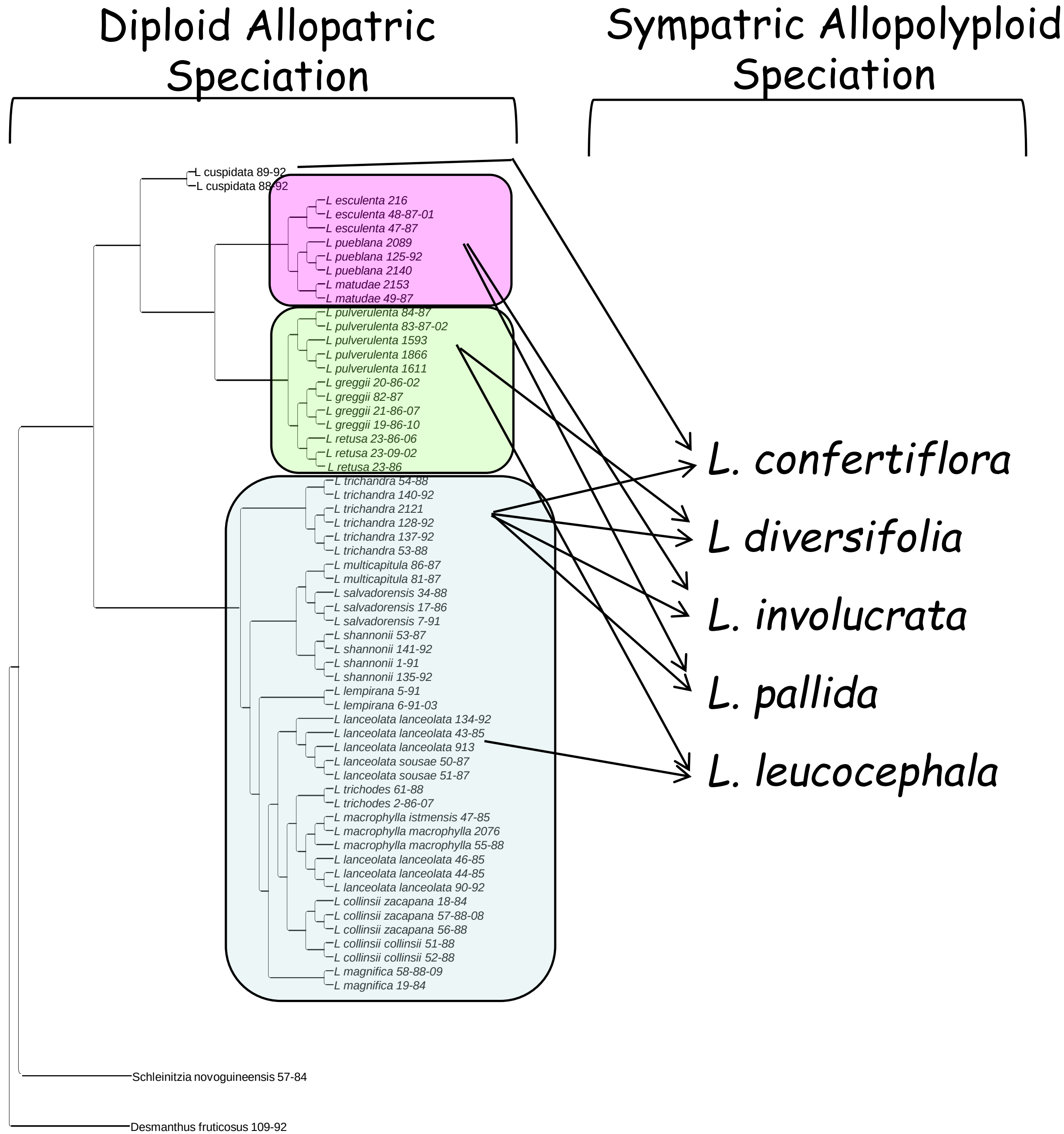
A2

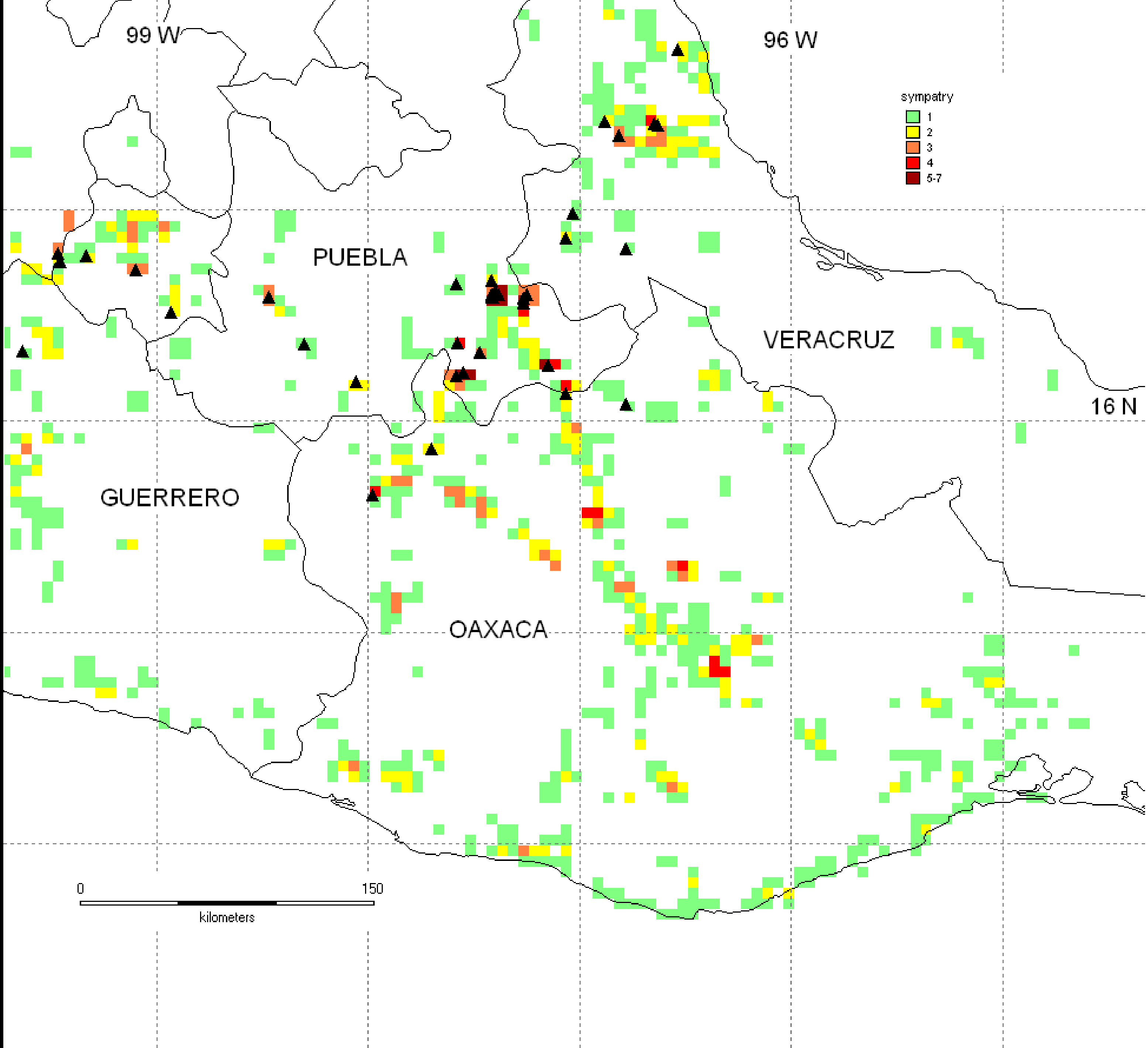


1) Crosses involve taxa from divergent clades.

2) *L. trichandra* is involved as maternal/paternal contributor in the origin of 4/5 allopolyploids

3) At least four unique allopolyploidizations between diploids are required to explain these patterns

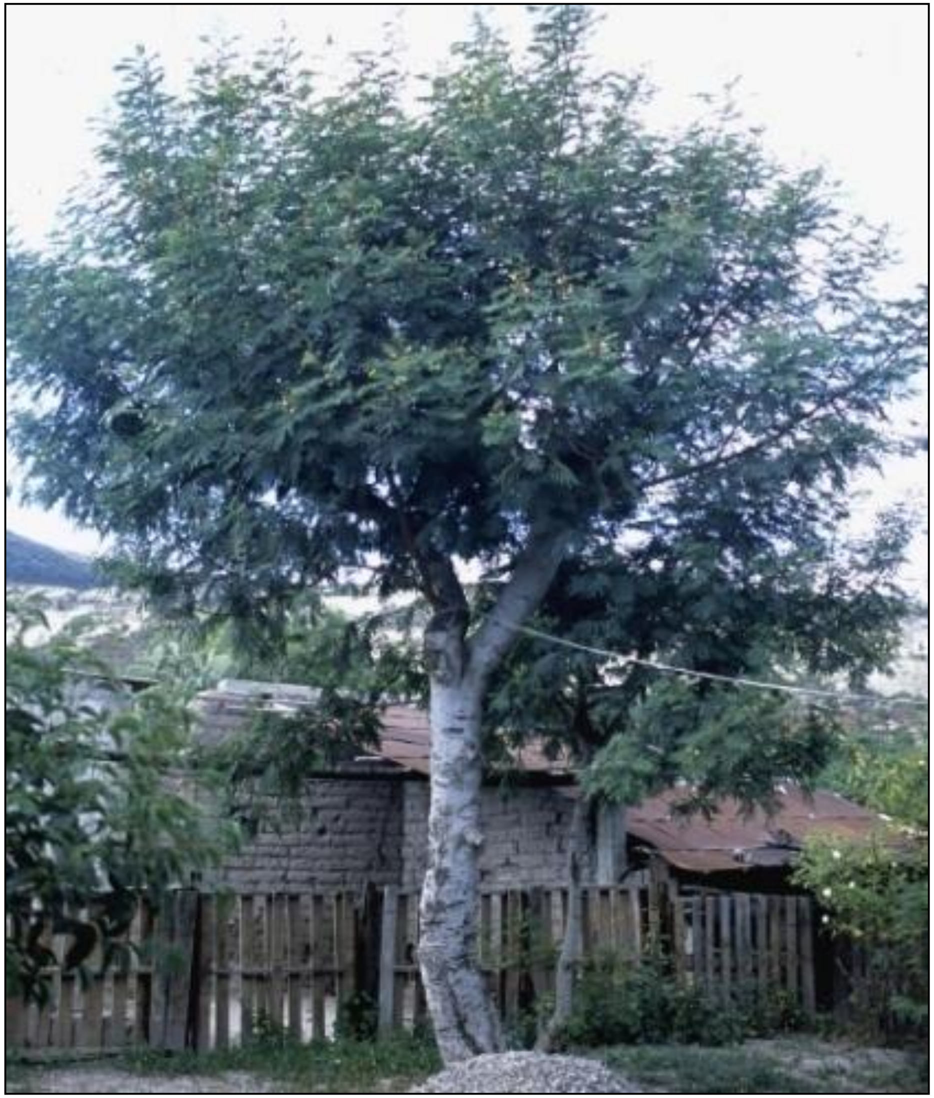


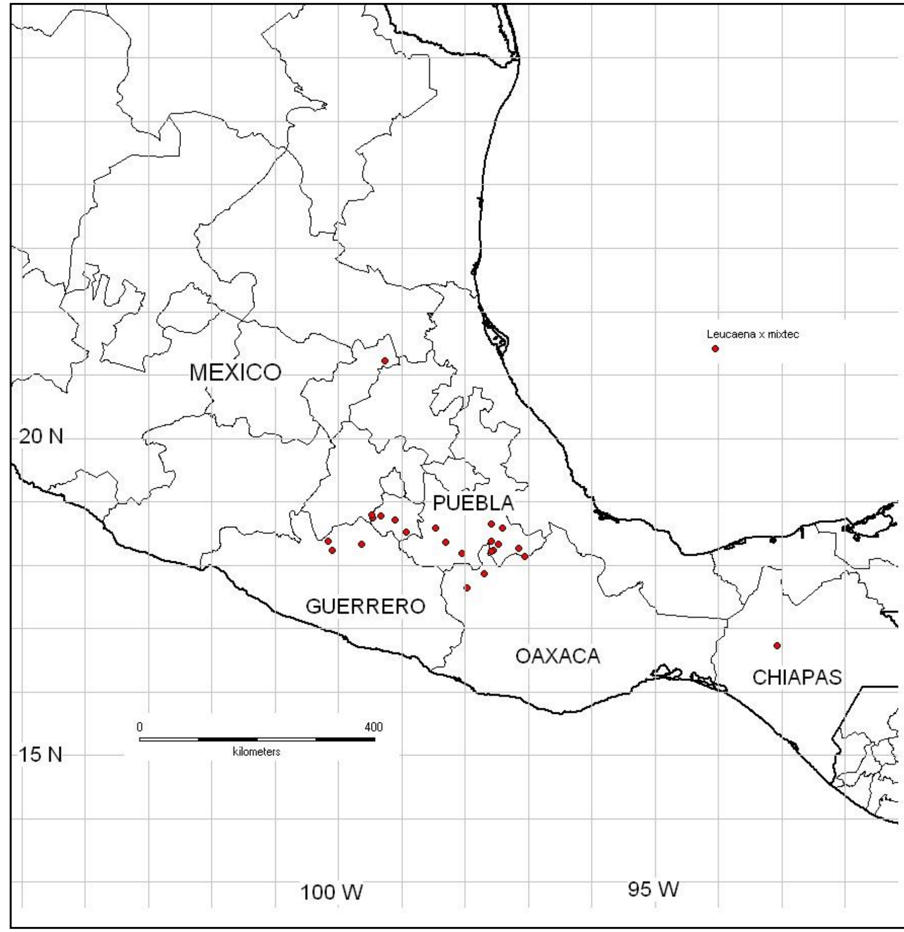


99 W
96 W
sympatry
1
2
3
4
5-7
PUEBLA
VERACRUZ
16 N
GUERRERO
OAXACA
0
150
kilometers

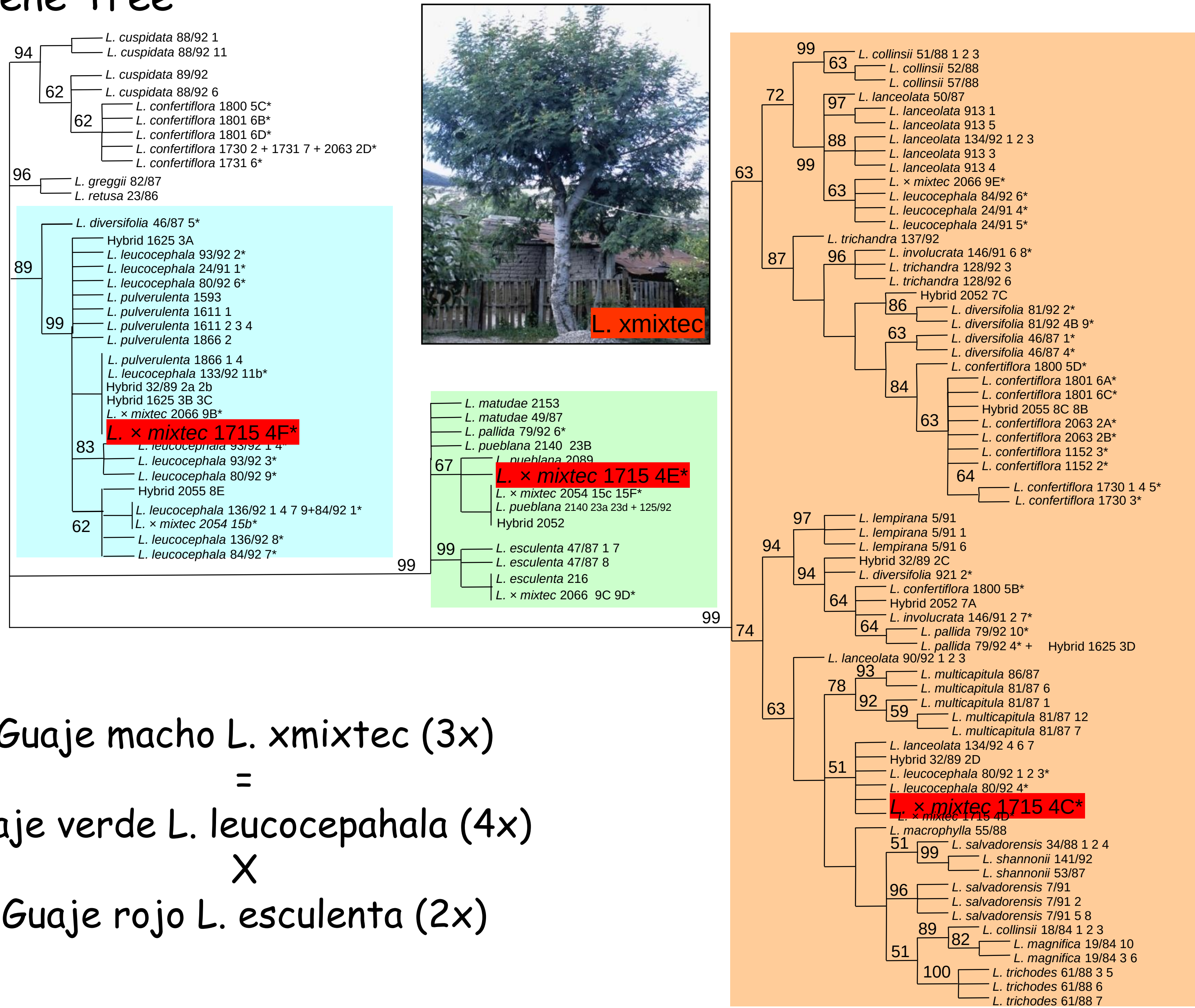
Tetraploid
Leucaena leucocephala

Guaje macho - Leucaena x mixtec - sterile





23L Gene Tree



Guaje macho L. xmixtec (3x)

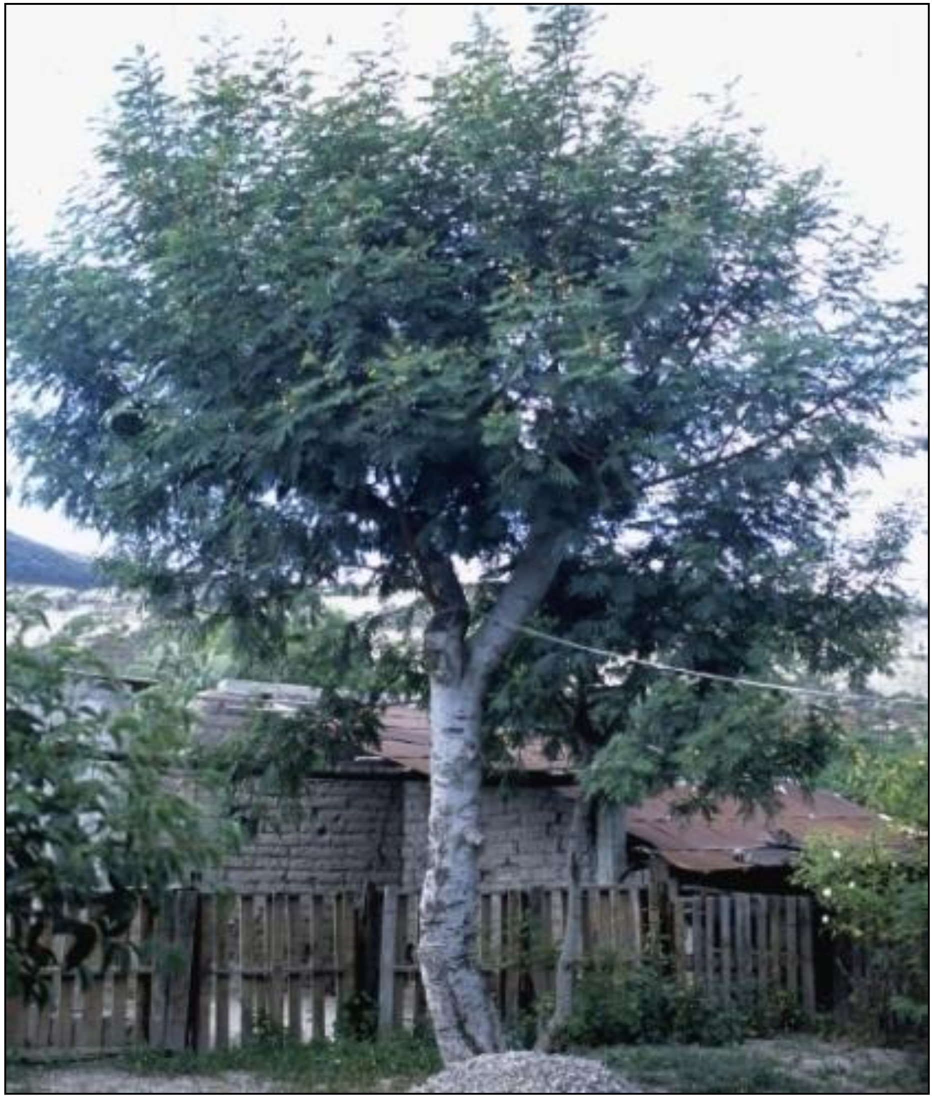
=

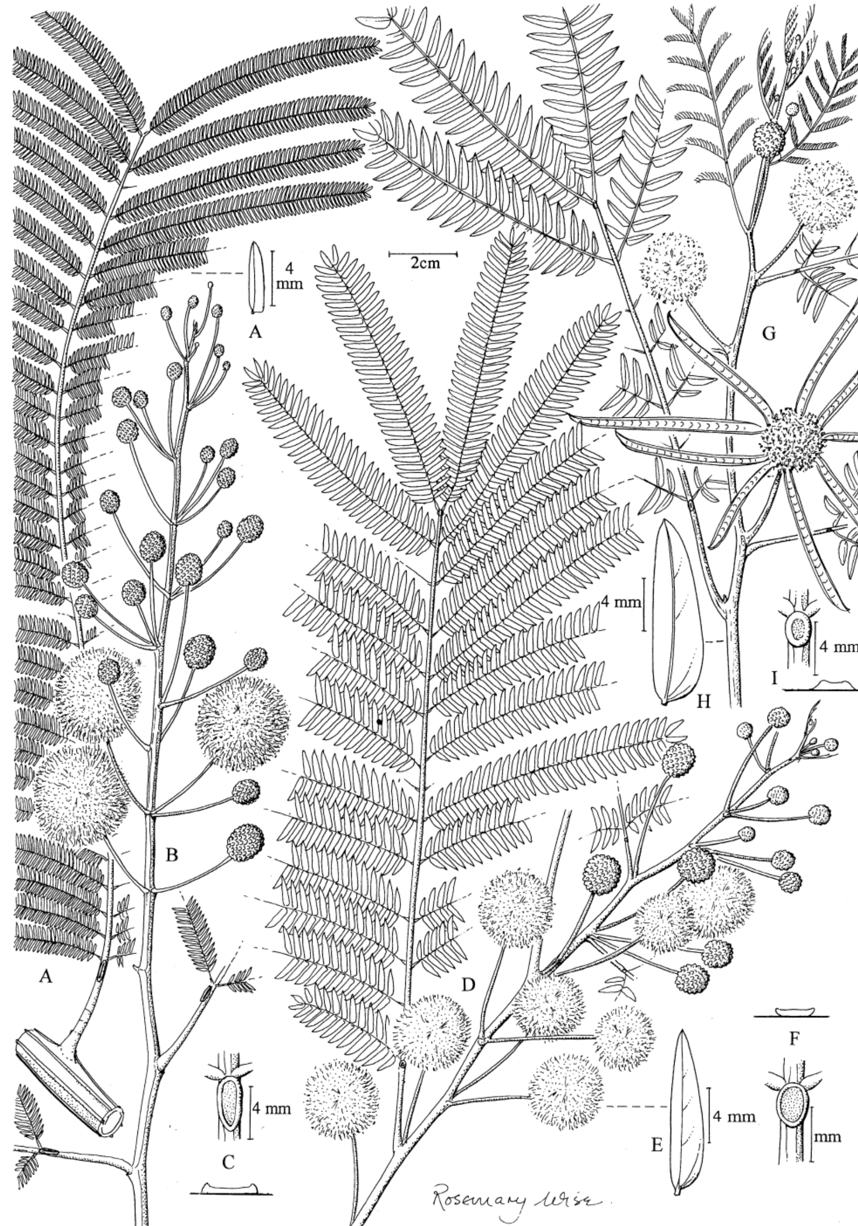
Guaje verde L. leucocepahala (4x)

X

Guaje rojo L. esculenta (2x)

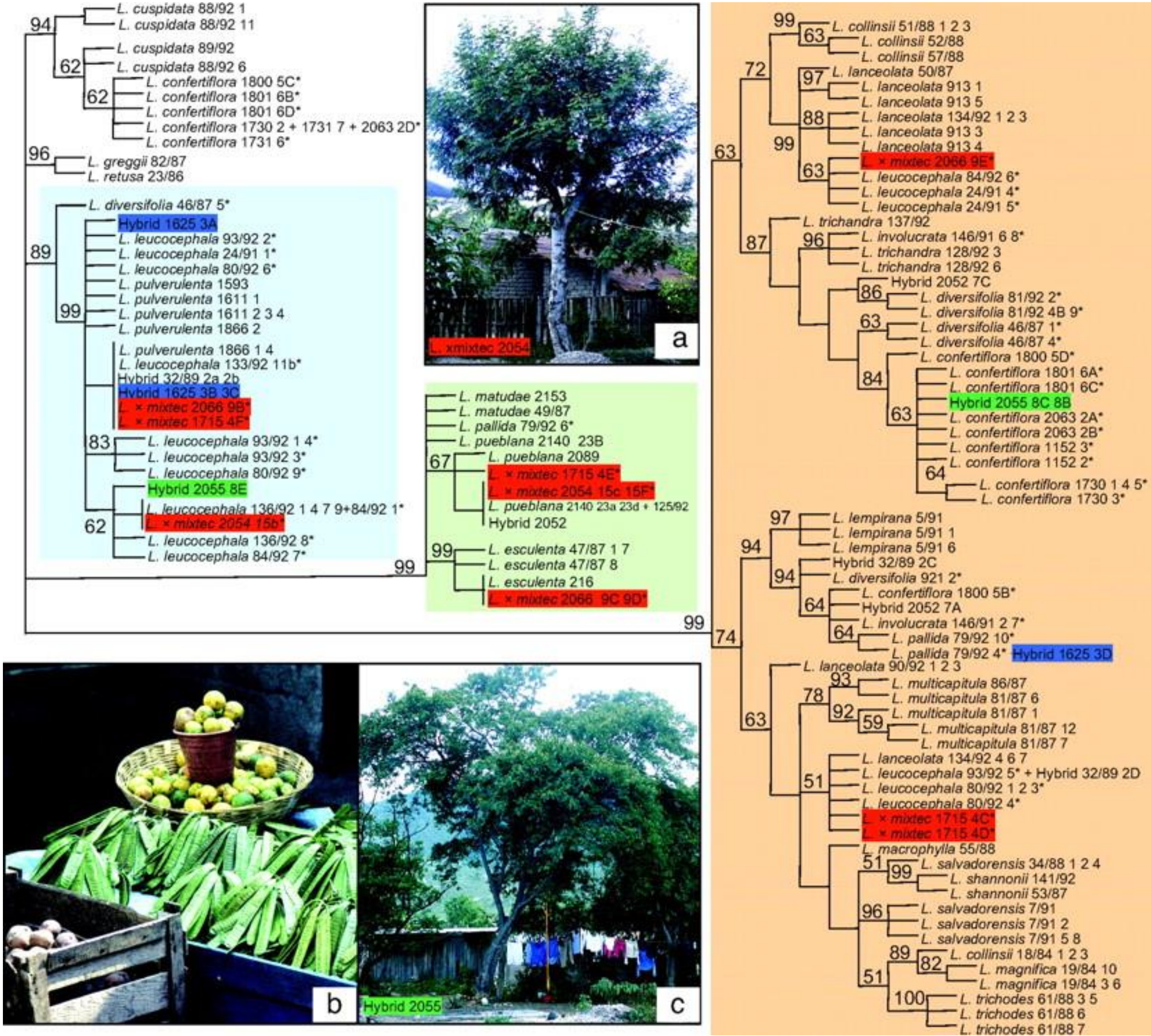
Hughes et al. 2007 - PNAS





Guaje macho L. xmixtec (3x)
=
Guaje verde L. leucocepahala (4x)
X
Guaje rojo L. esculenta (2x)

CEH 2055, San Pedro Chapulco



L. cuspidata 88/92 1
L. cuspidata 88/92 11
L. cuspidata 89/92
L. cuspidata 88/92 6
L. confertiflora 1800 5C*
L. confertiflora 1801 6B*
L. confertiflora 1801 6D*
L. confertiflora 1730 2 + 1731 7 + 2063 2D*
L. confertiflora 1731 6*
L. greggii 82/87
L. retusa 23/86
L. diversifolia 46/87 5*
Hybrid 1625 3A
L. leucocephala 93/92 2*
L. leucocephala 24/91 1*
L. leucocephala 80/92 6*
L. pulverulenta 1593
L. pulverulenta 1611 1
L. pulverulenta 1611 2 3 4
L. pulverulenta 1866 2
L. pulverulenta 1866 1 4
L. leucocephala 133/92 11b*
Hybrid 32/89 2a 2b
Hybrid 1625 3B 3C
L. × mixtec 2066 9B*
L. × mixtec 1715 4F*
L. leucocephala 93/92 1 4*
L. leucocephala 93/92 3*
L. leucocephala 80/92 9*
Hybrid 2055 8E
L. leucocephala 136/92 1 4 7 9+84/92 1*
L. × mixtec 2054 15b*
L. leucocephala 136/92 8*
L. leucocephala 84/92 7*
L. xmixtec 2054
a
L. matudae 2153
L. matudae 49/87
L. pallida 79/92 6*
L. pueblana 2140 23B
L. pueblana 2089
L. × mixtec 1715 4E*
L. × mixtec 2054 15c 15F*
L. pueblana 2140 23a 23d + 125/92
Hybrid 2052
L. esculenta 47/87 1 7
L. esculenta 47/87 8
L. esculenta 216
L. × mixtec 2066 9C 9D*
L. collinsii 51/88 1 2 3
L. collinsii 52/88
L. collinsii 57/88
L. lanceolata 50/87
L. lanceolata 913 1
L. lanceolata 913 5
L. lanceolata 134/92 1 2 3
L. lanceolata 913 3
L. lanceolata 913 4
L. × mixtec 2066 9E*
L. leucocephala 84/92 6*
L. leucocephala 24/91 4*
L. leucocephala 24/91 5*
L. trichandra 137/92
L. involucrata 146/91 6 8*
L. trichandra 128/92 3
L. trichandra 128/92 6
Hybrid 2052 7C
L. diversifolia 81/92 2*
L. diversifolia 81/92 4B 9*
L. diversifolia 46/87 1*
L. diversifolia 46/87 4*
L. confertiflora 1800 5D*
L. confertiflora 1801 6A*
L. confertiflora 1801 6C*
Hybrid 2055 8C 8B
L. confertiflora 2063 2A*
L. confertiflora 2063 2B*
L. confertiflora 1152 3*
L. confertiflora 1152 2*
L. confertiflora 1730 1 4 5*
L. confertiflora 1730 3*
L. lempirana 5/91
L. lempirana 5/91 1
L. lempirana 5/91 6
Hybrid 32/89 2C
L. diversifolia 921 2*
L. confertiflora 1800 5B*
Hybrid 2052 7A
L. involucrata 146/91 2 7*
L. pallida 79/92 10*
L. pallida 79/92 4* Hybrid 1625 3D
L. lanceolata 90/92 1 2 3
L. multicapitula 86/87
L. multicapitula 81/87 6
L. multicapitula 81/87 1
L. multicapitula 81/87 12
L. multicapitula 81/87 7
L. lanceolata 134/92 4 6 7
L. leucocephala 93/92 5* + Hybrid 32/89 2D
L. leucocephala 80/92 1 2 3*
L. leucocephala 80/92 4*
L. × mixtec 1715 4C*
L. × mixtec 1715 4D*
L. macrophylla 55/88
L. salvadorensis 34/88 1 2 4
L. shannonii 141/92
L. shannonii 53/87
L. salvadorensis 7/91
L. salvadorensis 7/91 2
L. salvadorensis 7/91 5 8
L. collinsii 18/84 1 2 3
L. magnifica 19/84 10
L. magnifica 19/84 3 6
L. trichodes 61/88 3 5
L. trichodes 61/88 6
L. trichodes 61/88 7
b
Hybrid 2055
c

Leucaena

Seeds of 13 species are used as food

Prevalent throughout S-C Mexico and NW fringes of Guatemala

Wild – managed – cultivated (8 of the 13 species) – incipiently domesticated

Home consumption – local & regional marketing

Very local – regional – wider translocation

Numerous repeated and spatially and temporally independent wild to cultivated transitions

High levels of artificial sympatry

Spontaneous hybrids are common – *L. xmixtec*, and likely account for at least the origin of the most important polyploid species *L. leucocephala*, which subsequently itself hybridized with another polyploid *L. confertiflora* to form CEH2055.

Agave – Maguey
Tequila & Mezcal


Opuntia - Nopales



Agave & Opuntia

Archaeobotanical records of use – 6,000-9,000 years

Several species are utilized

Finely differentiated cognitive systems

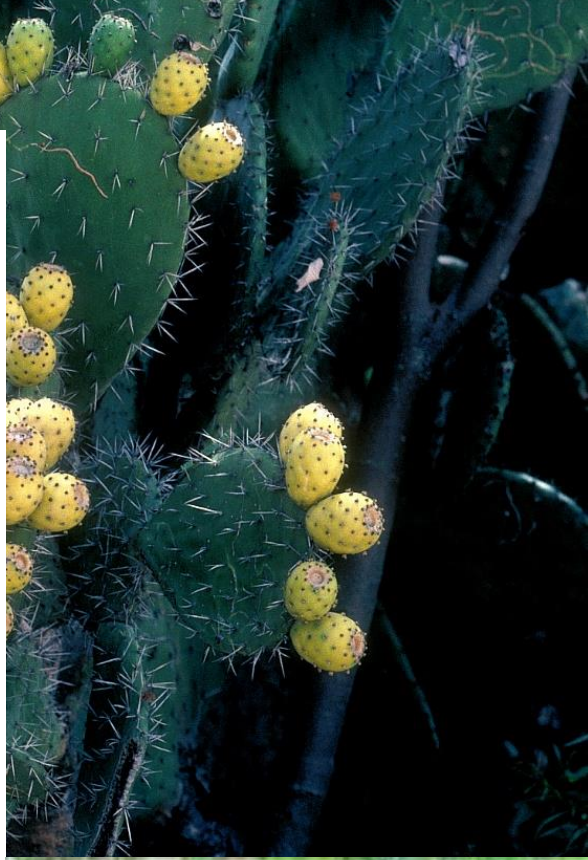
Widespread and complex mosaic of wild, managed and cultivated populations spanning a large area

Sympatry resulting from juxtaposition in cultivation is common

Compelling evidence for spontaneous interspecific hybridization

Spontaneous hybrid origins for major Agave and Opuntia domesticates

Ease of vegetative propagation of spontaneous hybrids



Agave Opuntia

Perennial Mesoamerican Domesticates

Leucaena

Serendipitous Backyard Hybridization & the Origin of Crops – Conclusions

Disturbed sites such as backyards, kitchen middens, and informal orchards are important sites for spontaneous hybridisation, where otherwise isolated plant species were brought into sympatry following cultivation.

For Guajes, Nopales & Maguey – three of the dominant perennial plants cultivated in south-central Mexico - predomestication cultivation has resulted in extensive artificial sympatry, and a complex series of geographically dispersed hybrids and polyploids.

In each case, there is evidence to suggest that the most prominent species in cultivation – *Leucaena leucocephala*, *Opuntia ficus-indica*, and *Agave tequilana*, have had hybrid origins most likely following cultivation.

The simple step of bringing species together, casually or consciously in dump heaps and informal orchards has played a key role in domestication of these crops.

Incipient or semi-domesticates like these can provide powerful insights into the early stages of domestication

Leucaena leucocephala

A fast growing, nitrogen-fixing, readily managed, multipurpose agroforestry tree for firewood, poles, high quality animal fodder and green manure

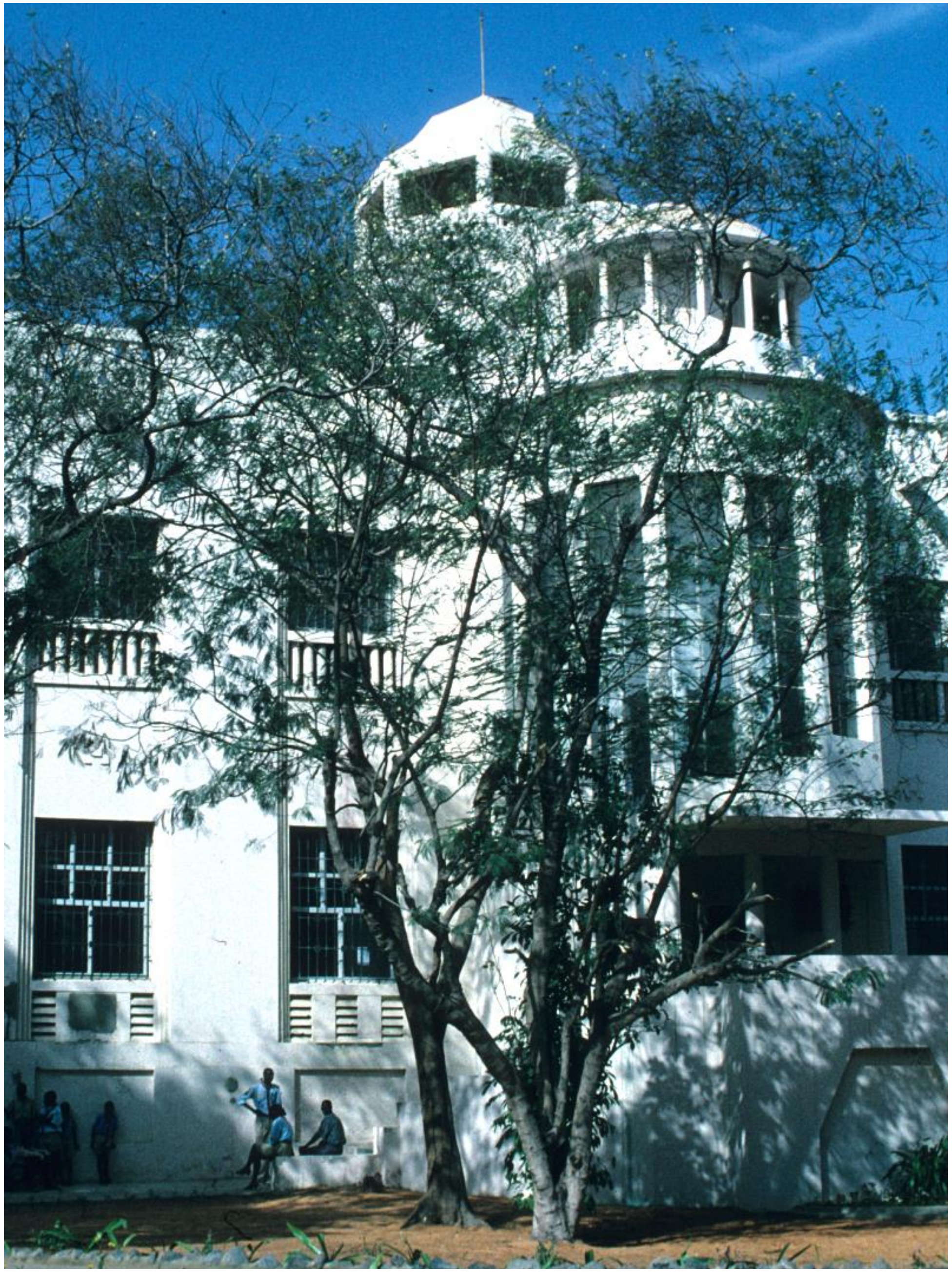
The 'alfalfa of the tropics'; 'Miracle tree'

Pantropically cultivated

Leucaena leucocephala

A pantropical invasive weed

Self fertile, massive seed production, fast growing



Guaje macho L. xmixtec (3x)
=
Guaje verde L. leucocepahala (4x)
X
Guaje rojo L. esculenta (2x)

In Dakar, Senegal, West Africa

Leucaena leucocepahala

Anthropogenic origin several millennia ago as a result of spontaneous hybridization following backyard cultivation of Leucaena as an incipiently domesticated food crop in south-central Mexico.

Widely cultivated throughout Mexico for edible seeds.

Introduced to the Old World in the 16th Century and now pantropically introduced and cultivated as a 'miracle tree' or the 'alfalfa of the tropics'.

Now naturalized and a pantropical invasive plant.

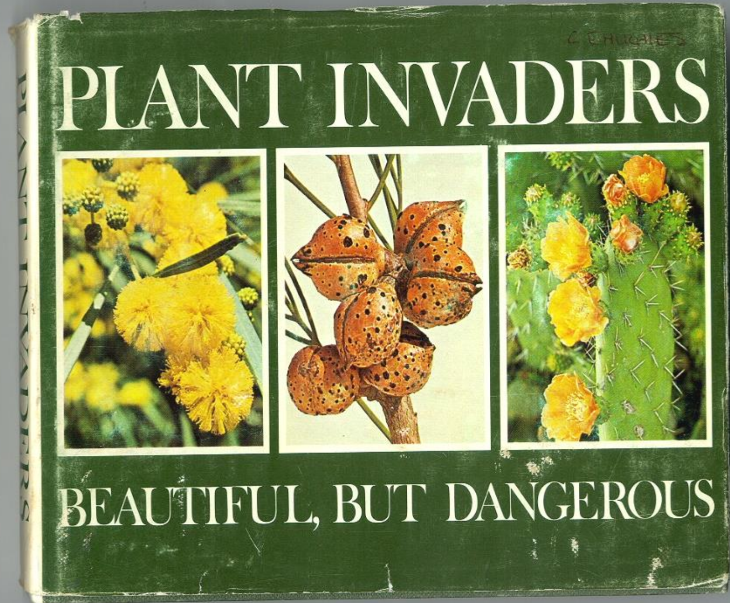
The intertwining of plants and people over several millennia and multiple continents

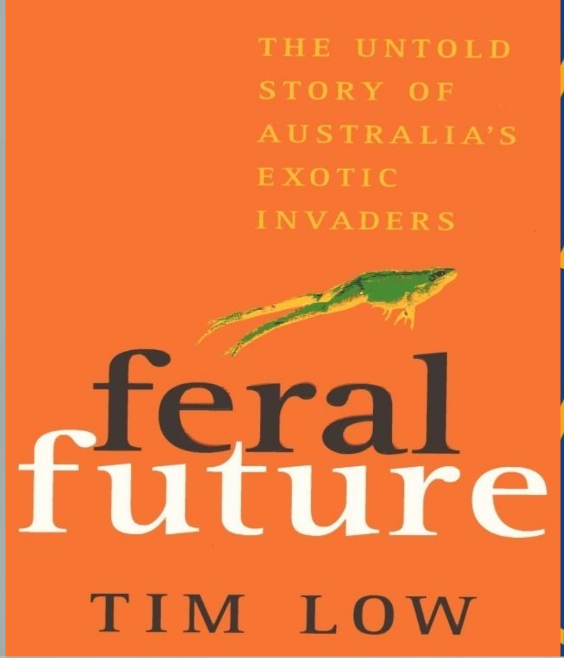
Invasive Species

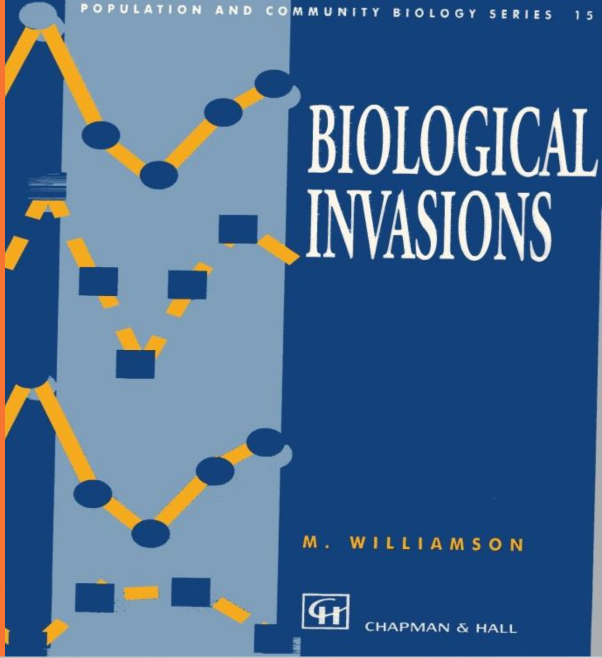
an alien plant spreading naturally (without the direct assistance of humans) in natural or semi-natural habitats to produce significant change in terms of composition, structure or ecosystem processes

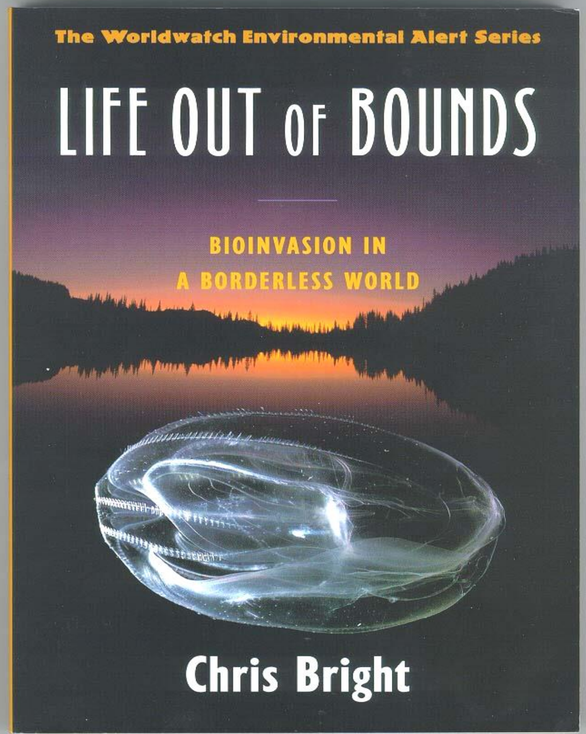
Darwin (1860)

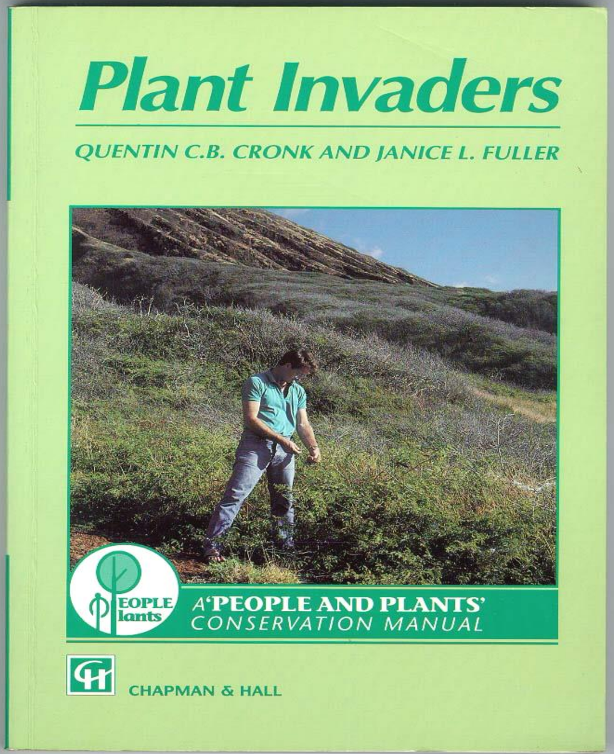
'Cases could be given of introduced plants which have become common throughout whole islands in a period of less than 10 years..... Let it be remembered how powerful the influence of a single introduced tree or mammal (species) *has been shown to be'*

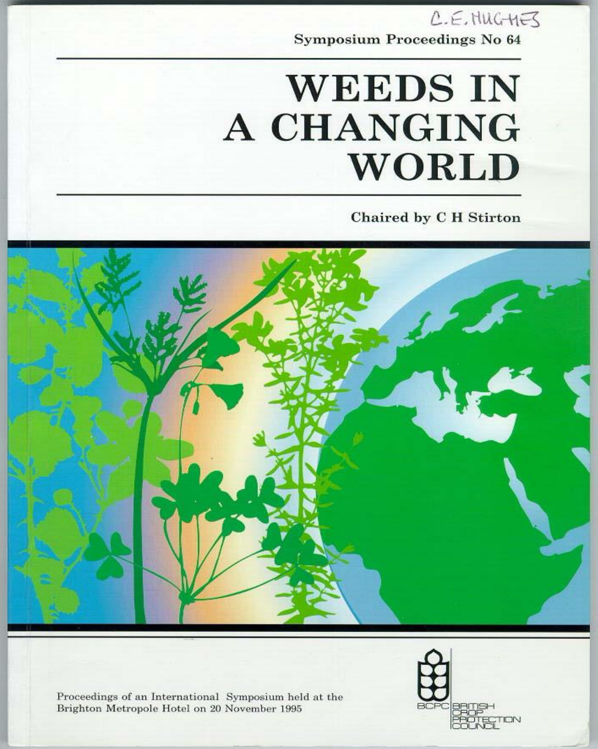

PLANT INVADERS
BEAUTIFUL, BUT DANGEROUS
PLANT INVADERS


THE UNTOLD STORY OF AUSTRALIA'S EXOTIC INVADERS
feral future
TIM LOW


POPULATION AND COMMUNITY BIOLOGY SERIES 15
BIOLOGICAL INVASIONS
M. WILLIAMSON
CHAPMAN & HALL


The Worldwatch Environmental Alert Series
LIFE OUT OF BOUNDS
BIOINVASION IN A BORDERLESS WORLD
Chris Bright


Plant Invaders
QUENTIN C.B. CRONK AND JANICE L. FULLER
PEOPLE Plants
A 'PEOPLE AND PLANTS' CONSERVATION MANUAL
CHAPMAN & HALL


C.E. HUGHES
Symposium Proceedings No 64
WEEDS IN A CHANGING WORLD
Chaired by C H Stirton
Proceedings of an International Symposium held at the Brighton Metropole Hotel on 20 November 1995
BCPC BRITISH CROP PROTECTION COUNCIL

Evolution in Reverse

- Effective collapse of the world's ecological barriers represents a vast and unprecedented, but little noticed, biotic upheaval
- Current movements of weeds, pests and pathogens
  - *frequency*: 1000s of times faster than natural rate
  - *pervasiveness*: occasional regional events now a chronic global phenomenon
  - *'impossible' migration, is now not only possible, but common*

‘we bring strangers together to make strange bedfellows, and we remake the beds they lie in, all at once……. Thus our disturbances hybridize both the environment and the species. ***We are hybridizing the planet***’

[Weiner, 1994: The Beak of the Finch]

Background paper:
Hughes et al. 2006. Serendipitous backyard hybridization and the origin of crops. *Proceedings of the National Academy of Sciences* **103**: 10334-10339

Anderson, E. 1954. Plants, Man & Life.

Renny-Byfield S. & Wendel J.F. 2014. Doubling down on genomes: polyploidy and crop plants. American Journal of Botany 101: 1711-1725.

C.E. Hughes
October 2018
colin.hughes@systbot.uzh.ch