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Volume: 16 Issue: 1
Month/Year: 2003
Pages: 41-48

Article Author:
Article Title: Rico, Lourdes; Geographical patterns in neotropical Acacia

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Geographical patterns in neotropical *Acacia* (Leguminosae: Mimosoideae)

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Abstract. Native neotropical species of *Acacia*, totalling 230 species, are represented by two subgenera, *Acacia* and *Aculeiferum*. The number of taxa per country and their distribution are presented. For subgenus *Aculeiferum*, the species of section *Filicinae* are the richest in Mexico, while species of section *Monacantha* are the most diverse in Brazil, Bolivia and Mexico. The species of subgenus *Acacia* have three main areas of diversity, with Mesoamerica being the most important region for the myrmecophyllous species and Mexico, the United States and Cuba for the non-myrmecophyllous species.

Introduction

The tribe Acacieae is currently monotypic containing the single genus *Acacia* Mill.; genus *Faidherbia* A.Chev. is officially excluded from the tribe (Bisby *et al.* 1994; Polhill 1994). Close morphological similarities are with the tribe *Ingeae*, particularly with the genus *Lysiloma* (Barneby and Grimes 1996; Jawad *et al.* 2000). *Acacia* is characterised by having many stamens, their filaments free or basally adherent to the corolla as part of a stemonozone (term as defined by Lewis and Elias 1981). Only a few species with male flowers have a more prominent staminal tube, examples of these are seen in *Acacia hindsii*, *A. mayana* and *A. farnesiana*.

As presently understood, pantropical *Acacia* is a single genus divided into three subgenera [*Acacia* Vassal, *Aculeiferum* Vassal and *Phyllodineae* (DC.) Ser.]. Australia has over 950 species (Maslin 2001), most of them members of subgenus *Phyllodineae*, some of which have been successfully introduced into other countries as ornamental trees and for social and commercial utilisation. In Malesia, there are only 29 species but these include native species of the three subgenera (Nielsen and Hopkins 1992). For other regions of the world, native species fall within only two subgenera, *Acacia* and *Aculeiferum*. These play important ecological and geographical roles, mainly in the arid lands of Africa and the Middle East with more than 130 species (Ross 1979), India with about 18 species (Timberlake *et al.* 1999) and the Americas with 230 species, including introduced taxa (L. Rico-Arce, unpubl. data). Today in Africa and America, the most widespread taxon is subgenus *Acacia*, characterising large areas of bushland and seasonal forest. In contrast, subgenus *Aculeiferum* is less abundant but more diverse in the moist and wet tropical forest where most species are vines.

The native neotropical species of *Acacia* belong to two subgenera. Subgenus *Aculeiferum* (=series *Vulgares* of Benthham) is subdivided into two sections, *Monacantha* and *Filicinae* (Vassal 1972), and subgenus *Acacia* (=series *Gummiferae* of Benthham) comprises two informal groups, the non-myrmecophyllous group (= *Vachellia* Wight & Arnott, *Poponax* Rafinesque, *Acaciopsis* Britton & Rose and *Feracacia* Britton & Leon) and the myrmecophyllous or swollen thorn acacia group (*Tauroceras* Britton & Rose and *Myrmecodendron* Britton & Rose).

Materials and methods

Data were gathered during collaborative field work and from regional *Acacia* treatments by various authors (Rudd and Carter 1983; Cialdella 1984; McVaugh 1987; Barneby and Zanoni 1989; Lee *et al.* 1989; Madsen 1990; da Silva 1990; Zamora 1991; Rico-Arce 1994; Acevedo-Rodríguez 1996; Fortunato and Cialdella 1996; Bässler 1998; Isely 1998; Rico and Rodríguez 1998; Ebinger *et al.* 2000; Jawad *et al.* 2000; García and Mejía 2000; Rico 2001a, 2001b, unpubl. data; Echeverry and Vester 2002; Casiva *et al.* 2002; L. Rico and Fonseca, unpubl. data) together with unpublished material from a conspectus of neotropical *Acacia* (L. Rico-Arce, unpubl. data).

For the analysis of these regions, all species of *Acacia* in the neotropics were divided into the following four groups: subgenus *Aculeiferum*—sections *Monacantha* and *Filicinae*, and subgenus *Acacia*—non-myrmecophyllous and myrmecophyllous groups (Table 1).

The geographical distribution of the neotropical species has been recorded in a database and excel spread sheet and this data was analysed. Introduced and 'naturalised' species were omitted from this study, data gathering being restricted to native species only.

Initially, a map with the political divisions of the American continent was used (Fig. 1), with the number of species for each country plotted. This shows that Mexico, Brazil, Argentina, Bolivia and Paraguay are the countries with most species diversity.

These political divisions were, however, inappropriate for data interpretation purposes because they cross phytogeographical

Table 1. List of native neotropical *Acacia* (accepted species only) with subgenera/groups and inflorescence type

Species	Subgenus/group	Inflorescence type	Species	Subgenus/group	Inflorescence type
<i>A. acatensis</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. daemon</i> Ekman & Urban	<i>Acacia</i>	Capitate
<i>A. adhaerens</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. dolichostachya</i> S.F.Blake	<i>Aculeiferum</i>	Spicate
<i>A. albicorticata</i> Burkart	<i>Acacia</i>	Capitate	<i>A. durangensis</i> (Britton & Rose) Jaward, Seigler & Ebinger	<i>Aculeiferum</i>	Spicate
<i>A. alemquerensis</i> Huber	<i>Aculeiferum</i>	Spicate	<i>A. eliasana</i> (Britton & Killip) Standl.	<i>Aculeiferum</i>	Capitate
<i>A. allenii</i> Janzen	<i>Acacia</i> , myrmecophyllous	Capitate	<i>A. emilioana</i> Fortunato & Cial.	<i>Aculeiferum</i>	Spicate
<i>A. altiscandens</i> Ducke	<i>Aculeiferum</i>	Spicate	<i>A. emoryana</i> Benth.	<i>Aculeiferum</i>	Spicate
<i>A. amambayensis</i> Hassler	<i>Aculeiferum</i>	Capitate	<i>A. etilis</i> Speg.	<i>Aculeiferum</i>	Spicate
<i>A. amazonica</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. farnesiana</i> (L.) Willd.	<i>Acacia</i>	Capitate
<i>A. amentacea</i> DC.	<i>Acacia</i>	Spicate	<i>A. feddeana</i> Harms	<i>Aculeiferum</i>	Spicate
<i>A. ampeloclada</i> Rusby	<i>Acacia</i>	Capitate	<i>A. fiebrigii</i> Hassler	<i>Aculeiferum</i>	Spicate
<i>A. anegadensis</i> Britton	<i>Acacia</i>	Capitate	<i>A. furcatispina</i> Burkart	<i>Aculeiferum</i>	Capitate
<i>A. angustissima</i> (Mill.) Kuntze	<i>Filicinae</i>	Capitate	<i>A. gaumeri</i> S.F.Blake	<i>Aculeiferum</i>	Spicate
<i>A. anisophylla</i> S.Watson	<i>Aculeiferum</i>	Capitate	<i>A. gentlei</i> Standl.	<i>Acacia</i> , myrmecophyllous	Spicate
<i>A. aroma</i> Gilles ex Hook. & Arn.	<i>Acacia</i>	Capitate	<i>A. glandulifera</i> S.Watson	<i>Acacia</i>	Capitate
<i>A. articulata</i> Ducke	<i>Aculeiferum</i>	Spicate	<i>A. globulifera</i> Saff.	<i>Acacia</i> , myrmecophyllous	Capitate
<i>A. atramentaria</i> Benth.	<i>Acacia</i>	Capitate	<i>A. goldmanii</i> (Britton & Rose) Wiggins	<i>Filicinae</i>	Capitate
<i>A. bahiensis</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. grandistipula</i> Benth.	<i>Aculeiferum</i>	Capitate
<i>A. barahonensis</i> Urban & Ekman	<i>Acacia</i>	Capitate	<i>A. greggii</i> A.Gray	<i>Aculeiferum</i>	Spicate
<i>A. barrancana</i> H.Gentry	<i>Filicinae</i>	Capitate	<i>A. guarensis</i> L.Cárdenas & F.García	<i>Aculeiferum</i>	Spicate
<i>A. belairioides</i> Urban	<i>Acacia</i>	Capitate	<i>A. hartwegii</i> Benth.	<i>Filicinae</i>	Capitate
<i>A. berlandieri</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. hayesii</i> Benth.	<i>Aculeiferum</i>	Spicate
<i>A. biaciculata</i> S.Watson	<i>Acacia</i>	Capitate	<i>A. hindsii</i> Benth.	<i>Acacia</i> , myrmecophyllous	Spicate
<i>A. (Acaciella) bicolor</i> (Britton & Rose)	<i>Filicinae</i>	Capitate	<i>A. hirtipes</i> Saff.	<i>Acacia</i> , myrmecophyllous	Spicate
<i>A. bilimekii</i> Macbride	<i>Acacia</i>	Spicate	<i>A. (Acaciella) houghii</i> (Britton & Rose)	<i>Filicinae</i>	Capitate
<i>A. bonariensis</i> Gilles ex Hook. & Arn.	<i>Aculeiferum</i>	Spicate	<i>A. huberi</i> Ducke	<i>Aculeiferum</i>	Spicate
<i>A. brandegeana</i> I.M.Johnston	<i>Acacia</i>	Spicate	<i>A. huilana</i> (Britton & Killip) García. Barr. & Forero-Gonzalez	<i>Aculeiferum</i>	Capitate
<i>A. (Acaciella) brevircemosa</i> (Britton & Rose)	<i>Filicinae</i>	Capitate	<i>A. igualensis</i> (Britton & Rose) Bullock	<i>Filicinae</i>	Capitate
<i>A. bucheri</i> Vict.	<i>Acacia</i>	Capitate	<i>A. insulae-jacobi</i> Ridley	<i>Acacia</i>	Capitate
<i>A. catharinensis</i> Burkart	<i>Aculeiferum</i>	Capitate	<i>A. interior</i> (Britton & Rose) McVaugh	<i>Aculeiferum</i>	Capitate
<i>A. caurina</i> Barneby & Zanoni	<i>Acacia</i>	Capitate	<i>A. janzenii</i> Ebinger & Seigler	<i>Acacia</i> , myrmecophyllous	Capitate
<i>A. caven</i> (Molina) Molina	<i>Acacia</i>	Capitate	<i>A. kallunkiae</i> Grimes & Barneby	<i>Aculeiferum</i>	Spicate
<i>A. cedilloi</i> L.Rico	<i>Acacia</i> , myrmecophyllous	Spicate	<i>A. kelloggiana</i> Carter & Rudd	<i>Aculeiferum</i>	Capitate
<i>A. centralis</i> (Britton & Rose) Lundell	<i>Aculeiferum</i>	Spicate	<i>A. klugii</i> Standl. ex J.F.Macbr.	<i>Aculeiferum</i>	Capitate
<i>A. chamelensis</i> L.Rico	<i>Filicinae</i>	Capitate	<i>A. kuhlmannii</i> Ducke	<i>Aculeiferum</i>	Spicate
<i>A. chiapensis</i> Saff.	<i>Acacia</i> , myrmecophyllous	Capitate	<i>A. lacerans</i> Benth.	<i>Aculeiferum</i>	Spicate
<i>A. choriophylla</i> Benth.	<i>Acacia</i>	Capitate	<i>A. langsdorfii</i> Benth.	<i>Aculeiferum</i>	Capitate
<i>A. chrysantha</i> DC.	<i>Aculeiferum</i>	Capitate	<i>A. lasiophylla</i> Benth.	<i>Aculeiferum</i>	Capitate
<i>A. cochliacantha</i> Humb. & Bonpl. ex Willd.	<i>Acacia</i>	Capitate	<i>A. lemmonii</i> Rose	<i>Filicinae</i>	Capitate
<i>A. collinsii</i> Saff.	<i>Acacia</i> , myrmecophyllous	Spicate	<i>A. lorentensis</i> Macbride	<i>Aculeiferum</i>	Capitate
<i>A. compacta</i> Rose	<i>Aculeiferum</i>	Spicate	<i>A. lozanii</i> Rose, ined.	<i>Aculeiferum</i>	Capitate
<i>A. constricta</i> Benth. ex A.Gray	<i>Acacia</i>	Capitate	<i>A. macbridei</i> Britton & Rose ex Macbride	<i>Aculeiferum</i>	Spicate
<i>A. cookii</i> Saff.	<i>Acacia</i> , myrmecophyllous	Capitate	<i>A. macilentia</i> Rose	<i>Aculeiferum</i>	Spicate
<i>A. cornigera</i> (L.) Willd.	<i>Acacia</i> , myrmecophyllous	Spicate	<i>A. macracantha</i> Humb. & Bonpl. ex Willd.	<i>Acacia</i>	Capitate
<i>A. couleri</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. magnibracteosa</i> Burkart	<i>Aculeiferum</i>	Capitate
<i>A. crassifolia</i> A.Gray	<i>Aculeiferum</i>	Capitate	<i>A. mammifera</i> Schldl.	<i>Aculeiferum</i>	Spicate
<i>A. cucuyo</i> Barneby & Zanoni	<i>Acacia</i>	Capitate	<i>A. martii</i> Benth.	<i>Aculeiferum</i>	Capitate
<i>A. cundinamarcae</i> (Britton & Killip) García. Barr. & Forero-Gonzalez	<i>Aculeiferum</i>	Capitate	<i>A. martiusiana</i> (Steudel) Burkart	<i>Aculeiferum</i>	Capitate
<i>A. cupeyensis</i> Leon	<i>Acacia</i>	Capitate	<i>A. maschalocephala</i> Griseb.	<i>Aculeiferum</i>	Capitate
<i>A. curvifructa</i> Burkart	<i>Acacia</i>	Capitate	<i>A. mayana</i> Lundell	<i>Acacia</i> , myrmecophyllous	Spicate

Table 1. (continued)

Species	Subgenus/group	Inflorescence type	Species	Subgenus/group	Inflorescence type
<i>A. melanoceras</i> Beurling	<i>Acacia</i> , myrmecophyllous	Capitate	<i>A. rojasii</i> Hassler	<i>Aculeiferum</i>	Spicate
<i>A. miersii</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. rorudiana</i> Christoph.	<i>Acacia</i>	Capitate
<i>A. mikanii</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. rosei</i> Standl.	<i>Filicinae</i>	Capitate
<i>A. millefolia</i> S.Watson	<i>Aculeiferum</i>	Spicate	<i>A. ruddiae</i> Janzen	<i>Acacia</i> , myrmecophyllous	Capitate
<i>A. mirandae</i> L.Rico	<i>Aculeiferum</i>	Spicate	<i>A. rugata</i> (Lam.) Buch.-Ham ex Fawcett & Rendle	<i>Aculeiferum</i>	Capitate
<i>A. monacantha</i> Willd.	<i>Aculeiferum</i>	Spicate	<i>A. rurrenabaqueana</i> Rusby	<i>Aculeiferum</i>	Capitate
<i>A. multipinnata</i> Ducke	<i>Aculeiferum</i>	Capitate	<i>A. russelliana</i> Britton & Rose	<i>Aculeiferum</i>	Spicate
<i>A. muricata</i> (L.) Willd.	<i>Aculeiferum</i>	Spicate	<i>A. rynchocarpa</i> Rusby	<i>Aculeiferum</i>	Capitate
<i>A. nitidifolia</i> Speg.	<i>Aculeiferum</i>	Capitate	<i>A. (Senegalia) saltilloensis</i> (Britton & Rose)	<i>Aculeiferum</i>	Capitate
<i>A. occidentalis</i> Rose	<i>Aculeiferum</i>	Capitate	<i>A. santosii</i> G.P.Lewis	<i>Aculeiferum</i>	Capitate
<i>A. olivensana</i> G.P.Lewis	<i>Aculeiferum</i>	Spicate	<i>A. schaffneri</i> (S.Watson) F.J.Herm.	<i>Acacia</i>	Capitate
<i>A. ouyrarema</i> DC.	<i>Acacia</i>	Capitate	<i>A. schottii</i> Torrey	<i>Acacia</i>	Capitate
<i>A. oviedoensis</i> R.García & M.Mejía	<i>Acacia</i>	Capitate	<i>A. sericea</i> Martens & Galeotti	<i>Aculeiferum</i>	Spicate
<i>A. pacensis</i> Rudd & Carter	<i>Aculeiferum</i>	Capitate	<i>A. serra</i> Benth.	<i>Aculeiferum</i>	Capitate
<i>A. paraensis</i> Ducke	<i>Aculeiferum</i>	Spicate	<i>A. skleroxyla</i> Tussac.	<i>Aculeiferum</i>	Spicate
<i>A. parviceps</i> (Speg.) Burkart	<i>Aculeiferum</i>	Capitate	<i>A. sororia</i> Standl.	<i>Aculeiferum</i>	Spicate
<i>A. parviflora</i> Little	<i>Aculeiferum</i>	Capitate	<i>A. sousae</i> L.Rico	<i>Filicinae</i>	Capitate
<i>A. pedicellata</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. sphaerocephala</i> Schldl. & Cham.	<i>Acacia</i> , myrmecophyllous	Spicate
<i>A. peninsularis</i> (Britton & Rose) Standl.	<i>Aculeiferum</i>	Capitate	<i>A. subangulata</i> Rose	<i>Aculeiferum</i>	Capitate
<i>A. pennatula</i> (Schldl. & Cham.) Benth.	<i>Acacia</i>	Capitate	<i>A. subpaniculata</i> Hoehne	<i>Aculeiferum</i>	Capitate
<i>A. piauiensis</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. tamarindifolia</i> (L.) Willd.	<i>Aculeiferum</i>	Capitate
<i>A. picachensis</i> Brandegee	<i>Aculeiferum</i>	Capitate	<i>A. tenuifolia</i> (L.) Willd.	<i>Aculeiferum</i>	Capitate
<i>A. pinctorum</i> F.J.Herm.	<i>Acacia</i>	Capitate	<i>A. tequilana</i> S.Watson	<i>Filicinae</i>	Capitate
<i>A. piptadenioides</i> G.P. Lewis	<i>Aculeiferum</i>	Spicate ^A	<i>A. tortuosa</i> (L.) Willd.	<i>Acacia</i>	Capitate
<i>A. plumosa</i> Lowe, Mart. ex Colla	<i>Aculeiferum</i>	Spicate	<i>A. trijuga</i> Rizz.	<i>Aculeiferum</i>	Capitate
<i>A. polyphylla</i> DC.	<i>Aculeiferum</i>	Capitate	<i>A. tucumanensis</i> Griseb.	<i>Aculeiferum</i>	Capitate
<i>A. polypyrrigenes</i> Greenman ex Combs	<i>Acacia</i>	Capitate	<i>A. usumacintensis</i> Lundell	<i>Aculeiferum</i>	Spicate
<i>A. praecox</i> Griseb.	<i>Aculeiferum</i>	Capitate	<i>A. velutina</i> DC.	<i>Aculeiferum</i>	Spicate
<i>A. pringlei</i> Rose	<i>Acacia</i>	Spicate	<i>A. velvae</i> L.Rico	<i>Filicinae</i>	Capitate
<i>A. pteridifolia</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. villaregalis</i> Mcvaugh	<i>Acacia</i>	Capitate
<i>A. purpusii</i> Brandegee	<i>Aculeiferum</i>	Capitate	<i>A. villosa</i> (Sw.) Willd.	<i>Filicinae</i>	Capitate
<i>A. recurva</i> Benth.	<i>Aculeiferum</i>	Capitate	<i>A. visco</i> Lorentz ex Griesb.	<i>Aculeiferum</i>	Capitate
<i>A. reniformis</i> Benth.	<i>Aculeiferum</i>	Spicate	<i>A. weberbaueri</i> Harms	<i>Aculeiferum</i>	Spicate
<i>A. retusa</i> (Jacq.) R.Howard	<i>Aculeiferum</i>	Capitate	<i>A. willardiana</i> Rose	<i>Aculeiferum</i>	Spicate
<i>A. riparia</i> Kunth	<i>Aculeiferum</i>	Capitate	<i>A. zapatensis</i> Urban & Ekman	<i>Acacia</i>	Capitate
<i>A. roemeriana</i> Scheele	<i>Aculeiferum</i>	Capitate			
<i>A. roigii</i> Leon	<i>Acacia</i>	Capitate			

^ASpecies not included in the discussion of the paper.

boundaries. For example, Brazil has 44 species in total, but this value obscures the fact that the Brazilian Amazon contains only 12. So, a modified and more detailed division of America was used for data interpretation with the political areas divided into 50 geographical areas as shown in Table 2. For example, Mexico was divided into several regions, including Mexico Central, Mexico North-east, Mexico South-east, and others; Brazil was divided into Brazil West-Central, Brazil North-east, Brazil South-east, Brazil North and Brazil South. These regions largely follow the geographical areas used in the 'World Geographical Scheme for Recording Plant Distributions' (Brummitt 2001).

Results and discussion

Table 3 shows the combined data. *Aculeiferum* section *Filicinae* (equivalent to *Acaciella* of Britton and Rose 1928) comprises a highly distinctive but little-known group of the

genus which is widely distributed from southern USA to Colombia, Venezuela, Ecuador and Peru, with one species extending to Bolivia and Argentina. Its altitudinal range is from near sea level up to 2800 m. Bentham (1842) listed 11 species. Britton and Rose (1928) published these under the genus *Acaciella* and in subsequent works added 42 taxa to give a total of 53 for the genus. They proposed *Acacia villosa* as the type. Recently, more new species have been described either as *Acacia* or *Acaciella* (Killip 1934; Britton and Killip 1936; Standley 1937; Wiggins 1942; Gentry 1948; Isely 1973; Rico 1987; Turner 1996). There are about 85 species names that fall into the *Filicinae* (= *Acaciella*) (L. Rico-Arce, unpubl. data).

The group is characterised by the lack of many traditional *Acacia* characters such as prickles, spines, extra floral

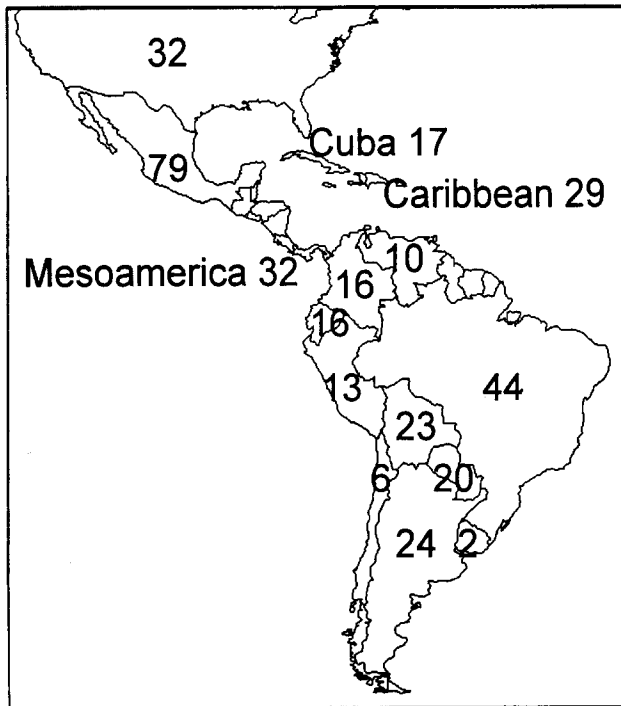


Fig. 1. Political division of the American continent with the number of species for each country. Mesoamerica is defined as southern Mexico and Central American countries.

nectaries and staminal glands, and is distinctive in having polyads with eight grains. The only feature which retains species of *Filicinae* within the genus *Acacia* is the presence of many free stamens, sometimes more than 300 per flower. All species have pedicellate flowers in very short racemes. The pedicels are not homologous to those in *Aculeiferum* section *Monacantha* because they disarticulate directly below the calyx and not at the base of the pedicel. Persistent pedicel 'pegs' on the inflorescence rachis are a feature of *Filicinae* species.

Acacia angustissima is one of the two most widely distributed species, it is found from southern USA to Colombia (as *Acaciella santanderensis* Britton & Killip 1936) Venezuela (as *Acaciella valenzuelana* Britton & Rose 1928), Bolivia and Argentina (as *Acacia boliviana* Rusby, Cialdella 1984), almost equalling the distribution of the whole *Filicinae*. A second widely distributed species is *Acacia villosa* from central Mexico to Colombia, Ecuador and Peru. Both species are found in oak and pine forest at altitudes up to 2800 m. Both are nitrogen-fixing species and both are acid-soil tolerant. Distribution of section *Filicinae* (= *Acaciella*) species is given in Fig. 2. Most species are riparian. Under normal tropical conditions the species are not gregarious but often become weedy in disturbed forest and thickets, along roadsides, or in pastures on sandy soils. Species such as *A. tequilana*, *A. chamelensis* and *A. sousae* extend the spectrum of habitats into arid regions where they

Table 2. Fifty geographical working areas

United States	Trinidad-Tobago
Mexico Central	Venezuelan Antilles
Mexico North-east	Windward Is
Mexico Gulf	French and British Guyana
Mexican Pacific	Surinam
Mexico North-west	Venezuela
Mexico South-west	Bolivia
Mexico South-east	Colombia
Belize	Ecuador
Costa Rica	Galapagos
Central America	Peru
El Salvador	Brazil West-Central
Guatemala	Brazil North-east
Honduras	Brazil South-east
Nicaragua	Brazil North
Panama	Brazil South
Bahamas	Argentina North-west
Cayman Is	Argentina North-east
Cuba	Argentina South
Dominican Republic	Chile Central
Haiti	Chile North
Jamaica	Chile South
Puerto Rico	Paraguay
South-west Caribbean	Uruguay
Turks-Caicos Is	Falkland Is

occur as isolated perennial herbs, shrubs or treelets. Some species, such as *A. sousae*, *A. lemmoni* and *A. rosei* are so rare that their genetic diversity may be threatened. As presently understood by L. Rico-Arce (unpubl. data), there is

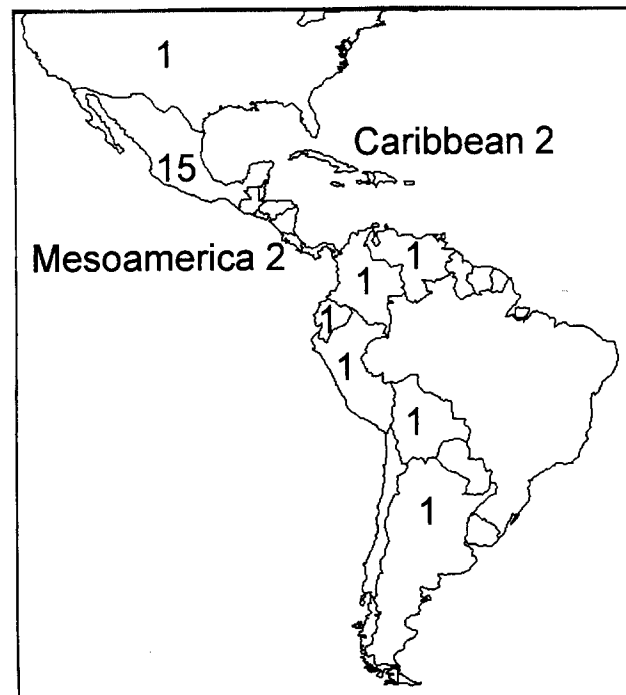


Fig. 2. General distribution of the species of subgenus *Aculeiferum* section *Filicinae* in the neotropics.

a total of 15 species and 10 varieties in section *Filicinae*. All 15 species occur in Mexico, mainly in low deciduous forest and dry scrub.

Subgenus *Aculeiferum* Vassal section *Monacantha* Vassal are spindly shrubs, vines or large trees up to 35 m tall, usually armed with prickles and always with leaves bearing extrafloral nectaries. All have pollen in 16-grain polyads, with the individual grains being porate (Guinet 1969, 1979, 1986, 1990; Caccavari 1976; Guinet and Lugardon 1976; Caccavari and Dome 2000; Rico and Banks 2001). This section is the most abundant in the continent, represented by 100 native species. Altitudinal tolerance ranges from near sea level up to 2300 m. Deciduous seasonal forest is the most common habitat of section *Monacantha*. Species collected from lowland evergreen tropical forest, especially the vines, are the least known in the section.

Species from lowland deciduous or scrub forest are mostly represented by collections of *Acacia riparia* Kunth. and *A. tenuifolia* (L.) Willd.

There are three species-rich areas for *Monacantha*: Brazil with 41 species (27 endemic), Mexico with 38 (25 endemic) and Bolivia with 16 (three endemic) (Fig. 3). Common species shared between these are *Acacia tenuifolia*, *A. paniculata*, *A. riparia*, *A. polyphylla* and *A. hayesii*. It is worth mentioning that *A. tenuifolia* and *A. paniculata* have many morphological similarities with the group of *A. pennata*, *A. montigena* and *A. kamerunensis* (amongst other species) of Asia and Africa. The North-east is the richest area in Brazil for section *Monacantha*. In Mexico, the Central and North-west areas are the most species rich for this section (Table 3).

Subgenus *Acacia* consists of shrubs or trees up to 15 m tall, with spiny stipules, leaves with well-developed extrafloral nectaries and pollen in 16-grain polyads, with the individual grains characteristically syncolpate. Subgenus *Acacia* is represented by 57 taxa and has the following three broad species-rich areas: (1) United States + Mexico + Mesoamerica; (2) Ecuador + Colombia + Venezuela; and (3) Argentina + Paraguay + Bolivia.

The non-myrmecophyllous group with capitate inflorescences occurs mainly in the two South American regions (areas 2 and 3). The only exception is Colombia where *Acacia collinsii* and *A. cornigera* are present. These two species are myrmecophyllous and have spicate inflorescences, but have a broader area of distribution in the neotropics. Both species could be considered as outliers of the Mesoamerican region. *A. cornigera* has been introduced into several regions, including the Caribbean area (Rudd 1964; Isely 1973, 1998; Janzen 1974; Bässler 1998).

Non-myrmecophyllous species commonly found in all three areas of the continent are *Acacia pennatula*, *A. macracantha*, *A. tomentosa* and the pantropically distributed *A. farnesiana*. These share many morphological similarities with the group of *Acacia tortuosa* from Asia and

A. gummifera, *A. haematoxylon* and *A. nilotica* from Africa. The most interesting area in terms of non-myrmecophyllous *Acacia* is, however, Mexico where spicate species are well represented. Mexico North-west and Cuba are richest in capitate non-myrmecophyllous species as shown in Table 3.

In contrast, the Mesoamerican region is the richest in obligate myrmecophyllous *Acacia*. In India and Africa, there are a few myrmecophyllous species such as *A. drepanolobium* from Africa, but the inflorescence structure of these species is 'simpler' than in the myrmecophyllous taxa of the Neotropics, and so far, all the extra-American myrmecophyllous species have capitate inflorescences whereas the neotropical ones are spicate. Pedley (1986) suggested that myrmecophyly in *Acacia* has reached its greatest development among the Central American species, some of which depend on ants for their survival. In addition, several levels of complexity are found in the Mesoamerican myrmecophyllous species. An example, *Acacia mayana*, which is restricted to south-eastern Mexico, has spicate inflorescences, where the involucre at the base is modified into a nectary, in addition to a functional gland on a stalk of a modified leaf. It is an evergreen forest species of very restricted distribution. As soon as its habitat is cut, this species does not regenerate in contrast with other myrmecophyllous taxa, for example, *A. collinsii* and *A. cornigera*, that grow in both evergreen forest and drier areas. *A. mayana* is thus highly threatened.

In the Caribbean area, there are no native obligate myrmecophyllous *Acacia* species, although *Acacia daemon*

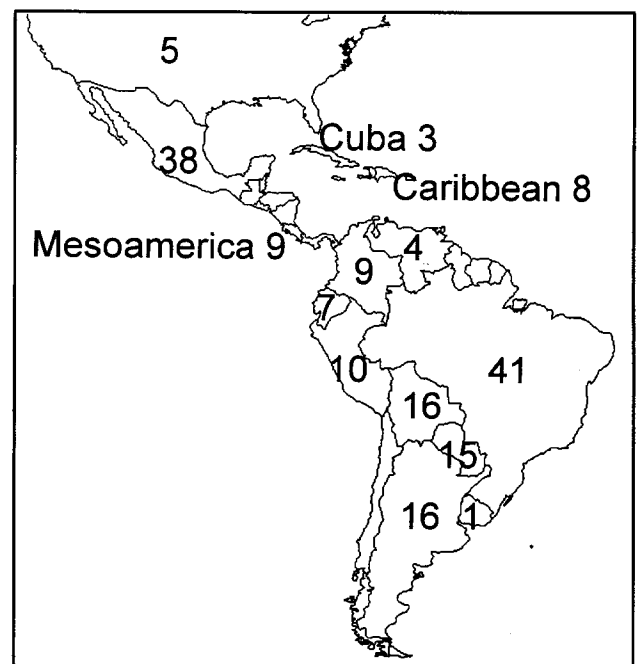


Fig. 3. General distribution of subgenus *Aculeiferum* section *Monacantha* in the neotropics.

Table 3. The fifty neotropical geographical areas with *Acacia* groups

Values in parentheses indicate the species with capitate/spiculate inflorescences; values outside parentheses are the total values. If there is only one value in column 1 (non-myrmecophyllous) this corresponds to species with capitate inflorescences. All taxa in section *Filicinae* (column 4) have short racemose inflorescences

Area	<i>Acacia</i> , non-myrmecophyllous	<i>Acacia</i> , myrmecophyllous	<i>Aculeiferum</i> - <i>Monacantha</i>	<i>Aculeiferum</i> - <i>Filicinae</i> , all short, racemose	<i>Acacia</i> , total
United States	8	(0/1) 1	(2/2) 4	1	4
Mexico Central	(3/2) 5		(6/8) 14	7	26
Mexico North-east	(3/1) 4		(5/3) 8	1	13
Mexico Gulf	5	(0/2) 2	(3/1) 4	2	13
Mexico Pacific	(6/1) 7	(0/2) 2	(7/4) 11	8	28
Mexico North-west	(7/4) 11		(9/5) 14	4	29
Mexico South-west	3		(9/5) 1	1	5
Mexico South-east	(4/1) 5	(4/8) 12	(4/5) 9	2	28
Belize	1	(3/5) 8	(2/2) 4	2	15
Costa Rica	2	(4/3) 7	(3/1) 4	2	15
Central America	3	(1/3) 4	(4/0) 4	2	13
El Salvador	2	(0/3) 3	(4/1) 5	2	12
Guatemala	3	(0/6) 6	(3/3) 6	2	21
Honduras	2	(0/3) 3	(2/1) 3	2	13
Nicaragua	2	(0/3) 3	(3/0) 3	2	11
Panama	1	(0/1) 1	(3/1) 4	2	11
Bahamas	2				2
Cayman Is	3		(1/1) 2		5
Cuba	11	(1/1) 2	(3/0) 3	1	17
Dominican Republic	5		(1/1) 2		7
Haiti	3				3
Jamaica	2		(2/0) 2	1	5
Puerto Rico	3		(1/1) 2		5
South-west Caribbean	3	(0/1) 1	(4/1) 5		9
Turks-Caicos Is	1				1
Trinidad-Tobago	1				1
Trinidad Antilles	1		(1/0) 1		2
Windward Is	1				1
French Guiana and Guyana	3		(2/1) 3		6
Surinam	2		(2/1) 3		5
Venezuela	4		(2/1) 3	1	9
Bolivia	6		(10/6) 16	1	23
Colombia	4	(0/2) 2	(8/1) 9	1	16
Ecuador	7		(4/4) 8	1	16
Galapagos	4				4
Peru	4		(4/5) 9	1	14
Brazil West-Central	—		(1/1) 2		2
Brazil North-east	1		(11/10) 2		22
Brazil South-east	1		(2/0) 2		3
Brazil North	1		(5/6) 11		12
Brazil South	3		(11/3) 14		17
Argentina North-west	7		(9/4) 13	1	21
Argentina North-east	7		(5/3) 8	1	16
Argentina South	5		(0/2) 2		7
Chile Central	3				3
Chile North	5		(0/1) 1		6
Chile South	3				3
Paraguay	5		(9/6) 15		20
Uruguay	1		(1/0) 1		2
Falkland Is	—	—	—	—	—

in Cuba has been reported to be myrmecophyllous by Berazain (in Bässler 1998). I have seen this species in several localities in Cuba. None of the trees observed showed true domatia, although it is worth noting that this is the most spiny species of *Acacia* known. Adult trees have a polyarchic growth and form a dense impenetrable vegetation type known as 'cubales'. In the National Botanical Garden in La Habana, there are a few trees of *A. daemon* which grow in less competition with other species. There, the tree architecture is more sympodial than polyarchic, showing that different growth strategies for the species are possible in different environments. The spines in this case tend to be 'swollen' but lack any ant-holes as in the typical swollen thorns of all other obligate myrmecophyllous species. For the current study, *Acacia daemon* is considered as a non-myrmecophyllous taxon, as are other species occasionally reported to have ants, such as *A. rigidula* and *A. caven* (Seigler *et al.* 1982; Aronson 1992).

Conclusions

- (i) Neotropical *Acacia* is represented by two subgenera.
- (ii) Brazil, Mexico and Bolivia are richer in subgenus *Aculeiferum* section *Monacantha* than in *Acacia* subgenus *Acacia*.
- (iii) Mexico is the richest in subgenus *Aculeiferum* section *Filicinae*, with 15 species, eight of which are in the Pacific area.
- (iv) The subgenus *Acacia* has three main areas of species diversity, with Mesoamerica being the most important region for the myrmecophyllous species and Mexico North-west, the United States and Cuba for the non-myrmecophyllous species.

Acknowledgments

I am grateful to Gwilym Lewis and Tim Windsor-Shaw for their support during production of this paper and to Bruce Maslin and Joe Miller for the initial invitation to present this contribution at the Fourth International Legume Conference in Canberra.

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Manuscript received 18 October 2001, accepted 16 October 2002