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Seed Storage Protein Size Variations and Their Significance in the Evolution and the Systematics of *Acacia* and *Prosopis* (*Mimosaceae*)

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Abstract

Phylogenetic relationships among 20 species (38 accessions) of *Acacia* and ten (13 accessions) of *Prosopis* were estimated using data from seed storage protein size variations. Thirty-two different bands were detected (245 to 29 kD). The studied tetraploid, hexaploid and octoploid accessions of subgenus *Acacia* had almost the same numbers of bands. WAGNER parsimony analysis revealed six equally parsimonious trees of 72 steps with consistency index = 81.5% and retention index = 78%. The 50% majority rule consensus tree revealed four clades consistent with the three subgenera of *Acacia* and the genus *Prosopis*. Subgenus *Aculeiferum* appeared ancestral to subgenera *Acacia* and *Heterophyllum*. *Prosopis africana* appeared ancestral to the other studied *Prosopis* species and *Acacia polyacantha* ancestral to the other studied species of *Aculeiferum*. The two accessions of *A. albida* clustered within

the ten accessions of the subgenus *Aculeiferum*. The results indicated that hexaploidy and octoploidy in *Acacia* were geologically more recent than tetraploidy, and that the evolution in *Acacia* proceeded towards a reduction in the concentration and number of variable protein molecules in the seed.

Key words: parsimony, phylogeny, SDS-PAGE, seed storage proteins.
FDC: 160.203; 161.34; 164.8; 165.1/4; 176.1 *Acacia*; 176.1 *Prosopis*.

Introduction

The genus *Acacia* (TOURN.) MILLER comprises 1200 known species with a large number of subspecies and varieties (Ross, 1979). BENTHAM (1875) subdivided the genus *Acacia* into five series (*Phyllodineae*, *Pulchelae*, *Botryocephala*, *Vulgares* and *Gummiferae*). Later, VASSAL (1972) classified *Acacia* into three subgenera (*Heterophyllum*, *Aculeiferum* and *Acacia*) and six sections (*Monocantha*, *Aculeiferum*, *Acacia*, *Pulchelloidea*, *Heterophyllum*, and *Uninervata*) excluding *A. albida*. The genus *Prosopis* (L.) BURKART includes 45 species, 41 of which are indigenous to tropical America (HUNZIKER *et al.*, 1986). The genus *Acacia* fits in the tribe *Acacieae* and *Prosopis* in *Mimosaceae* (BENTHAM, 1875). Although these two genera belong to

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different tribes, they are similar in thorniness, form and morphology (BURKART, 1976). They are adapted to arid conditions (BURKART, 1976; ROSS, 1981), have similar flowering and fruit production strategies (SOLBRIG and CANTINO, 1975; ROSS, 1979), provide wood, gum, shade, fodder, etc., and most of them fix atmospheric nitrogen (BASAK and GOYAL, 1975). Due to their ecological and economic importance, and their morphological and biological similarities, *Prosopis* and *Acacia* are very often studied together.

Prosopis and *Acacia* have similar chromosome morphology (BUKHARI, 1997b), share several strategies of ecological adaptation and have low flower to pod ratios (SOLBRIG and CANTINO, 1975; ROSS, 1979). However, diploid species of *Prosopis* have approximately two thirds of the amount of nuclear DNA of diploid *Acacia* (BUKHARI, 1997a). In addition, chromosome size and nuclear DNA mass in tetraploid *Acacia* are lower than that in diploid relatives, whereas the hexaploid and octoploid cytotypes of *Acacia* have similar nuclear DNA amounts as their relative tetraploids (BUKHARI, 1997a and b). The significance of such difference on the evolution of seed storage proteins and the systematics of *Acacia* and *Prosopis*, however, remains uncovered.

Subgenus *Aculeiferum* possesses the least advanced morphological characters among the three subgenera of *Acacia* (ATCHISON, 1948; VASSAL, 1972; GUNET and VASSAL, 1978), whereas subgenera *Acacia* and *Heterophyllum* share a common decent (ATCHISON, 1948; VASSAL, 1972; VASSAL and LESCALLE, 1976; GUINET and VASSAL, 1978; BRAIN, 1990).

Several tools have been used to further the systematics of *Acacia* and *Prosopis*: shoot and pollen morphology (BENTHAM, 1875; VASSAL, 1969 and 1972; GUINET and VASSAL, 1978); histology (ROBBERTSE, 1975a, b and c; VASSAL, 1975); cytology (GHIMPU, 1929; ATCHISON, 1948; KHAN, 1951; VASSAL, 1972, 1975; HAMANT *et al.*, 1975; VASSAL and LESCALLE, 1976; GUINET and VASSAL, 1978; BUKHARI, 1997a and b); isozyme (HUNZIKER *et al.*, 1986; MORAN, 1992; PLAYFORD *et al.*, 1993; MANDAL *et al.*, 1995; OBALLA, 1996; SAIDMAN *et al.*, 1996); immunology (EL-TINAY *et al.*, 1979; BRAIN, 1990; BRAIN and MASLIN, 1996). The majority of the characters used in the above studies were quantitative and have continuous overlapping variation (GUINET and VASSAL, 1978). Such evidence tends to classify taxa on the basis of overall present phenetic similarity. Consequently, convergent evolution and functional adaptation may influence the estimated relatedness (PALMER *et al.*, 1988). Estimating phylogenies using parsimony is perceived to be a better alternative (CAMIL and SOKAL, 1965; FARRIS, 1970).

Seed storage proteins of angiosperms evolved from a few genes into multi-gene families. Each gene family may contain a few genes with several allelic forms (SHEWRY *et al.*, 1984; PAYNE, 1987; HÄGER *et al.*, 1995), and differences in repetitive domains of the products of these genes account for most of the polymorphism in seed storage proteins (D'OIDIO *et al.*, 1996). Recently evolved allotetraploids possess all parental seed storage protein or new combinations of multimeric protein may cause deviation from parental profiles. However, the redundant protein loci, resulting from polyploidy, would have more chances to mutate in the course of evolution (MURRAY *et al.*, 1970; BULINSKA-RADOMSKA and LESTER, 1986). Data on seed storage protein have frequently been used for estimating relatedness among taxa at various taxonomic levels (BULINSKA-RADOMSKA *et al.*, 1986; NAVOT and ZAMIR, 1987; BIANCHI-HALL *et al.*, 1993; CIAFFI *et al.*, 1993; LANHAM *et al.*, 1994) and for identifying plant ancestry (BULINSKA-RADOMSKA and LESTER, 1988). Little is known about the evolution of seed storage proteins in *Acacia* and *Prosopis*, although VASSAL (1972) and EL-TINAY *et al.* (1979)

pointed out the necessity of using all possible approaches to improve the systematics of *Acacia*. In this study, we analyze the patterns of size variations of seed storage proteins for 39 accessions of *Acacia* and 12 accessions of *Prosopis* to test the relevance of such data for classification purposes in *Acacia* and *Prosopis*.

Materials and Methods

Seeds of 39 accessions of *Acacia* and 12 accessions of *Prosopis* were included in this study. Of these, 36 were provided by the Forest Seed Center of the Danish International Development Agency; 12 by the Sudan Tree Seed Center; and three by the Tanzanian National Tree Seed Programme. Detailed information on the seed material is given in *table 1*. The seeds were received in June 1993 and stored at 4°C to reduce metabolic activity (BIANCHI-HALL *et al.*, 1993). Twenty-five seeds of each accession were randomly selected in January 1997. After removing the seed coats, the cotyledons were frozen in liquid nitrogen for three min. The frozen cotyledons were then ground to coarse powder (about 0.3 mm in diameter) using a mortar and pestle. Protein extraction was performed using a slightly modified method from REN *et al.* (1996). From each sample, 40 mg of powder were suspended in 2 ml of extraction and loading buffer (50 mM Tris-HCl, pH 8.5; 2% (w/v) sodium dodecyl sulphate; 0.1% bromphenol blue; 10% glycerol; 2% freshly added 2β-mercaptoethanol). The samples were kept at 22°C for 1 h and then heated in a boiling water bath for 10 min. The material was then centrifuged at 14,000 g at 22°C for 15 min and the supernatant was used for electrophoresis. Seven different samples from each accession were studied.

From each sample, 12 µl were used for electrophoresis through 10% SDS-PAGE (sodium dodecyl sulphate polyacryl amide gel electrophoresis). Gels were 12 cm long, 17 cm wide and 1.5 mm thick. The separation gel contained 10% acryl amide, 0.12% SDS, 370 mM Tris-HCl (pH 8.8), 1% APS and 0.1% TEMED. The stacking gel contained 4% acryl amide, 0.12% SDS, 125 mM Tris-HCl (pH 6.8), 1% APS and 0.1% TEMED. Electrophoresis was performed in a BioRad Protein II apparatus (BioRad, Richmond, Calif., USA). The running buffer consisted of 25 mM Tris-HCl, 250 mM glycine, 0.1% SDS, pH 8.3. All 51 samples were run concurrently at a fixed current (30 mA per gel) for the first 30 min, and thereafter the amperage was doubled. Electrophoresis was stopped when the tracking dye was 4 mm from the bottom of the gel. The gels were stained in a solution of Coomassie (10 g Coomassie R250) dissolved in 25% isopropanol and 10% acetic acid) for about 12 h. De-staining was performed in 5 changes (15 min each) of boiling 10% aqueous acetic acid. The gels were then photographed.

Molecular masses of the separated bands were estimated from the mobilities of molecular markers containing myosin, 200 kD; β-galactosidase, 116.3 kD; phosphorylase B 97.4 kD; bovine serum albumin 66.2 kD; ovalbumin, 45 kD; carbonic anhydrase, 31 kD. (BioRad, 161-0317). Electrophoretic bands were given Arabic numerals; the slowest-moving band was numbered 1 and the fastest 32. Equally-migrating band were recorded as present, absent or unclear (when they do not appear regularly in gels replications). The latter class of data were excluded from the phylogenetic analysis. Bands were subjectively considered to be major or minor depending on their intensity (LEONARDI *et al.*, 1991). A matrix was created from the above data and analyzed using the computer program Phylogenetic Analysis Using Parsimony (PAUP for Apple MacIntosh, version 3.1.1; SWOFFORD, 1993). Heuristic search was performed

Table 1. – Accessions included in the study, their source and somatic chromosome number (BUKHARI, 1997a).

Accession	Code	Country	Latitude°	Longitude°	2n	Donor
Subgenus <i>Acacia</i> VASSAL						
<i>A. caven</i> BENTH.	01589/86	Chile	31S	71W		DANIDAFSC
<i>A. drepanolobium</i> HARMS ex SJÖSTEDT	751/91A	Tanzania	5S	35E	52	TNTSP
<i>A. nilotica</i> ssp. <i>adstringens</i> chiov.	01112/83	Sudan	13N	30E	104	DANIDAFSC
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01219/83	India	17N	78E	52	DANIDAFSC
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01074/82	India	31N	76E	—	DANIDAFSC
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01423/84	India	28N	76E	52	DANIDAFSC
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01643/86	India	26N	73E	52	DANIDAFSC
<i>A. nilotica</i> ssp. <i>nilotica</i> (BENTH.) HILL.	01441/84	India	26N	73E	52	DANIDAFSC
<i>A. nilotica</i> ssp. <i>tomentosa</i> (BENTH.) HILL.	01037/82	Senegal	16N	17W	104	DANIDAFSC
<i>A. nilotica</i> ssp. <i>tomentosa</i> (BENTH.) HILL.	01644/86	Sudan	14N	32E	52	DANIDAFSC
<i>A. nubica</i> BENTH.	01890/92	Kenya	0	37E	56	DANIDAFSC
<i>A. radiana</i> (SAV.) BRENAN	01284/84	Israel	31N	35W	78	DANIDAFSC
<i>A. radiana</i> (SAV.) BRENAN	01195/83	Senegal	17N	16W	104	DANIDAFSC
<i>A. seyal</i> var. <i>fistula</i> (SCHWEINF.) OLIV.	—/84	Sudan	11N	34E	104	STSC
<i>A. sieberana</i> DC.	—/93	Sudan	13N	35E	26	STSC
<i>A. tortilis</i> ssp. <i>sirocarpa</i> (HOCH.) BRENAN	01669/86	Sudan	15N	2E	104	STSC
<i>A. tortilis</i> (FORSSK.) HAYNE	—/84	Sudan	15N	2E	104	STSC
<i>A. tortilis</i> (FORSSK.) HAYNE	01285/84	Israel	31N	35W	78	DANIDAFSC
<i>A. tortilis</i> (FORSSK.) HAYNE	01509/85	Yemen	15N	45E	52	DANIDAFSC
<i>A. albida</i> DEL. (Syn. <i>Faidherbia albida</i> (DEL.) A. CHEV)						
<i>A. albida</i> DEL.	01193/83	Senegal	17N	33E	26	STSC
<i>A. albida</i> DEL.	—/93	Sudan	13N	24E	26	STSC
Subgenus <i>Aculeiferum</i> VASSAL						
<i>A. caffra</i> (THNUB.) WILLD.	01810/88	Kenya	3S	7E	26	DANIDAFSC
<i>A. mellifera</i> (VAHL.) BENTH.	01808/88	Kenya	01N	36E	26	DANIDAFSC
<i>A. polyacantha</i> , BRENAN	0271/92A	Tanzania	5S	35E	56	TNTSP
<i>A. senegal</i> (L.) WILLD.	01427/84	India	26N	73E	26	DANIDAFSC
<i>A. senegal</i> (L.) WILLD.	A/93	Sudan	12N	35E	26	STSC
<i>A. senegal</i> (L.) WILLD.	11A/91	Tanzania	6S	36E	26	TNTSP
<i>A. senegal</i> (L.) WILLD.	B/93	Sudan	13N	35E	26	STSC
<i>A. senegal</i> (L.) WILLD.	c/93	Sudan	13N	31E	26	STSC
<i>A. senegal</i> (L.) WILLD.	d/93	Sudan	13N	32E	26	STSC
Subgenus <i>Heterophyllum</i> VASSAL						
<i>A. dealbata</i> var. <i>dealbata</i> LINK.	01876/92	Australia	41S	147E	26	DANIDAFSC
<i>A. holosericea</i> CUN. ex DON.	01645/92	Senegal	5N	15W	52	DANIDAFSC
<i>A. implexa</i> BENTH.	01877/92	Australia	36S	134E	26	DANIDAFSC
<i>A. mearnsii</i> WILLD.	01892/92	Kenya	1S	38E	26	DANIDAFSC
<i>A. melanoxylon</i> ROXB.	01878/92	Australia	41S	144E	26	DANIDAFSC
<i>A. sophorae</i> WILLD.	01879/92	Australia	42S	148E	26	DANIDAFSC
<i>A. sophorae</i> WILLD.	—/93	Sudan	10N	29E	—	STSC
The genus <i>Prosopis</i> (L.) BURKART						
<i>P. alba</i> GRISEB.	01574/86	Chile	23S	68W	28	DANIDAFSC
<i>P. chilensis</i> (MOLINA) STUNTZ	—/93	Sudan	15N	32E	56	STSC
<i>P. chilensis</i> (MOLINA) STUNTZ	01591/86	Chile	31S	71W	28	DANIDAFSC
<i>P. cineraria</i> (L.) DRUCE	01451/84	Yemen	13N	45E	28	DANIDAFSC
<i>P. cineraria</i> (L.) DRUCE	01445/84	Pakistan	32N	71E	28	DANIDAFSC
<i>P. cineraria</i> (L.) DRUCE	01204/84	Yemen	13N	45E	28	DANIDAFSC
<i>P. flexuosa</i> DC.	01585/86	Chile	27S	70W	28	DANIDAFSC
<i>P. glandulosa</i> var. <i>torreyana</i> TORR.	01211/83	Mexico	25N	101W	28	DANIDAFSC
<i>P. juliflora</i> (SWARTZ) DC.	01214/83	Mexico	24N	104W	28	DANIDAFSC
<i>P. lampa</i> LINK.	01595/86	Chile	33S	71W	28	DANIDAFSC
<i>P. pallida</i> (WILLD.) HBK.	01668/86	Peru	11S	76W	28	DANIDAFSC
<i>P. siliquastrum</i> WILLD.	01579/86	Chile	28S	70W	28	DANIDAFSC

DANIDAFSC, Danish International Development Agency Forest Seed Centre; TNTSP, Tanzania National Tree Seed Programme; STSC, Sudan Tree Seed Centre.

ed under WAGNER parsimony and phylogenetic trees were reconstructed. Random tree branch swapping functions were employed to examine alternative trees of identical length. The statistical significance of the characters being independent was tested by performing 100 bootstrap resampling replicates according to FELSENSTEIN (1985).

Results

Thirty-two electrophoretically different bands were observed among all the studied accessions. Molecular sizes for these bands ranged from 225 kD to 29 kD. The number of bands in *Prosopis* accessions ranged from eight (*P. africana*) to 26 (*P. flexuosa*). For subgenus *Aculeiferum*, *A. polyacantha*

Species	A. No.	Protein bands and their molecular weights (kD)		
Subgenus <i>Aculeiferum</i> VASSAL		245 240 238 205 195 190 170 152 120 116 112 109 107 100	88 96 94 90 87 84 80 76 74 70 66 57 50 52 45 43 41 35 29	
<i>A. caffra</i> (THUNB.) WILLD.	01810/88	[■]	[■]	11 7
<i>A. mellifera</i> (VAHL.) BENTH.	01808/88	[■]	[■]	16 10
<i>A. polyacantha</i> ssp. <i>campylac</i> BRENNAN	0271/92A	[■]	[■]	20 9
<i>A. senegal</i> (L.) WILLD.	01427/84	[■]	[■]	11 7
<i>A. senegal</i> (L.) WILLD.	A/93	[■]	[■]	14 9
<i>A. senegal</i> (L.) WILLD.	011/91A	[■]	[■]	14 9
<i>A. senegal</i> (L.) WILLD.	B/93	[■]	[■]	14 9
<i>A. senegal</i> (L.) WILLD.	C/93	[■]	[■]	14 9
<i>A. senegal</i> (L.) WILLD.	E/93	[■]	[■]	14 9
<i>A. senegal</i> (L.) WILLD.	01388/84	[■]	[■]	14 9
<i>A. albida</i> DEL. (Syn. <i>Faidherbia albida</i> CHEV.)				
<i>A. albida</i> DEL.	01193/83	[■]	[■]	16 9
<i>A. albida</i> DEL.	/93	[■]	[■]	16 9
Subgenus <i>Acacia</i> VASSAL				
<i>A. caven</i> BENTH.	01589/86	[■]	[■]	17 5
<i>A. elatior</i> BRENNAN	01810/88	[■]	[■]	16 5
<i>A. drepanolobium</i> HARMUS, ex Siös.	571/91A	[■]	[■]	16 5
<i>A. nilotica</i> ssp. <i>adstringens</i> (BENTH.) HILL.	01112/83	[■]	[■]	14 5
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01219/83	[■]	[■]	15 4
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01074/82	[■]	[■]	15 4
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01423/84	[■]	[■]	15 4
<i>A. nilotica</i> ssp. <i>indica</i> (BENTH.) HILL.	01643/86	[■]	[■]	15 4
<i>A. nilotica</i> ssp. <i>nilotica</i> (BENTH.) HILL.	01441/84	[■]	[■]	15 4
<i>A. nilotica</i> ssp. <i>tomentosa</i> (BENTH.) HILL.	01037/82	[■]	[■]	17 5
<i>A. nilotica</i> ssp. <i>tomentosa</i> (BENTH.) HILL.	01644/86	[■]	[■]	17 1
<i>A. nubica</i> BENTH.	01890/92	[■]	[■]	19 5
<i>A. radiana</i> (SAVL.) BRENA	01284/84	[■]	[■]	18 4
<i>A. radiana</i> (SAVL.) BRENA	01195/83	[■]	[■]	20 4
<i>A. seyal</i> var. <i>fistula</i> (SCHW.) OLIV.	/84	[■]	[■]	15 5
<i>A. sieberana</i> DC.	/92	[■]	[■]	12 4
<i>A. tortilis</i> ssp. <i>spiracarpa</i> BRENNAN	01669/86	[■]	[■]	20 5
<i>A. tortilis</i> (FORSSK.) HAYNE	01285/84	[■]	[■]	21 4
<i>A. tortilis</i> (FORSSK.) HAYNE	01509/85	[■]	[■]	21 4
<i>A. tortilis</i> (FORSSK.) HAYNE	/84	[■]	[■]	21 4
Subgenus <i>Heterophyllum</i> VASSAL				
<i>A. dealbata</i> LINK, var. <i>dealbata</i>	01876/92	[■]	[■]	8 5
<i>A. holosericea</i> CUN. ex DON.	01645/92	[■]	[■]	13 5
<i>A. implexa</i> BENTH.	01877/92	[■]	[■]	8 4
<i>A. mearnsii</i> WILLD.	01892/92	[■]	[■]	9 5
<i>A. melanoxylon</i> ROXB.	01878/92	[■]	[■]	8 5
<i>A. sophorae</i> WILLD.	01879/92	[■]	[■]	8 6
The Genus <i>Prosopis</i> (L.) BURK.				
<i>P. africana</i> (GUILL.) TAUBERT	/93	[■]	[■]	8 4
<i>P. alba</i> GRISEB.	01574/86	[■]	[■]	21 4
<i>P. chilensis</i> (MOLINA) STUNTZ	01591/86	[■]	[■]	23 8
<i>P. chilensis</i> (MOLINA) STUNTZ	/93	[■]	[■]	19 6
<i>P. cineraria</i> (L.) DRUCE	01451/84	[■]	[■]	19 6
<i>P. cineraria</i> (L.) DRUCE	01445/84	[■]	[■]	19 6
<i>P. cineraria</i> (L.) DRUCE	01204/84	[■]	[■]	19 6
<i>P. flexuosa</i> DC.	01585/86	[■]	[■]	26 9
<i>P. glandulosa</i> TORR. var. <i>torreyana</i>	01211/83	[■]	[■]	19 5
<i>P. juliflora</i> (SWARTZ) DC.	01214/83	[■]	[■]	10 4
<i>P. lajena</i> WILLD.	01595/86	[■]	[■]	14 4
<i>P. pallida</i> (WILLD.) HBK.	01668/86	[■]	[■]	20 4
<i>P. siliqueastrum</i> WILLD.	01579/86	[■]	[■]	15 4

Figure 1. – Map of seed storage protein bands in 51 accessions of *Acacia* and *Prosopis* (after LANHAM *et al.*, 1994). ■, intense band; ▨, light band; ▨, not certain; ▨, no band. The column at the extreme right hand side shows the number of intense protein band and the column next to it indicates the number of total protein bands detected. More information on the material are available in table 1.

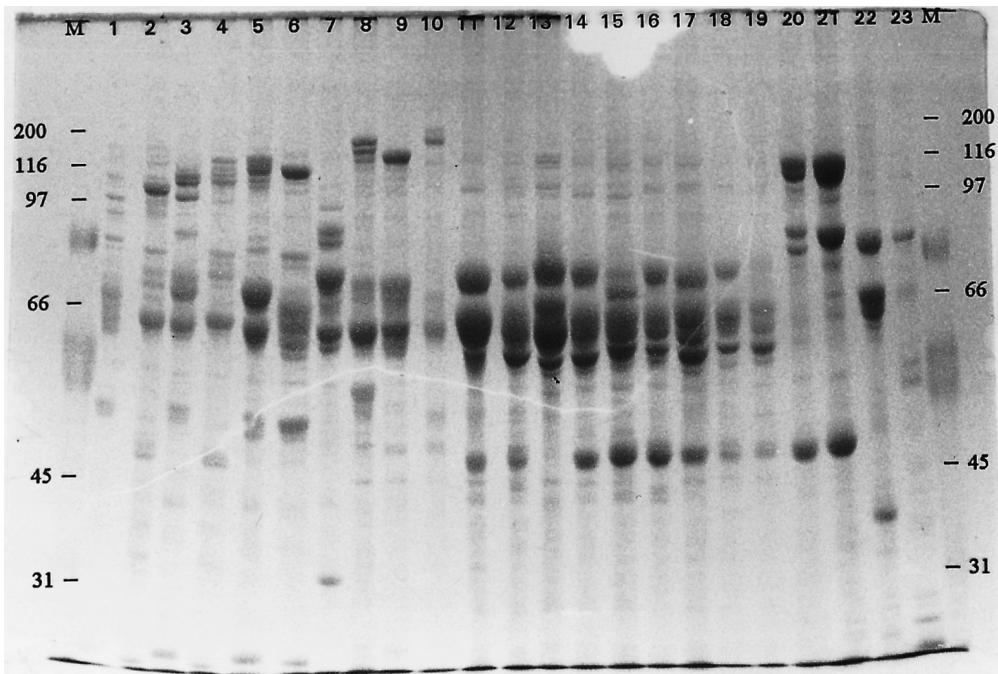


Figure 2. – Electrophoretic pattern of seed storage proteins of 23 accessions from the three subgenera of *Acacia* and the genus *Prosopis*. Laines 1 to 6, subgenus *Heterophyllum*; 7, *A. albida*; 8 to 10, subgenus *Aculeiferum*; 11 to 20, subgenus *Acacia*; 21 to 23, the genus *Prosopis*. Accession numbers and origins are given in bracket 1. *A. implexa* BENTH. (01877/92, Australia); 2, *A. holosericea* CUN. ex DON (01645/92, Senegal); 3, *A. mearnsii* WILLD. (01892/92, Kenya); 4, *A. dealbata* LINK. (01876/92, Australia); 5, *A. melanoxylon* ROXB. (01878/92, Australia); 6, *A. sophorae* WILLD. (01879/92, Australia); 7, *A. albida* DEL. (-/93, Sudan); 8, *A. senegal* (L.) WILLD. (-/93, Sudan); 9, *A. mellifera* (VAGL.) BENTH. (0180/88, Kenya); 10, *A. caffra* (THUNB.) WILLD. (754/91, TANZANIA); 11, *A. sieberiana* DC (-/92, Sudan); 12, *A. nilotica* ssp. *tomentosa* (BENTH.) HILL. (01644/86, Sudan); 13, *A. caven* BENTH. (01589/86, Chile); 14, *A. tortilis* ssp. *spiroparpa* (HOC.) BRENAN (01509/86, Yemen); 15, *A. radiana* (SAVL.) BRENAN (01284/84, Israel); 16, *A. tortilis* ssp. *spiroparpa* (HOC.) BRENAN (01669/86, Sudan); 17, *A. drepanolobium* HARMS ex SJÖSTEDT (751/91A, Tanzania); 18, *A. seyal* var. *fistula* (SCHWEINF.) OLIV. (-/84, Sudan); 19, *A. nilotica* ssp. *indica* (BENTH.) HILL. (01074/82, India); 20, *A. nubica* BENTH. (01890/92, Kenya); 21, *P. chilensis* (MOLINA) STUNTZ (-/91, Sudan); 22, *P. glandulosa* var. *torreyana* TORR. (01211/83, Mexico); 23, *P. africana* (GUIL.) TAUBERT (-/93, Sudan).

showed 20 bands, *Acacia caffra* 11, *A. mellifera* 16. Number of bands in the accessions of *A. senegal* ranged from 11 to 14. *A. albida* showed 16 bands. In subgenus *Heterophyllum*, *A. holosericea* showed 13 bands and bands of the other five species ranged from 8 to 9. For subgenus *Acacia*, *A. radiana* from Senegal showed 20 bands, *A. tortilis* ssp. *spiroparpa* 20, and *A. nilotica* ssp. *adstringens* 14 bands; band number in other accessions ranged from 12 to 21. The six species of subgenus *Heterophyllum* showed the lowest number of bands in all materials studied whereas the tetraploid accessions of subgenus *Acacia* showed the highest number. The studied tetraploid, hexaploid and octoploid accessions of subgenus *Acacia* (Table 1) had nearly the same numbers of bands (Figure 1).

Several accessions of subgenus *Acacia* had four fast-moving bands occurring irregularly (Figure 1) regarding different gels. Such bands were excluded from the phylogenetic analysis as well as from the total number of bands given in figure 1. The number of intense, light, irregular and total bands detected in the accessions together with their estimated molecular weights are shown in figure 1. The banding patterns of 23 selected accessions from the three subgenera of *Acacia* and the genus *Prosopis* are shown in figure 2.

Parsimony analysis of the seed protein data produced six equally parsimonious trees of 72 steps and consistency index = 81.5%, retention index = 78% and tree length 72. The 50%

majority rule consensus tree of the six equally parsimonious trees revealed four clades representing the three subgenera of *Acacia* and the genus *Prosopis*. The clade of *Prosopis* appeared basal to the clades of *Acacia* but supported with only 51 bootstrap level. The 13 accessions of *Prosopis* were separated from the *Acacia* in the cluster analysis. *P. africana* appeared ancestral to the other studied accessions of *Prosopis*. The two accessions of *A. albida* clustered within ten accessions of the subgenus *Aculeiferum* whereas *Acacia polyacantha* formed a subclade with the remaining studied accessions of subgenus *Aculeiferum*. In addition, the phylogram revealed interspecific variations in *A. senegal* and *A. nilotica*, whereas interspecific total similarities were revealed between some other species. Figure 3 shows phyletic relationships among the studied 51 accessions and table 2 shows mean distance and absolute numbers of unshared bands.

The present phylogenetic tree revealed interspecific variations in *A. senegal* and *A. nilotica*. The four accession of *A. nilotica* ssp. *indica* formed one clade and the other four subspecies formed an other clade with zero branch length. Similarly, the four Sudanese accessions of *A. senegal* had zero branch length and so were the other three accessions. *P. chilensis* from Sudan was different from that from Chile. Interspecific total similarities were revealed in other species. For instances, *P. alba* and *P. lampas* have zero branch length. The same applies to *P. glandulosa* and *P. chilensis* from Chile.

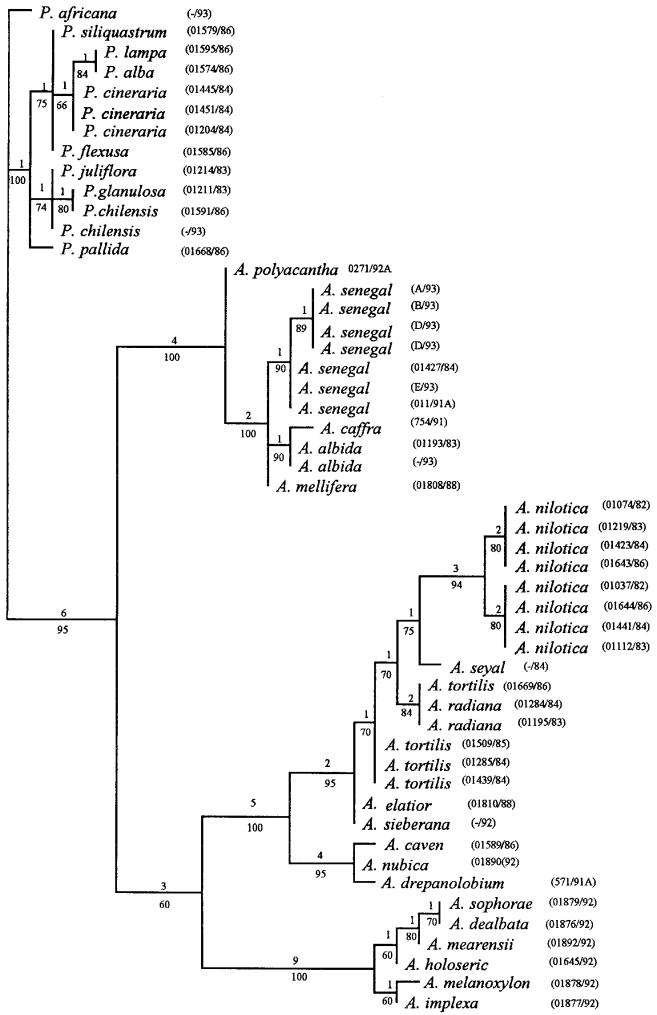


Figure 3. – 50% majority rule consensus of six equally parsimonious trees of 51 accessions of *Acacia* and *Prosopis* based on seed protein electrophoretic patterns. The phylogram was reconstructed using the WAGNER parsimony (SWOFFORD, 1993). The FELSENSTEIN's bootstrap confidence levels from 100 replicates of heuristic search analysis are given below each branch. Estimated number of character state changes following divergence from the nearest ancestral node are given above each branch. Branch lengths are proportional to distance between taxa. Consistency index for the tree = 81.5%, retention index = 78% and tree length 72.

Discussion

In the present study, the number of seed storage protein bands of tetraploid cytotypes of *Acacia* and *Prosopis* was higher than that of their diploid relatives, whereas the number of bands tended not to change with further increase in ploidy levels. MURRAY *et al.* (1970) showed that seed storage protein profiles of allotetraploid cytotypes may possess all the parental bands or, a varying degree of loss and gain of bands may occur. Recently speciated polyploids usually have all ancestral seed storage protein bands represented while ancient polyploids may lose some ancestral bands and may acquire new ones (BULINSKA-RADOMSKA and LESTER, 1986). New combinations of the subunits of multimeric proteins could account for the loss of some bands and the gain of new ones (BULINSKA-RADOMSKA and LESTER, 1986). The latter phenomenon is, however, negligible in this study, since the proteins were reduced to monomers by adding mercaptoethanol. Earlier studies on *Acacia*

species showed reduction in chromosome size with increasing polyploidy (BUKHARI, 1997b). The less than expected increase in the number of seed storage protein bands revealed in hexa- and octoploid acacias and the reduction in chromosome size and nuclear DNA mass observed earlier indicate that most polyploidies in *Acacia* are a geologically ancient event that permitted high degree of evolution and differentiation in their seed storage protein.

In this study, subgenus *Aculeiferum*, including *A. albida* had approximately double the number of intense bands compared with that of subgenera *Acacia* and *Heterophyllum*. In previous studies (GUINET and VASSAL, 1979; BUKHARI, 1997b), subgenus *Acacia* appeared to be the most evolved while subgenus *Aculeiferum* appeared as ancestral to subgenus of *Acacia*. BUKHARI (unpublished data) reported that seed mass and total seed protein were higher in members of subgenus *Aculeiferum*, lower in subgenus *Acacia* and lower still in subgenus *Heterophyllum*. It appears that the evolution of *Acacia* proceeded towards a reduction in the number and amounts of major seed storage proteins.

In the present study, the numbers of protein bands in tetra- and octoploid species were similar. On the basis of chromosomal data, BUKHARI (1997b) has also observed that some 4x cytotypes of *Acacia* are allotetraploid and 8x ones are auto-octoploids which were very likely derived recently, in geological time scale, from allotetraploid relatives. The octoploid accessions of *Acacia* had exactly twice the amount of nuclear DNA mass as their tetraploid relatives. It is possible that the duplicated genes resulting from polyploidization (forming the 8x cytotypes) have not had enough time to differentiate. As a result of polyploidization, the duplicated homologous loci would give similar polypeptides that would tend to have similar electrophoretic mobilities.

Prosopis africana was placed ancestral to the other *Prosopis* species studied. It is the only *Prosopis* species native to Africa (BURKART, 1976). Unlike most of the species of *Prosopis* which are often native to dry areas and usually in shrub form, *P. africana* survives in high rainfall zones of Africa and grows up to 21 m high (SAHNI, 1968). This present phyletic relationships to the other species of *Prosopis* support the results of BURKART (1976) who assigned *P. africana* to a separate series.

The present phylogenetic tree showed that *Acacia* evolved from *Prosopis*. This has weak bootstrap support. Previous morphological and chromosomal evidence suggested that section *Filicinae* (not included in the present study) is ancestral to the other sections of subgenus *Aculeiferum* whereas subgenera *Acacia* and *Heterophyllum* were derived from a common descent (ATCHISON, 1948; VASSAL, 1972; VASSAL and LESCALLE, 1976; GUINET and VASSAL, 1978; BRAIN, 1990). Thus, the previous hypothesis about the common ancestry of *Acacia* appears more plausible than the present one. Other studies showed that subgenus *Aculeiferum* possesses the least advanced morphological characters (ATCHISON, 1948; VASSAL, 1972; GUINET and VASSAL, 1978). Contrarily, the present study showed closer association between subgenera *Acacia* and *Heterophyllum*.

Protein electrophoretic data of the present study showed that *A. albida* fits in subgenus *Aculeiferum*. Pollen morphology (COETZEE, 1955), chromosome number, morphology and nuclear DNA mass (BUKHARI, 1979a and b) have also shown that *A. albida* fits in subgenus *Aculeiferum*. ROSS (1979) noted that *A. albida* can possess morphological characters of both subgenera *Acacia* and *Aculeiferum*. However, on morphological (VASSAL, 1972; ROBBERTSE, 1975b and c) and immunological (EL-TINAY *et al.*, 1979) grounds, *A. albida* would not be placed in the genus

Table 2. – Pairwise comparison distance matrices of 51 accessions of *Acacia* and *Prosopis* based on seed storage protein size variations obtained using PAUP 3.1.1. software package (SWOFFORD, 1993). The figures above the diagonal represent mean distance and the ones below the diagonal show the absolute numbers of unshared bands.

No.	Accession	Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	<i>A. caven</i>	01589/8	.44	.38	.50	.41	.50	.50	.50	.50	.50	.50	.44	.34	.41	.38	.38	.31	.34	.31	.31	.41	.41	
2	<i>A. drepanolobium</i>	751/91	14	-	.31	.38	.22	.38	.38	.38	.38	.38	.38	.41	.34	.19	.31	.31	.41	.31	.31	.53	.47	
3	<i>A. elatior</i>	01810/8	12	10	-	.31	.28	.38	.31	.38	.38	.38	.25	.22	.16	.31	.00	.06	.22	.06	.47	.47		
4	<i>A. nilotica</i>	01219/8	16	12	10	-	.16	.06	.06	.06	.06	.06	.06	.25	.16	.16	.19	.31	.31	.16	.31	.31	.47	.47
5	<i>A. nilotica</i>	01074/8	13	7	9	5	-	.16	.16	.16	.16	.16	.16	.22	.25	.13	.03	.28	.28	.25	.28	.56	.50	
6	<i>A. nilotica</i>	01423/8	16	12	12	2	5	-	.06	.00	.00	.00	.00	.25	.22	.22	.19	.38	.38	.22	.38	.47	.47	
7	<i>A. nilotica</i>	01643/8	16	12	10	2	5	2	-	.06	.06	.06	.06	.25	.16	.16	.19	.31	.31	.16	.31	.31	.53	.53
8	<i>A. nilotica</i>	01441/8	16	12	12	2	5	0	2	-	.00	.00	.00	.25	.22	.22	.19	.38	.38	.22	.38	.47	.47	
9	<i>A. nilotica</i>	01037/8	16	12	12	2	5	0	2	0	-	.00	.00	.25	.22	.22	.19	.38	.38	.22	.38	.47	.47	
10	<i>A. nilotica</i>	01112/8	16	12	12	2	5	0	2	0	0	-	.00	.25	.22	.22	.19	.38	.38	.22	.38	.47	.47	
11	<i>A. nilotica</i>	01644/8	16	12	12	2	5	0	2	0	0	0	-	.25	.22	.22	.19	.38	.38	.22	.38	.47	.47	
12	<i>A. nubica</i>	01890/9	14	12	8	8	7	8	8	8	8	8	8	-	.22	.16	.25	.25	.25	.22	.25	.47	.47	
13	<i>A. radiana</i>	01284/8	11	13	7	5	8	7	5	7	7	7	7	-	.13	.28	.22	.22	.00	.22	.22	.50	.50	
14	<i>A. rsadiana</i>	01195/8	13	11	5	5	4	7	5	7	7	7	5	4	-	.16	.16	.16	.13	.16	.16	.50	.50	
15	<i>A. seyal</i>	-8	12	6	10	6	1	6	6	6	6	6	8	9	5	-	.31	.28	.31	.31	.53	.47		
16	<i>A. sieberana</i>	-9	12	10	0	10	9	12	10	12	12	12	8	7	5	10	-	.06	.22	.06	.06	.47	.47	
17	<i>A. tortilis</i>	01669/8	10	10	2	10	9	12	10	12	12	12	8	7	5	10	2	-	.22	.00	.00	.47	.47	
18	<i>A. tortilis</i>	-8	11	13	7	5	8	7	5	7	7	7	7	0	4	9	7	7	-	.22	.22	.50	.50	
19	<i>A. tortilis</i>	01285/8	10	10	2	10	9	12	10	12	12	12	8	7	5	10	2	0	7	-	.00	.47	.47	
20	<i>A. tortilis</i>	01509/8	10	10	2	10	9	12	10	12	12	12	8	7	5	10	2	0	7	0	-	.47	.47	
21	<i>A. albida</i>	01193/8	13	17	15	15	18	15	17	15	15	15	15	16	16	17	15	15	15	15	15	-	.13	
22	<i>A. albida</i>	-9	13	15	15	15	16	15	17	15	15	15	15	16	16	15	15	15	15	15	15	4	-	
23	<i>A. caffra</i>	01810/8	14	14	12	14	15	12	14	12	12	12	12	15	15	14	12	14	15	14	14	13	13	
24	<i>A. mellifera</i>	01808/8	15	17	11	15	16	13	15	13	13	13	13	15	14	14	17	11	13	14	13	13	10	8
25	<i>A. polyacantha</i>	0271/92	9	15	17	15	14	15	15	15	15	15	15	17	12	16	13	17	15	12	15	15	14	14
26	<i>A. senegal</i>	A/9	14	18	12	12	13	10	12	10	10	10	10	12	15	13	14	12	14	15	14	14	11	9
27	<i>A. senegal</i>	B/9	14	18	12	12	13	10	12	10	10	10	10	12	15	13	14	12	14	15	14	14	11	9
28	<i>A. senegal</i>	c/9	13	15	13	17	18	15	17	15	15	15	15	18	18	17	13	13	18	13	13	12	10	
29	<i>A. senegal</i>	d/9	15	17	13	15	18	13	15	13	13	13	13	16	18	19	13	13	16	13	13	12	10	
30	<i>A. senegal</i>	01427/8	13	15	13	17	18	15	17	15	15	15	15	15	18	18	17	13	13	18	13	13	12	10
31	<i>A. senegal</i>	011/91	15	17	13	15	18	13	15	13	13	13	13	16	18	19	13	13	16	13	13	12	10	
32	<i>A. senegal</i>	1388/8	16	18	12	12	13	10	12	10	10	10	10	14	15	13	14	12	14	15	14	14	11	9
33	<i>A. dealbata</i>	01876/9	13	13	17	15	10	15	15	15	15	15	15	18	14	9	17	17	18	17	17	18	16	
34	<i>A. holosericea</i>	01645/9	20	14	16	14	15	16	14	16	16	16	18	17	15	14	16	16	17	16	17	19		
35	<i>A. implexa</i>	01877/9	17	19	23	15	16	15	17	15	15	15	17	20	20	20	15	23	20	23	23	14	14	
36	<i>A. mearensii</i>	01892/9	14	20	20	18	17	16	18	16	16	16	16	20	21	19	16	20	20	21	20	20	15	15
37	<i>A. melanoxylon</i>	01878/9	15	15	17	15	12	15	13	15	15	15	15	17	18	14	11	17	17	18	17	17	20	18
38	<i>A. sophorae</i>	01879/9	15	17	17	15	12	15	13	15	15	15	15	17	18	14	11	17	17	18	17	17	18	18
39	<i>P. africana</i>	-9	15	17	17	13	14	11	13	11	11	11	11	17	18	16	13	17	19	18	19	19	10	14
40	<i>P. alba</i>	01574/8	16	10	10	14	15	14	12	14	14	14	14	11	11	14	10	10	11	10	10	15	13	
41	<i>P. chilensis</i>	-9	20	20	12	14	17	14	14	14	14	14	16	13	13	18	12	14	13	14	14	17	19	
42	<i>P. chilensis</i>	01591/8	18	20	16	16	21	16	16	16	16	16	14	13	17	22	16	14	13	14	14	17	17	
43	<i>P. cineraria</i>	01451/8	16	10	10	14	15	14	12	14	14	14	14	11	14	10	10	11	10	10	15	13		
44	<i>P. cineraria</i>	01445/8	16	10	10	14	15	14	12	14	14	14	14	11	14	10	10	11	10	10	10	15	13	
45	<i>P. cineraria</i>	01204/8	16	10	10	14	15	14	12	14	14	14	14	11	14	10	10	11	10	10	10	15	13	
46	<i>P. Fleuxusa</i>	01585/8	10	12	10	14	15	16	14	16	16	16	16	10	9	11	14	10	8	9	8	8	15	17
47	<i>P. glandulosa</i>	01211/8	19	21	15	17	20	17	17	17	17	17	16	16	21	15	15	16	15	15	18	20		
48	<i>P. juliflora</i>	01214/8	16	16	10	12	13	14	12	14	14	14	12	13	11	14	10	12	13	12	12	13	15	
49	<i>P. lampa</i>	01595/8	14	14	12	12	13	14	12	14	14	14	10	11	9	12	12	10	11	10	10	15	17	
50	<i>P. pallida</i>	01668/8	18	16	16	16	19	16	16	16	16	16	16	15	15	18	16	16	15	16	16	15	15	
51	<i>P. siliquastrum</i>	01579/8	15	17	13	15	16	15	13	15	15	15	15	13	12	12	15	13	13	12	13	18	20	

Acacia. VASSAL (1972) and EL-TINAY *et al.* (1979) pointed out the need for other tools beside plant morphology to classify *Acacia* since morphological characters can be influenced by the environmental factors. In several *Acacia* species, key floral and vegetative characters, such as spines, petiolar glands and type of inflorescence, can be shared among the species of subgenera *Acacia* and *Aculeiferum*. For instance, *A. lahti*, *A. horrida*, and *A. bussei* (subgenus *Acacia*) have spicate inflorescence and *A. mellifera* ssp. *detinens* (subgenus *Aculeiferum*) has capitate inflorescence (ROSS, 1979). It appears that *A. albida*, which has been removed from *Acacia* and given the generic status of *Faidherbia* (CHEVALIER, 1934) consisting of only one species (*F. albida*) is like other species of *Acacia* that belong to subgenus

Aculeiferum, although it possesses some characters that are unique to subgenus *Acacia* such as spinescent stipules (ROBBERTSE, 1975a) or capitate inflorescence (ROSS, 1979). On the other hand, as this study shows, *A. polyacantha* (subgenus *Aculeiferum*) only formed a sister clade with all the other studied accessions of subgenus *Aculeiferum*. This species is similar to subgenus *Acacia* in petiole morphology (ROBBERTSE, 1975c) and is tetraploid (BUKHARI, 1997b). It is comparable to *A. albida* in having morphological characters of both subgenera *Acacia* and *Aculeiferum*.

The phyletic tree of the present study revealed interspecific variations in some cases and interspecific total similarities in other cases. The intraspecific variations in *A. nilotica* coincided

(continuation table 2)

No.	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	
1	.44	.47	.28	.44	.44	.41	.47	.41	.47	.50	.41	.63	.53	.44	.47	.47	.47	.50	.63	.56	.50	.50	.50	.31	.59	.50	.44	.56	.47	
2	.44	.53	.47	.56	.56	.47	.53	.56	.41	.44	.59	.63	.47	.53	.53	.31	.63	.63	.31	.31	.31	.38	.66	.50	.44	.50	.53			
3	.38	.34	.53	.38	.38	.41	.41	.41	.38	.53	.50	.72	.63	.53	.53	.31	.38	.50	.31	.31	.31	.47	.31	.38	.50	.46				
4	.44	.47	.47	.38	.38	.53	.47	.53	.47	.38	.47	.44	.47	.56	.47	.47	.41	.44	.44	.50	.44	.44	.44	.53	.38	.50	.47			
5	.47	.50	.44	.41	.41	.56	.56	.56	.41	.31	.47	.50	.53	.38	.38	.44	.47	.53	.66	.47	.47	.47	.47	.63	.41	.41	.59	.50		
6	.38	.41	.47	.31	.31	.47	.41	.47	.41	.31	.47	.50	.47	.47	.47	.34	.44	.44	.50	.44	.44	.44	.50	.53	.44	.44	.50	.47		
7	.44	.47	.47	.38	.38	.53	.47	.53	.47	.38	.47	.44	.53	.56	.41	.41	.38	.44	.50	.38	.38	.38	.44	.53	.38	.38	.50	.41		
8	.38	.41	.47	.31	.31	.47	.41	.47	.41	.31	.47	.50	.47	.50	.47	.47	.34	.44	.44	.50	.44	.44	.44	.50	.53	.44	.44	.50	.47	
9	.38	.41	.47	.31	.31	.47	.41	.47	.41	.31	.47	.50	.47	.50	.47	.47	.44	.44	.44	.50	.44	.44	.44	.50	.53	.44	.44	.44	.50	
10	.38	.41	.47	.31	.31	.47	.41	.47	.41	.31	.47	.50	.47	.47	.47	.34	.44	.44	.50	.44	.44	.44	.50	.53	.44	.44	.44	.50	.47	
11	.38	.41	.47	.31	.31	.47	.41	.47	.41	.31	.47	.50	.47	.47	.47	.34	.44	.44	.50	.44	.44	.44	.50	.53	.44	.44	.44	.50	.47	
12	.38	.47	.53	.38	.38	.47	.41	.47	.41	.44	.47	.56	.53	.63	.53	.53	.53	.44	.50	.44	.44	.44	.44	.31	.53	.38	.31	.50	.41	
13	.47	.44	.38	.47	.47	.56	.50	.56	.50	.47	.56	.53	.63	.66	.56	.56	.56	.34	.41	.41	.34	.34	.28	.50	.41	.34	.47	.38		
14	.47	.44	.50	.41	.41	.56	.56	.56	.41	.44	.47	.63	.59	.44	.44	.50	.34	.41	.53	.34	.34	.34	.50	.34	.28	.47	.38			
15	.44	.53	.41	.44	.44	.53	.59	.53	.44	.28	.44	.44	.47	.50	.34	.34	.41	.44	.56	.69	.44	.44	.44	.44	.66	.44	.38	.56	.47	
16	.38	.34	.53	.38	.38	.41	.41	.41	.38	.53	.50	.72	.63	.53	.53	.53	.31	.38	.50	.31	.31	.31	.47	.31	.38	.50	.41			
17	.44	.41	.47	.44	.44	.41	.41	.41	.44	.44	.44	.72	.63	.53	.53	.59	.31	.44	.44	.31	.31	.31	.25	.47	.38	.31	.50	.41		
18	.47	.44	.38	.47	.47	.56	.50	.56	.50	.47	.56	.53	.63	.66	.56	.56	.56	.34	.41	.41	.34	.34	.28	.50	.41	.34	.47	.38		
19	.44	.41	.47	.44	.44	.41	.41	.41	.41	.44	.53	.50	.72	.63	.53	.53	.59	.31	.44	.44	.31	.31	.25	.47	.38	.31	.50	.41		
20	.44	.41	.47	.44	.44	.41	.41	.41	.41	.44	.53	.50	.72	.63	.53	.53	.59	.31	.44	.44	.31	.31	.31	.25	.47	.38	.31	.50	.41	
21	.41	.31	.44	.34	.34	.38	.38	.38	.34	.56	.53	.44	.47	.63	.56	.56	.31	.47	.53	.53	.47	.47	.47	.47	.56	.41	.47	.56		
22	.41	.25	.44	.28	.28	.31	.31	.31	.31	.28	.50	.59	.44	.47	.56	.44	.41	.59	.53	.41	.41	.41	.53	.63	.47	.53	.47	.63		
23	-	.28	.59	.19	.19	.09	.16	.09	.16	.19	.41	.50	.41	.38	.41	.41	.28	.38	.38	.50	.47	.38	.38	.44	.28					
24	9	-	.56	.16	.16	.25	.25	.25	.16	.63	.66	.63	.53	.63	.63	.44	.34	.41	.41	.34	.34	.59	.50	.41	.59	.41	.44			
25	19	18	-	.59	.59	.56	.56	.56	.56	.59	.50	.53	.50	.47	.56	.56	.56	.53	.53	.47	.53	.53	.53	.41	.56	.66	.53	.53	.56	
26	6	5	19	-	.00	.16	.16	.16	.16	.06	.47	.63	.47	.38	.47	.47	.34	.44	.44	.50	.44	.44	.44	.63	.47	.38	.50	.44	.47	
27	6	5	19	0	-	.16	.16	.16	.16	.16	.06	.47	.63	.47	.38	.47	.47	.34	.44	.44	.50	.44	.44	.44	.63	.47	.38	.50	.44	.47
28	3	8	18	5	5	-	.06	.06	.16	.16	.50	.59	.50	.41	.50	.50	.38	.34	.53	.41	.34	.34	.47	.44	.47	.41	.38			
29	5	8	18	5	5	5	2	-	.06	.06	.16	.56	.66	.50	.47	.56	.56	.44	.41	.53	.34	.41	.41	.47	.44	.47	.44			
30	3	8	18	5	5	0	2	-	.06	.16	.50	.59	.50	.41	.50	.50	.38	.34	.53	.41	.34	.34	.47	.44	.47	.41	.41	.38		
31	5	8	18	5	5	2	0	2	-	.16	.56	.66	.50	.47	.56	.56	.44	.41	.53	.34	.41	.41	.47	.44	.47	.44				
32	6	5	19	2	2	5	5	5	5	-	.47	.56	.47	.38	.47	.47	.28	.44	.44	.50	.44	.44	.44	.63	.47	.38	.50	.47		
33	13	20	16	15	16	18	16	18	15	-	.28	.19	.22	.06	.13	.38	.66	.72	.72	.66	.66	.66	.59	.69	.47	.72	.50			
34	16	21	17	20	20	19	21	19	21	18	9	-	.28	.31	.28	.28	.41	.50	.50	.56	.50	.50	.56	.53	.38	.38	.50	.47		
35	13	20	16	15	15	16	16	16	15	6	9	-	.16	.25	.25	.31	.78	.66	.59	.78	.78	.78	.78	.72	.63	.47	.53	.66	.56	
36	12	17	15	12	12	13	15	13	15	12	7	10	5	-	.22	.22	.34	.69	.50	.56	.69	.69	.69	.47	.56	.50	.56	.47		
37	13	20	18	15	15	16	18	16	18	15	2	9	8	7	-	.06	.38	.59	.66	.59	.59	.59	.63	.47	.66	.44				
38	13	20	18	15	15	16	18	16	18	15	4	9	8	7	2	-	.31	.59	.59	.66	.59	.59	.59	.59	.61	.38				
39	9	14	18	11	11	12	14	9	12	13	10	11	12	10	-	.59	.59	.72	.59	.59	.59	.66	.63	.34	.53	.59	.50			
40	12	11	17	14	11	13	11	13	14	21	16	25	22	19	19	19	-	.38	.44	.00	.00	.00	.38	.41	.38	.25	.25			
41	16	13	17	14	14	17	17	17	14	23	16	21	16	21	19	19	12	-	.31	.38	.38	.38	.56	.09	.38	.25	.34			
42	14	13	15	16	16	13	11	13	11	16	23	18	19	18	21	21	23	14	10	-	.44	.44	.44	.31	.22	.63	.44	.31		
43	12	11	17	14	14	11	13	14	21	16	25	22	19	19	19	0	12	14	-	.00	.00	.38	.41	.38	.25	.25	.28			
44	12	11	17	14	14	11	13	14	21	16	25	22	19	19	19	0	12	14	0	-	.00	.38	.41	.38	.25	.25	.28			
45	12	11	17	14	14	11	13	14	21	16	25	22	19	19	19	0	12	14	0	0	-	.38	.41	.38	.25	.25	.28			
46	16	19	13	20	20	15	15	15	20	19	18	23	22	19	19	21	12	18	10	12	12	12	-	.47	.63	.31	.44	.41		
47	15	16	18	15	15	14	14	15	22	17	20	15	20	18	20	13	7	3	7	13	13	13	15	-	.47	.28	.22	.31		
48	12	13	21	12	12	15	15	15	12	15	18	15	13	11	12	12	20	12	12	12	20	15	-	.31	.50	.34				
49	12	19	17	16	16	13	15	15	16	15	12	17	16	15	13	17	8	12	14	8	8	8	10	9	10	-	.31	.16		
50	14	13	17	14	14	13	15	13	15	16	23	16	21	18	21	19	19	8	8	10	8	8	8	14	7	16	10	-	.34	
51	9	14	18	15	15	12	14	12	14	15	16	15	18	15	14	12	16	9	11	13	9	9	9	13	10	11	5	11		

with sub-specific levels. An in-depth study on *A. senegal* and *Prosopis chilensis*, and perhaps on other species of *Acacia* and *Prosopis*, may identify additional subspecies in future. However, the interspecific total similarities revealed by the present analysis indicate that the use of only one character may not always be appropriate.

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Genetic Parameters Estimated From a Wild Cherry Diallel: Consequences for Breeding

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Summary

Height, girth at breast height and susceptibility to cherry leaf spot were measured periodically up to seven years at three plantations of a 14-parent half diallel of wild cherry. Variance components were interpreted according to an additive-dominance genetic model and used to estimate potential gains from

selection under various selection and deployment strategies. Height increment over five growing seasons, girth increment over two growing seasons and susceptibility to cherry leaf spot had moderate to high narrow and broad sense heritabilities. For these traits, the ratio of additive to total genetic variance was higher than 0.60 in the three studied tests. Genotype by site interaction was quite high for stem height increment but was low or null for girth increment and susceptibility to cherry leaf spot. Height increment and girth increment were highly genetically correlated with each other as well as with susceptibility to cherry leaf spot. Clonal means of the parents of the diallel were generally well correlated with their general combining abilities, so that gains from selection in clonal tests of parents for clonal seed orchards and for the next breeding

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