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Full Length Research Paper

Spatial prototype and phenotypes of variation in populations of prickly acacia in semi-arid regions in India

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Acacia nilotica **is a complex species with nine subspecies, of which six are native to the African tropics and three others are native to the Indian subcontinent. It occurs from sea level to over 2000 m and can withstand extremes of temperature (>50°C) and air dryness but is frost is sensitive when young. It is considered as a very important economic plant since early times as a source of tannins, gums, timber, fuel, fodder and medicine. Variability among populations was analyzed in five different regions of *A. nilotica* from spatially variable habitats. Populations of *A. nilotica* developed in response to their habitat conditions. The nature of morphological variability for vegetative traits appeared environmentally controlled. The level of variability was significantly high among the populations. Phenotypic variability was extremely high for leaf and stipular spine characteristics. The differentiation of leaf and stipular spine expression seems to have an adaptive significance for the species in terms of water economy. The study suggested that populations of *A. nilotica* are differentiated in relation to the heterogeneity of environment. These populations became adapted to their habitat through the variability of morphological expressions. The morphologically differentiated populations of the species had allowed them to maintain themselves in a wide array of environmental situations enabling *A. nilotica* to occupy ample ecological ranges.**

Key words: Prickly acacia, Babul, population variation, semi arid.

INTRODUCTION

The genus *Acacia* belongs to the family Leguminosae (Fabaceae), subfamily Mimosoideae. *Acacia* represents the largest genus of the angiosperms in which approximately 1,200 species of shrubs and trees are recorded, mainly in Australia and Africa. *Acacia* species are widely distributed in tropical and subtropical regions, including all continents and Pacific Islands, except Europe and Antarctica (Atchinson, 1948). About 700 species are endemic to Australia which is believed to be a center of speciation and evolution (Guinet and Vassal, 1978; Pedley, 1978). *Acacia* species have been found in the tropical lowland forest of west Gondwana land (Raven and Axelrod, 1974; Beadle, 1981). Speculation has extended to dispersal routes within Africa (Ross, 1981) and Australia (Beadle, 1981) after the breakup of Gondwana land into separate continents. Beadle (1981) suggested that a few species arrived in Australia before separation and its relative species evolved and spread southwards from tropical northern Australia. Tindale and Roux (1974) reported that the eastern Australia was the centre of origin of the Australian Acacia. Hoper and Maslin (1978) suggested that a major proliferation of

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species is now occurring in the south western areas of west Australia. The most abundantly found sp. *Acacia nilotica* has a broad native range including much of Africa, Middle-east and the Indian subcontinent (Dwivedi, 1993). Presently, this species is recognized into 9 subspecies with more or less distinctive morphological, ecological and geographical features. Out of these 9 ssp., 4 are reported to occur in India (Brenan, 1983; Sheikh, 1989), namely: *A. nilotica* ssp. *indica, A. nilotica* ssp. *cupressiformis, A. nilotica* ssp. *subalata* and *A. nilotica* ssp. *adstringens. Acacia nilotica* and its subspecies *indica* are widely distributed in India, particularly in Punjab, Rajasthan, Haryana, Uttar Pradesh, Gujarat, Madhya Pradesh, Maharashtra and Andhra Pradesh. It is Indigenous to the western part of the Indo-Gangetic plains and northern part of the Deccan Plateau (Brandis, 1921). It is commonly known as 'Babul'. *Acacia nilotica* ssp. *cupressiformis* is described as 'Ramkanta Babul' which occurs mostly in Uttar Pradesh, Punjab, and Rajasthan in agricultural lands (Troup, 1921; Joshi, 1944; Vahid, 1944). *Acacia nilotica* ssp. *subalata* occurs in East Africa, though it has only be It has also been recorded from Pakistan (Sind), India and Sri Lanka. *Acacia nilotica* ssp. *adstringens* is found in Libya and Algeria but whether they are indigenous to these areas is not certain. This ssp. is reported (Ali 1973) to occur in Pakistan (Sind) and India (Maharashtra). *Acacia nilotica* and its sp. is a tree 5-20 meters high with a dense spherical crown, stems and branches usually dark to black coloured, fissured bark, grey-pinkish slash, exuding a reddish low quality gum. The tree has thin, straight, light, grey spines in axillary pairs, usually in 3 to 12 pairs, 5 to 7.5 cm long in young trees, and mature trees are commonly without thorns. The leaves are bipinnate, with 3-6 pairs of pinnulae and 10-30 pairs of leaflets each, tomentose, rachis with a gland at the bottom of the last pair of pinnulae. Flowers in globulous heads 1.2-1.5 cm in diameter of a bright golden–yellow colour set up either auxiliary or whorly on peduncles 2-3 cm long located at the end of the branches. The flowers are small, massed into globose heads and function as units of reproduction and the small quantities of concentrated nectar, and has abundant pollen resources available to the pollinators (Gorain et al., 2012). Pods are strongly constricted, hairy, white-grey, thick and softly tomentose.

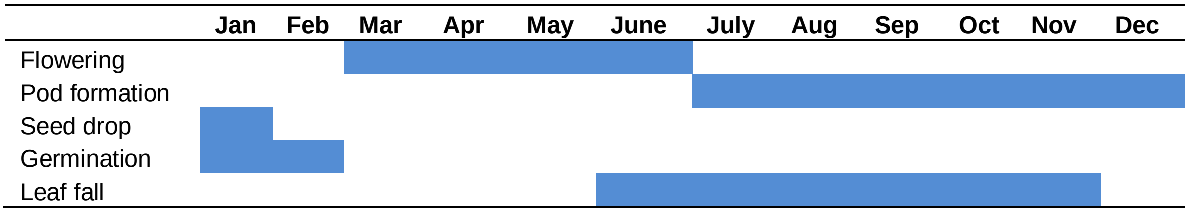
The habitat may vary due to the changing pattern of soil chemistry, water and nutrient availability, light and many other factors (Schmitt, 1993). Plants cope with the variability of their environment. They have to endure whatever the environment offers to them because of their sessile nature. Species with wide geographic ranges always develop locally adapted plant populations and show variation for morphological expressions (Elberse et al., 2003). The species of diverse habitats may show several modifications of various morphological traits (Thompson, 1990; Thompson and Rabinowitz (1989). This differentiation is usually pertinent to habitat conditions. Morphological variation is strongly influenced by various environmental factors. The morphological variability signifies the adaptation of the species to its environment and it may be genetically determined or environmentally induced. Thus morphological differentiation seems to have an evolutionary significance that results in the gradual adaptation of the species to its environment (Hussain and Mahmood, 2004; Mahmood and Abbas, 2003). *Acacia* is a large species complex and is represented by 900 species. *A. nilotica* has considerable variation with its nine subspecies presently recognized, three occurring in subcontinent and six occurring throughout Africa (asali) (Ali, 1973). The morphological variability can be extremely high in those species that have wide geographic distribution. *A. nilotica* has wide ecological amplitude and is found growing in a variety of habitats. The species is remarkably variable for various morphological expressions such as leaf, stipular spine morphology, pod and seeds characteristics. The populations of the species can be differentiated even at very short distances.

The growth pattern of *A. nilotica* germinates following rainfall in the wet season. Although 95% of seed become dead after two years, some seeds may still germinate up to 15 years after seed drop. Germination is aided when seeds are disturbed, for example, by fire or by passing through the digestive system of animals. Seedlings grow rapidly near water but more slowly in open grasslands. Trees can flower and fruit two to three years after germination, and more quickly after high rainfall years. It flowers between March and June, with pods forming between July and December. Most leaf fall corresponds to this dry period between June and November. Seedpods drop from October to January (Table 1).

Efforts for eradication

Lots of efforts have been made to eradicate *Acacia nilotica*, mechanically and chemically. There are two aspects to be considered (economic aspect and ecological aspect) when carrying out big programmes, because the activity or action applied in the conservation area is different from the action applied in the non conservation area. According to the management, eradication of *A. nilotica* by chemical method was not effective and efficient. This method spent a lot of budget, because it needed a lot of chemical material compared to area treatment. Though eradication by mechanical method by cutting is yet to be successful, these methods trigger the dormant seed to grow, and vegetative regeneration from coppice, one coppice resulting in 5-6 new branches. Besides, by using pulley is also not efficient, because it takes so long a time to do that. While using bulldozer is quite effective, but it can change the land structure. Now, the method that applied to eradicate this species is by cutting and burning the coppice and pulling it out of the seedling. These activities need a lot of

Table 1. General growth pattern of *Acacia nilotica* or prickly acacia.



labor, continuity, and monitoring. Until now, the speed eradication to this species is about 63 ha/year, so it need 73 years to eradicate this species, with assumption that there is no reinvasion to this area. Climatic modeling and genetic studies have indicated that the search for biological control agents should be concentrated in India (Dhileepan et al., 2010).

The main objectives of the study were to reveal differentiation among populations in relation to heterogeneous environmental situations. Study was also aimed at testing the hypothesis that populations are adapted to their environment through the variability of morphological expressions. The study focused on recognizing the pattern of morphological variability that allows a species to grow under a wide array of habitat situations. Particular attention was paid to understanding the way by which species is maintained in nature and occupies wide geographical ranges. The research was conducted at the Arid Forest Research Institute (Indian Council of Forestry Research and Education) Jodhpur, India during September to October, 2010.

MATERIALS AND METHODS

A field study was conducted during September - October, 2010 to study the morphological variation in five populations of *Acacia nilotica* from five edaphically, topographically and climatically variable sites of Gandhinagar, Nadiad, Anand, Junagarh and Bhuj in Gujarat, India. Detail of the study sites is provided in Table 2. These sites showed remarkable differences among them regarding the climate, topology, soil conditions, type and number of plant species growing and water availability. The sites were visited and observations were made for the stands of *Acacia nilotica* growing under natural environment. Ten individuals were selected from each site and five uniform branches were collected from each individual tree. Observations were also made for general characteristics of *Acacia* trees such as height and extent of branching Figure 1.

Collection protocols

Acacia nilotica trees of uniform age were selected by measuring the girth of the plants to assess the age. Plants of uniform size within one kilometer range were sampled almost at the same time of the year from all populations. The branches were sampled at the same height of the individual trees. For morphometric analysis (leaflet length, pinnules length, spine length pod length and seed size), consistent measurements were taken. Data were analyzed statistically using analysis of variance procedures, means, standard deviation and standard error of mean were compared with the one way anova test and multiple mean comparison test at $P < 0.001$ unless otherwise stated. All analyses were performed using SigmaStat 3.5 (Systat Software Inc., Richmond, USA).

RESULTS AND DISCUSSION

Number of compound leaves per 20 cm branch

The stems are whitish and either hairy or occasionally hairless when young, but turn a darker colour (that is, grey to brown) as they aged and become woody. They are usually covered in tiny whitish-coloured raised spots (that is, lenticels). The trunks of mature trees are rough with fissured bark towards their base that is brown, reddish-brown or black in colour.

The number of compound leaves on the branch of every 20 cm ranged from 11.36 at Junagarh to 14.26 at Gandhinagar. The results for number of compound leaves showed that all survey sites or population had significantly different number of compound leaves (Table 3). The highest number of compound leaves was observed in population at Gandhinagar while population at Junagarh had the lowest number of compound leaves. Populations at Nadiad and Anand did not show any marked difference between them. Population at Bhuj had significantly reduced number of leaves than the other populations. Analysis of variance revealed a significant ($P \leq 0.001$) contrast among populations (Table 4).

Number of leaflet per compound leaf

The twice-compound (that is, bipinnate) leaves are dark green in colour and have a feathery appearance. They are borne on a relatively short leaf stalk (that is, petiole) 4-20 mm long, which is finely hairy and sometimes has a small raised structure (that is, gland) just below the lowest pair of leaf branchlets (that is, pinnae). The

Table 2. The general description of the study sites of *Acacia nilotica* in semi-arid areas in Gujarat state.

Different survey site	Location	General habitat conditions
1. Gandhinagar	N23°14'58.9" E072°41'24.1" ELEV: 293ft	Sandy soil, low water availability, rain fed area, ground water brackish, non-irrigated field.
2. Nadiad (Khera)	N22°38'50.4" E072°55'54.4" ELEV: 173ft	Sandy soil, ample rainfall, soil with greater organic matter content
3. Anand	N22°30'34.9" E072°48'10.0" ELEV: 115ft	Medium black soil, rain red area, ground water non saline, non-irrigated soil.
4. Junagarh	N21°39'30.6" E070°32'07.5" ELEV: 259ft	Medium black soil, brakish ground water, non-irrigated.
5. Bhuj	N23°15'06.8" E069°23'25.1" ELEV: 522ft	Sandy loam, frequently irrigated, saline, water availability, rain red area.

Figure 1. (A) Mature tree of *A. nilotica*; (B) 20 cm branch of *A. nilotica*; (C) Leaflets; (D) Spines of *A. nilotica*; (E) A hole podes of *A. nilotica*; (F) Seeds of *A. nilotica*.

extension of the leaf stalk (that is, rachis) is 8-68 mm long and bears 2-10 pairs of small leaf branchlets (that is, pinnae). A small raised gland is usually present on the rachis, at the junction of the uppermost one or two pairs of leaf branchlets (that is, pinnae). Each of the leaf branchlets (1-5 cm long) bears numerous (7-30) pairs of small, oblong or narrowly oblong leaflets (that is, pinnules). These leaflets (2-7 mm long and 0.5-2 mm wide) are usually hairless (that is, glabrous), but sometimes have somewhat hairy (that is, ciliate) margins, and have rounded tips (that is, obtuse apices).

Number of leaflet per compound leaf of *A. nilotica* in populations at Bhuj was the highest and the lowest number of leaflet was in Anand and Nadiad though they did not differ significantly in the populations (Table 3). Populations sampled from different sites showed significant difference ($P \leq 0.001$) between them (Table 4). Similarly, population at Junagarh and Gandhinagar

Table 3. Overall mean values, standard deviation, and standard error of mean for various morphological attributes of *Acacia nilotica* sampled from different sites.

Populations differentiations					
Different parameters	**Gandhi-nagar**	**Nadiad**	**Ananad**	**Junagarh**	**Bhuj**
No. of compound leaves per 20 cm branch	14.26	14.1	14.04	11.36	12.98
No. of leaflets per compound leaf	7.1	6.86	6.76	8.24	10.42
Leaflet length (cm.)	5.34	5.36	5.03	4.2	2.67
No. of pinnules per leaflet	34.22	26.92	18.14	36.98	41.32
Pinnules length (cm.)	0.39	0.43	0.44	1.38	2.03
No. of spines per 20 cm branch	18.94	18.94	17.16	18.88	9.68
Length of spines (cm.)	2.61	3.16	2.31	1.82	3.09
Length of pods (cm.)	13.7	12.98	12.12	13.3	12.58
Seed size (cm.)	0.76	0.87	0.88	0.84	0.72
No. of seeds per pod	11.42	10.34	9.04	11.26	7.88

Table 4. Analysis of variance for various morphological attributes of *Acacia nilotica* in different populations.

Populations differentiations			
Attributes/ Different parameters	**Mean sq. values**	**F-values**	**Significance**
No. of compound leaves per 20 cm branch	14.09	15.15	<0.001
No. of leaflets per compound leaf	23.71	232.56	<0.001
Leaflet length (cm.)	12.89	111.15	<0.001
No. of pinnules per leaflet	833.31	173.71	<0.001
Pinnules length (cm.)	5.45	1050.01	<0.001
No. of spines per 20 cm branch	160.69	238.93	<0.001
Length of spines (cm.)	3.13	6.78	<0.001
Length of pods (cm.)	3.77	28.68	<0.001
Seed size (cm.)	0.04	3.92	<0.008
No. of seeds per pod	22.79	137.15	<0.001

having lower number of leaflets also differed considerably from all other populations Figure 2.

Leaflet length

Length of the leaflets of *A. nilotica* in various populations showed a significant ($P < 0.001$) difference (Table 4). A considerable reduction in leaflet length was observed at Bhuj and the lengths were highest at Gandhinagar. Other populations exhibited a variable length of leaflets (Table 4).

Number of pinnules per leaflet

Pinnule number varied considerably in a range of 18-41 pinnules per leaflet in populations of *A. nilotica* (Table 3). All populations showed significantly different number of pinnules. The two populations (Junagarh and Gandhinagar) had significantly higher number of pinnules but did not show any significant differences among them. The highest number of pinnules was observed in population at Bhuj, whille the lowest number of pinnules was in population at Anand. Number of pinnules per leaflet was significantly different ($P \leq 0.001$) between populations at various locations (Table 4).

Pinnule length

A. niloltica populations showed a significant difference for pinnule length except in the population sampled from populations at Nadiad and Anand. The population of pinnule length is highest at Bhuj and population at Gandhinagar had the longest pinnules, while populations at Nadiad and Anand had more expanded leaflets. The statistical analysis revealed a significant ($P \leq 0.001$) difference for pinnule length in populations that were sampled from spatially variable habitats (Table 3).

Number of stipular spines per 20 cm branch

Pairs of stout greyish-coloured spines (2-50 mm long, occasionally up to 10 cm in length) are borne at the base of each leaf (that is, near the leaf axils). Sometimes these spines may be inconspicuous (that is, they may

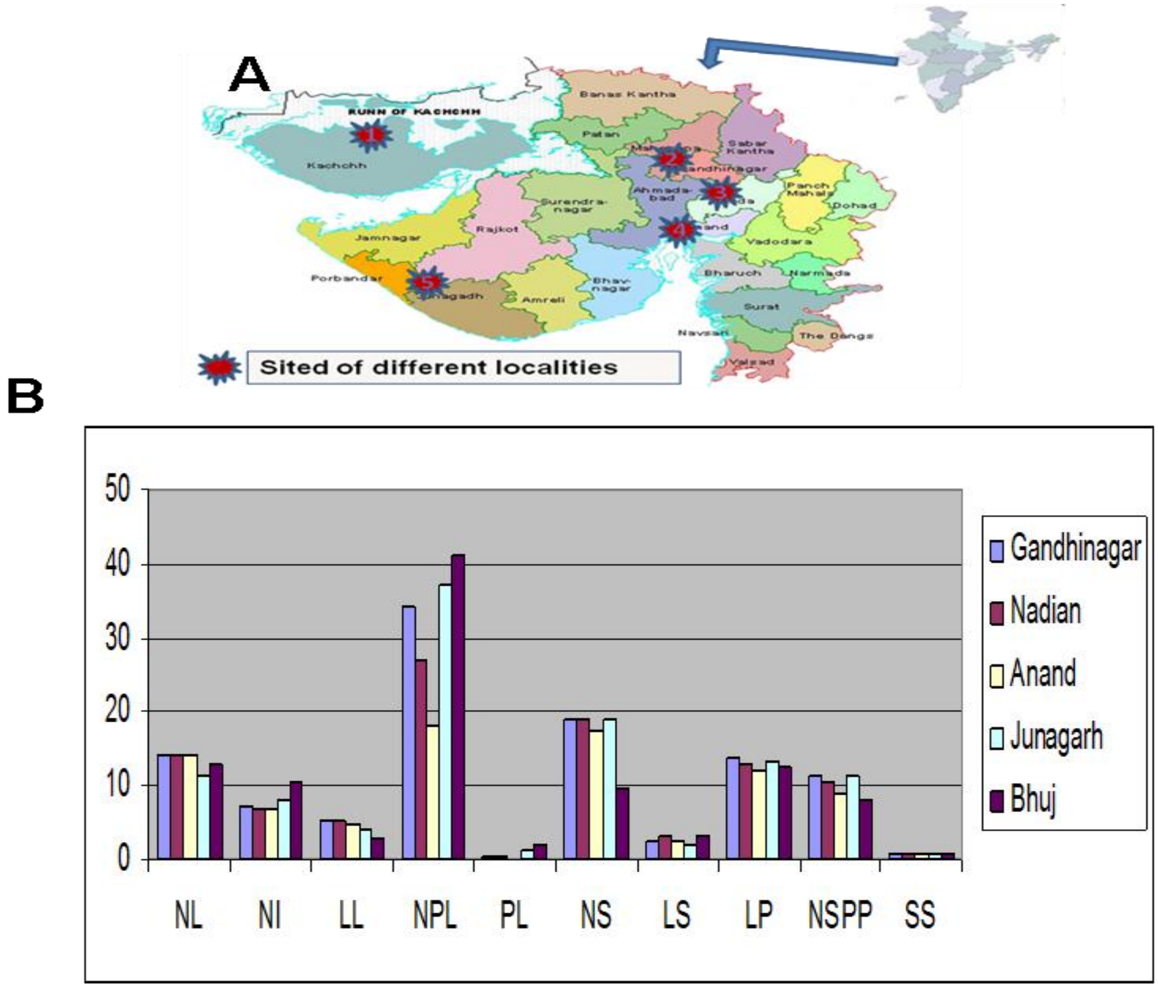


Figure 2. (A) Survey and population density on *Acacia nilotica* in different places in semi-arid region; (B) Graph showing the mean of all localities.
NL = Number of compound leaves per 20 cm branch; NI = Number of leaflet per compound leaf; LL = Leaflet length; NPL = Number of pinnules per leaflet; PL = Pinnule length; NS = Number of stipular spines per 20 cm branch; LS = Length of spines; LP = Stipular spine length; NSPP = Number of seeds per pod; SS = Seed size.

occasionally appear to be absent from some branches), and they are usually absent from the trunks and older branches.

A significant ($P \leq 0.001$) difference was observed for number of stipular spines per 20 cm branch. Number of stipular spine showed responses of the populations (Table 3). However, no significant difference was observed for populations at Nadiad and Gandhinagar as they had different number of spines. The occurrence of spines was more frequent for population at Gandhinagar and Nadiad, but the lowest population was at Bhuj which had a striking dissimilarity from all populations sampled from different sites Figure 3.

Stipular spine length

All the populations of *A. niloltica* showed a significant ($P \leq 0.001$) difference for stipular spine length (Table 3). The populations at Nadiad are the longest and the shortest is the population at Junagarh of the mean values. However, population at Nadiad had the longest spines and differed significantly ($P \leq 0.001$). Population at Junagarh had the shortest spines but also showed a marked difference ($P \leq 0.001$).

Pod length

The pod is slightly pubescent and light grayish yellow in colour and measures approximately 15 cm in length and 1.4 cm in breadth. In transverse section, it is oval in the seed region and oblong in between them. The seeds are closely surrounded by loose tissue which in turn is enclosed in a thick leathery tissue of the fruit wall. The inner loose tissue shrivels up as the fruit ripens making the seeds slightly loose. In a pod, the number of seeds varies from 8-16, and they lie along the middle line of the

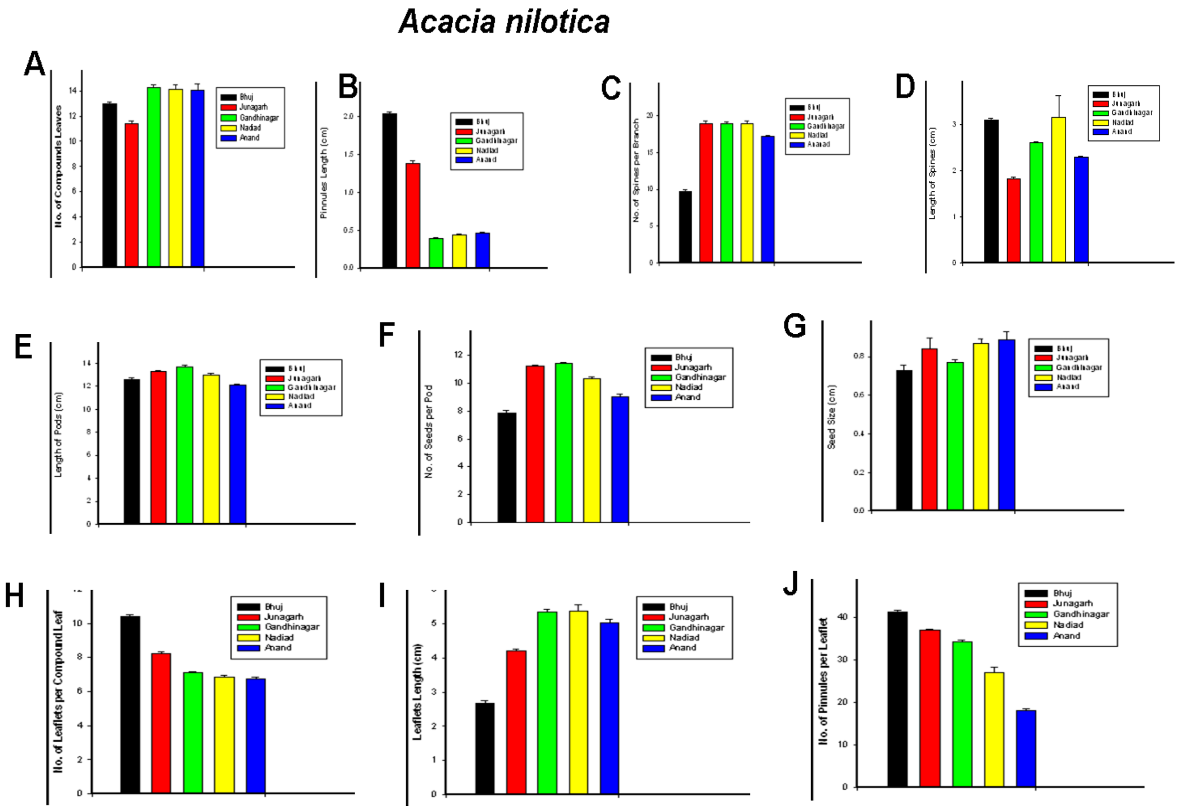


Figure 3. Graph showing the mean and error of mean of all localities. (A) Number of compound leaves per 20 cm branch; (B) Pinnule length; (C) Number of stipular spines per 20 cm branch; (D) Stipular spine length; (E) Length of pods; (F) Number of seeds per pod; (G) Seed size; (H) Number of leaflet per compound leaf; (I) Leaflet length; (J) Number of pinnules per leaflet.

fruit, with their long axes at the right angles to the long axis of the fruit.

Pods length of *A. niloltica* at various populations exhibited invariably different means for fruiting trait (Table 3). Although the population at Anand had the shortest pods, it did not differ significantly from all other populations. Population at Gandhinagar had the pods but the variability of the trait was statistically insignificant (Table 4).

Number of seeds per pod

The fruit is an elongated pod (6-25 cm long and 4-17 mm wide) that is swollen around each seed and strongly constricted between the seeds (that is, it is torulose), and therefore resembles a string of pearls. These greyish-green pods are covered in tiny soft hairs (that is, they are pubescent) that are somewhat flattened, and turn green to brown in colour when mature. However, very old pods may turn dark brown or black in colour after being shed from the plant. They contain several (8-15) seeds, do not split open at maturity (that is, they are indehiscent), and are most commonly present during late winter, spring and summer (that is, from May to January). The brown or blackish-brown coloured seeds (6-7 mm long and 4.5-6.5 mm wide) are almost round in shape (that is, sub-globular) and somewhat flattened. They are smooth in texture and have a hard seed coat.

The funicle or the seed stalk, which attaches the seed to the fruit wall, takes three turns. Just at the point of attachment of the stalk to the seed it bends away from the micropyle and after running close to the seed for a short distance towards the chalaza, it takes a sharp turn in the reverse direction. As soon as this turning is complete, it gain bends gradually backwards and after running some distance joins the fruit wall obliquely.

Number of seed per pod was considerably variable in different populations of *A. niloltica* (Table 3). However, the populations at Gandhinagar and Junagarh had similar seed number. Population at Gandhinagar had the maximum number of seed whereas population at Bhuj had the lowest number of seeds. The responses of populations were distinct except the two populations (Nadiad and Anand) which had invariably same number of seeds in their pods (Table 4).

Seed size

The dry seeds are approximately 8 × 7 mm and deep brown in colour. They have a peculiar marking on their flat surfaces in the form of a line running parallel to the contour of the flat surfaces leaving a border on the periphery. It is incomplete or open on the funicular side. In a mature seed, the outer integument forms a thick testa, and the inner integument disintegrates completely. The nucellus persists only at the chalazal end in the form of a cup-shaped structure.

A significant ($P < 0.008$) variability in seed size of *A. niloltica* was observed among all the populations. The seeds sampled from population at Anand were larger in size in contrast to the seeds of the population at Bhuj (Table 3). The seeds from other three populations also displayed a significant difference for seed size.

Conclusion

A considerable morphological variation was observed in five populations of *A. nilotica* sampled from five edaphically different sites. *A. nilotica* populations represented ample phenotypic variation from a wide array of environments. The pattern of morphological variation varies among sites particularly for leaf and stipular spine. Schmid and Weiner (1993) reported that the variability of morphological expressions could be related to their habitat types.

The differentiation of phenotypes may result from local variation of the environment, therefore phenotypic differentiation can be used as an indicative of environmental situations. Thus, those populations that occupy similar habitat might show parallel expressions. *A. nilotica* is an exceedingly variable tree and the characteristic growth forms are attributed to the abundance of foliage (Ali, 1973). Thus it may give an individual a characteristic appearance in the field. The individuals with greater number of compound leaves appeared as expanded trees while those having scanty foliage may have a bushy appearance. *A. nilotica* trees sampled from Junagarh and Bhuj appeared distinct for their shape. The former had well-developed individual trees, while the later exhibited more bushy appearance. *A. nilotica* trees from Bhuj had greater leaf number but did not exhibited extensive growth forms. Therefore, there seems to exist an incoherent pattern between foliage and growth form for these populations. Hence, an inconsistent relationship between foliage abundance and growth forms is in agreement with the observation of Cody (1989), who reported different growth forms in the same species of *A. aneura* sampled from different sites.

The number and size of the spines of *A. nilotica* were significantly higher for population at Gandhinagar and Bhuj as the terrain of this site possessed a marked dissimilarity from the other sites. The site of the population at Nadiad, which receives ample rainfall each year, showed the lowest values for these two attributes. Therefore, considerable modification of spines in population at Gandhinagar seems to provide some means of adaptation to the species in terms of water conservation. *A. nilotica* population at Nadiad also showed altered responses with respect to their habitat and had a few spines, as there is no need for resistance to desiccation. Independent study also demonstrated that the morphology of stipular spine varies in areas, which receives different rate of precipitation (Mahmood et al., 2005).

Floral and fruiting traits appeared to be under genetic control, therefore they are less liable to change (Schmid and Weiner, 1993), while certain character expressions (vegetative) may evolve very quickly in response to the variability of habitat and seems likely to be environmentally controlled. Consequently, variation in relation to different habitat situations can only be observed for the class of expressions, which are more prone to environmental changes. Thus genetically controlled expressions may not show any differentiation despite the variability of the environment (Jasienski et al., 1997). *A. nilotica* populations were not distinguished with respect to their pod morphology and all provenances exhibited similar pattern of differentiation. Although the population at Anand had the shortest pods, it has not shown any significant difference from all other populations. These results are in close agreement to many researchers who regarded fruiting characters as genetically controlled rather than environmentally induced. Therefore no significant variability for this attribute was observed even from contrasting sites. The response of the populations was variable with regard to seed number and size. Seed number and size were significantly different between populations. Although both seed attributes are genetically determined, the responses of populations were significantly variable.

Thompson (1992) reported that while *A. nilotica* is technically suitable for wood-chipping using modern techniques, an analysis concluded that it was uneconomical to harvest the plant commercially. Increases in the growth rates of *A. nilotica* with predicted climate change could alter the balance in favour of some form of economic harvesting, significantly reducing the cost of mechanical control of mature trees. Likewise, increased growth potential could also offer the opportunity of mixing pastoral and agroforestry activities on the same land, mitigating the effects of increasing CO_2 concentrations, or fuelling local bioenergy projects. The large potential for further spread and increased mitigation costs under both current and expected future climate conditions, and the relative ease of preventing further spread, means that this biological invasion may be containable. A crucial element in this response strategy will be adequate public education about the threat posed by *A. nilotica*, its identification and control techniques.

The study suggested that populations of *A. nilotica* are differentiated in relation to the heterogeneity of environment. These populations became adapted to their habitat through the variability of morphological expressions. The morphologically differentiated populations of the species had allowed them to maintain themselves in a wide array of environmental situations enabling *A. nilotica* to occupy ample ecological ranges.

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