Chapter 9

UNUSUAL PHYSIOLOGICAL PROPERTIES OF THE ARID ADAPTED TREE LEGUME PROSOPIS AND THEIR APPLICATIONS IN DEVELOPING COUNTRIES

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Introduction

Despite their traditional outward appearance, the nitrogen fixing trees and shrubs of the genus *Prosopis* possess drought and heat tolerance equivalent to more common “desert type” plants such as the cacti. These trees currently occur in some of the most impoverished and harshest arid ecosystems of the world, *i.e.*, in the African Sahel from Senegal to Somalia, in the Middle Eastern deserts of Yemen, Saudi Arabia, and the Rajasthan desert of India/Pakistan (Pasiecznik et al. 2001). Examples of the various forms in Death Valley, Texas and Haiti are shown in Fig. 9.1A-C.

There are three subfamilies in the family Leguminosae. The Papilionoideae contains the common economically important annual legumes such as beans (*Phaseolus*), soybeans (*Glycine max*), alfalfa (*Medicago sativa*), and a few tree legumes such as black locust (*Robinia*). The most primitive subfamily the Caesalpinioideae contains trees such as redbud (*Cercis*), honey locust (*Gleditsia*), and paloverde (*Parkinsonia* and *Cercidium*; Doyle and Luckow 2003). The subfamily Mimosoideae contains many arid trees such as the genera *Acacia* known for its photos of the African savannas and *Prosopis* which contains the mesquites of North America and the algarrobos of South America. From an economic utility standpoint, the major difference between the *Prosopis* and the *Acacias* is that there are many species of *Prosopis* that produce highly edible pods (with up to 40% sucrose) while almost none of the *Acacias* produce pods edible by humans.

Burkart (1976) described 44 species of *Prosopis* native to four continents (North and South America, Africa, and Asia) and suggested that the species evolved from the primitive *P. africana* species in Gondwanaland some 125 million years ago. Ramírez et al. (1999) examined RAPD profiles of species native to all 4 continents and were able to distinguish the species native to the individual continents (in the 5 sections of the genus) and revealed a molecular marker common to old and new world species. A more recent analysis of evolution in the legume family has suggested that the mimosoids and papilionoids evolved later in the Eocene when there was a land bridge connecting North America and Europe about 54 million years ago (Doyle and Luckow 2003). The hypothesis of Doyle and Luckow (2003) notwithstanding, the presence of well adapted native *Prosopis* in harsh deserts of North South America, Africa, the Middle East and India/Pakistan, and the absence of any Papilionoid genera on all 4 continents, suggests to this author that *Prosopis* is an older and more distinct genus than the others. The small size of the *Prosopis* genome (392 to 490 Mbp) also suggests that it is a primitive species.

One important asset of *Prosopis* that sets it apart from many potential economic plants of arid regions, is the presence of a rich interbreeding gene pool. All of the species have 2n = 28 except for some *P. juliflora* which are 4n (Harris et al. 2003). With the exception of the atypical shrubby *P. strombulifera*, with low gene heterozygosity that spreads by rhizomes
Figure 9.1. Growth-forms of *Prosopis*. *Prosopis glandulosa* var *torreyana* in Death Valley, California that is the hottest location in the Western hemisphere (A). Dense weedy stand of immature *Prosopis glandulosa* var *glandulosa* in Texas, see man for scale (B). Mature specimen of *Prosopis juliflora* in Haiti with the author's daughters (C).
(Hunziker *et al*. 1986) all the species studied to date are self-incompatible (Simpson 1977; Keys and Smith 1994). Bessega *et al*. (2000), using isozyme data, calculated a 15% selfing rate within most economically important North and South American species. Based on cytological grounds, Hunziker *et al*. (1975) proposed natural hybrids for the Argentine species *P. alba* by *P. nigra*, *P. hassleri* by *P. ruscifolia*, and *P. ruscifolia* by *P. alba*. Saidman and Vilardi (1987) using isozymes on the 7 most economically important arboreal species of Argentina stated that they were so close genetically that each of them should be considered a semi-or sub-species and that as a whole these 7 species would be a super-species or syngameon. We also have observed in replicated field trials (Felker *et al*. 1983) that progeny of the thornless South American species *P. alba* growing in proximity to North American species *P. glandulosa* var. *torreyana* were thorny and thornless and had many traits of the North American species. As described below, this rich genetic pool, in combination with the potential for interspecific hybridization, techniques for rooting trees of elite trees in some species, and grafting in almost all the economically important species, makes it possible to clonally propagate superior hybrids.

Probably due to their economic utility, the vast majority of the physiological and genetic studies have been done on members of the Papilionoideae subfamily with the implicit assumption that the physiology of the other genera would not be radically different. However the evolution of common annual legumes such as soybeans, beans, and alfalfa occurred in temperate and/or regions with rainfalls considerably greater than semi-arid regions. In contrast, the evolution of *Acacia* and *Prosopis* occurred in the world’s hottest (Death Valley, California) and lowest rainfall regions (Chilean Atacama Desert) and has lead to vast differences in physiological characters such as heat, drought, and salinity tolerance. For example as will be discussed in detail later, common legume genera such as *Pisum*, *Phaseolus* and *Glycine* very poorly tolerate salinities of 2 to 3 dS m⁻¹ while both *Prosopis* and *Acacia* have been shown to grow in salinities of 45 and 80 dS m⁻¹ respectively. Due to the great energetic cost, N fixation is very sensitive to water stress with nodules abscising or N fixation being greatly reduced even at moderate stress levels. Thus while N fixation in soybeans is reduced to zero at leaf xylem water potentials of −2.8 MPa (Huang *et al*. 1975), N fixation in *Prosopis* proceeds at high rates with xylem water potentials of −3.5 MPa and air temperatures of 45 °C.

**Photosynthesis and water relations**

In the 1970s, Stanford University scientists O. Björkman and H. Mooney setup a mobile laboratory in Death Valley National Monument in California to measure photosynthesis and water relations in phreatophytic plants like *Prosopis* and non phreatophytes such as *Larrea* (Mooney 1977). *Prosopis* is native to Death Valley and has rather extensive distribution in the valley as noted by Mesquite flats on Death Valley maps. This location was chosen as Death Valley is the hottest location in the western hemisphere and is close to being the hottest location on earth. The Greenland
Ranch meteorological station in Death Valley has a mean daily July maximum temperature of 46.6 °C (115.8 °F) and an absolute maximum temperature of 56.7 °C (134 °F) (47 years of record; U.S. Department of Commerce 1964). Here these workers measured photosynthesis in *Prosopis* at air temperatures of 45 °C and leaf water potentials of −4.5 MPa (Mooney et al. 1977). They measured a maximum light saturated photosynthesis rate of 30 mg CO₂/dm²/hr (18 µmol m⁻² s⁻¹) that they stated was among the highest photosynthetic rates for woody plants.

De Soyza et al. (1996) measured water stress and net photosynthesis for the short shrubby *Prosopis glandulosa* on 4 sampling dates on the northern edge of the Chihuahuan desert in New Mexico. Here the mean annual precipitation was 233 mm but unlike Death Valley, the trees did not tap into groundwater. While there were considerable differences between dates and for small and large shrubs, the daily maximum net photosynthesis was greater than 10 µmol m⁻² s⁻¹ and the maximum photosynthesis rate of about 22 µmol m⁻² s⁻¹ occurred for large shrubs at the end of the summer.

On a non-phreatophyte site in Texas with 322 mm annual rainfall, Hansen and Dye (1980) measured water stress and photosynthesis on *Prosopis*. These authors reported that maximum light saturated photosynthesis rates of 19 µmol m⁻² s⁻¹ were associated with xylem water potentials of −3.3 MPa at the beginning of the season and rates of 7.3 µmol m⁻² s⁻¹ were associated with leaf water potentials of −3.7 MPa at the end of the season. These authors stated that *Prosopis* net photosynthesis rate was high compared to reported maximum photosynthetic values for most woody deciduous species of 4.3 to 16 µmol m⁻² s⁻¹. This is particularly impressive given the low annual precipitation and the low xylem water potentials.

Although photosynthesis was not measured, Nilsen et al. (1981) measured leaf water potential, stomatal conductance, and leaf osmotic potential in *Prosopis* in a phreatophytic site in the Sonoran Desert of California where the mean annual rainfall was about 70 mm yr⁻¹ and the absolute July maximum temperatures were about 49 °C (Sharifi et al. 1983). Using daily comparisons of leaf conductance and water potential, they observed that the leaf stomata stayed open until a leaf water potential of about −4.8 MPa was reached.

In a more mesic (662 mm annual rainfall) site in northern Texas, Ansley et al. (1992) compared *Prosopis* water relations under rainout and irrigated conditions. The root systems were containerized to a 2.5 m depth with sheet metal and a plastic vertical barrier. These authors found that, in the treatment without rain or irrigation for 2 months in the summer, the leaf water potential did not go lower than −3.2 MPa. In spite of this lack of water, in the early morning hours the stomatal conductance in rainout treatment was still about 70% of that of the surplus water irrigated treatment.

Flowering and pod production in *Prosopis* is apparently stimulated by stress. Lee and Felker (1992) examined *Prosopis* flower production, pod production, nectar secretion, and xylem water potential in a 450 to 700 mm rainfall gradient over 5 sites in a normal and a dry year. In the wet
From grasslands to alpine environments

An average of 70 mm rainfall per month occurred for the first 6 months of the year which was the period of flowering and fruit production, but in the dry year only an average of 19 mm per month occurred as a mean for the same sites. Averaged over all 5 sites, the dry year produced a lower pre-dawn xylem water potential of \(-1.3\) MPa than the wet year of \(-1.0\) MPa and had greater inflorescence and 3 times greater pod production. In contrast, in drought tolerant strains of faba bean (\textit{Vicia faba}) being grown under semi-arid conditions (350 mm yr\(^{-1}\)) in Australia, the early podding stage was very susceptible to drought stress resulting in 50% reduction in seed yields and a drop in the photosynthetic rate to about 6 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). The well watered control plants had mid-day leaf water potentials less between \(-1.0\) and \(-0.6\) MPa while the stressed plants were in the \(-2.0\) to \(-1.5\) MPa range (Mwanamwenge et al. 1999). These results are not directly comparable since the \(-1.3\) MPa water potentials measured by Lee and Felker (1992) were predawn and would have been much lower at mid-day. Thus we see that \textit{Prosopis} has the interesting physiological trait of having its partitioning into reproductive organs, stimulated, rather than inhibited by drought stress.

In summary, in spite of the fact that many of the measurements on photosynthesis as a function of leaf water potential are 20 years old, the data is impressive. Photosynthesis rates on the order of 10 to 20 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) measured for \textit{Prosopis} are high for mesic woody trees. The photosynthesis and stomatal conductance of \textit{Prosopis} continued until leaf xylem water potentials reached about \(-4.8\) MPa which is unusually low. Even though the \textit{Prosopis} in Death Valley are tapping into permanent underground water sources, it is probable that even if the soil around the root systems of Papilionoid legumes were maintained at field capacity, most of them would not survive under daily maximum temperatures of 46 °C.

Roots and soil relations

Depth of water table

\textit{Prosopis} roots can reach water at extraordinary depths of 53 m (Philips 1963). However, it is probable that these roots do not contribute substantially to the growth of the plants since in a study of \textit{Prosopis} height as a function of ground water in the California desert, Meinzer (1927) found that \textit{Prosopis glandulosa} was 3.6 to 6 m tall when the ground water was 3 m deep but was only 0.6 to 0.9 cm tall when the depth to the groundwater was 14 meters.

\(N\) fixation and cross inoculation in \textit{Prosopis}

Nodulation was first reported for \textit{Prosopis} by Khudairi (1957) for \textit{P. stephaniana} in Iraq, then by Basak and Goyal (1972) in India, and by the Canadian, Bailey (1976), in Texas. Felker and Clark (1980) examined nodulation and nitrogen fixation (acetylene reduction) with a rhizobia strain isolated from a \textit{Prosopis} growing in the greenhouse on soil taken from
under *Prosopis* in the California desert. These authors examined a wide range of *Prosopis* species including the old world *P. africana*, Peruvian *P. pallida*, *P. tamarugo* from the Chilean Atacama salt deserts, *P. kuntzei* which only has photosynthetic stems (no leaves), the commercial *P. alba* and *P. nigra* from Argentina, and various *Prosopis* species from southwestern U.S.A. All of these species were demonstrated to nodulate, reduce acetylene to ethylene, and grow on N free media. However the primitive *P. africana* had the smallest plants, and the lowest N fixation rate. Thus it seemed as if one rhizobia strain probably could cross inoculate all *Prosopis* species. This rhizobia strain was later demonstrated to have exceptional salt tolerance with significant growth in 0.5 M NaCl (Hua et al. 1982).

**Water stress experienced when fixing N**

Due to the high energy cost of breaking the triple bond of atmospheric nitrogen gas to make ammonia, plants in the nitrogen fixing mode have a very high photosynthate requirement. Thus it makes sense that with any kind of stress, the N fixation process is halted to prevent the drain on photosynthate utilization.

In the common bean (*Phaseolus vulgaris*) when water was withheld for 5 or 8 days in greenhouse studies with 24/16 °C day/night temperatures there was a 60% decrease in specific nitrogenase activity (Ramos et al. 2003) and a change in leaf xylem water potential from about −0.9 to −0.5 MPa. In a study on the effect of drought stress on soybeans Huang et al. (1975) found that the acetylene reduction was completely inhibited at a leaf water potential of −2.8 MPa. For cow peas (*Vigna unguiculata*), which is probably the most drought tolerant of the annual legumes, Figueiredo et al. (1998) found that when the plants were grown in a greenhouse with minimum and maximum temperatures of 27 and 35 °C, when the leaf water potential reached −1.1 MPa, the nitrogenase activity declined from 10 µmol per plant per hour to 1 µmol per plant per hour. In contrast, when Felker and Clark (1982) measured *Prosopis* nitrogen fixation rates of 68 µmol per plant per hour in 3-m long soil columns whose tops were close to the roof of the greenhouse in California, the air temperatures ranged from 43 to 47 °C and the leaf water potential from −3.8 to −2.9 MPa. The *Prosopis* N fixation rates in this study compared favorably to values of 40 µmol per plant per hour for soybeans (Thibodeau and Jaworski 1975) and 60 µmol per plant per hour for alder seedlings (Huss-Daniel 1978). Thus not only were the N fixation rates comparable to other plants, but the N fixation occurred at leaf air temperatures and xylem water potentials which would totally inhibit N fixation in other Papilionoid legumes.

**Adaptation to low soil P levels in the field**

It is generally acknowledged that phosphorus is the most important macronutrient for N fixation in legumes and that addition of P fertilizer often stimulates N fixation and protein in the leaves. For arid soils, which are often alkaline, the sodium bicarbonate extraction technique of Olsen
and Sommers (1982) is most often used. For the forage legumes, alfalfa, alsike clover, birdsfoot trefoil, red clover and a grass-legume combination, Olsen soil test values of 0-3, 4-7, 8-11, 12-15, and 16+ mg kg\(^{-1}\) were very limiting, limiting, medium, high and very high, respectively (Dahnke et al. 1992).

In a survey of seven sites in South Texas where Prosopis naturally occurred, Geesing et al. (2000) found that the mean Olsen extractable P level was 4.6 mg kg\(^{-1}\) with a 95% confidence interval of 2.1. In spite of these low soil P levels, the mean N for all sites was 3.34 % with a 95% confidence interval of 0.13. This mean 3.34% N for all sites corresponds to a protein concentration of 20.8% which is substantial for this low level of soil P. Wightman and Felker (1990) examined various soil and leaf nutrients for the same Prosopis alba clone grown on experimental sites with contrasting productivity in south Texas. In spite of the fact that the maximum Olsen bicarbonate extractable P on the high productivity site was only 1.27 mg kg\(^{-1}\) (vs. 2.12 mg kg\(^{-1}\) on the low productivity site), the leaf N on the low productivity site ranged from 2.9 to 3.2% on the low productivity site vs. 3.0 to 4.2% N on the high productivity site (However, 60 kg P ha\(^{-1}\) was side dressed at the time of planting). The old work of Drake and Streckel (1955) may be relevant in understanding how Prosopis can function under such low native soil P levels. These authors found that due to their high cation exchange capacity the root systems of legumes were able to extract calcium from insoluble calcium-phosphorus complexes in the soil, thus effectively solubilizing P. Whatever the mechanism by which Prosopis is able to utilize low P containing soils while maintaining leaf protein concentrations of 20%, it would be valuable to exploit this potential in the field and to conduct further studies to determine the mechanism by which Prosopis functions on such low P concentrations.

\textit{N} fixation in natural stands

In spite of the fact that Prosopis had been demonstrated to nodulate and fix \textit{N} in greenhouse studies, there was doubt that Prosopis actually fixed \textit{N} in field settings since nodules could not be found on the root systems (Martin 1948). An intensive U.S. National Science Foundation study where Prosopis obtained its water from a 3.5- to 5-m deep perched water table on a harsh desert site in California with a mean July maximum temperature of 47 °C and 70 mm annual rainfall (Sharifi et al. 1983), was initiated to resolve this issue of \textit{N} fixation in natural stands. This study used \textit{N} balances and the natural abundance of \(^{15}\text{N}/^{14}\text{N}\) to unequivocally demonstrate that Prosopis fixed a minimum of about 30 kg N ha\(^{-1}\) yr\(^{-1}\) (Rundel et al. 1982; Shearer et al. 1983; Virginia et al. 1984). Rundel et al. (1982) suggested that Prosopis plantations with virtually complete canopy cover (vs. 30% on this site) might be able to achieve \textit{N} fixation rates of 150 kg N ha\(^{-1}\) yr\(^{-1}\). Virginia and Jarrell (1983) found that in the top 30 cm of soil there were 4,400 kg ha\(^{-1}\) more total \textit{N} and 790 kg ha\(^{-1}\) more nitrates under the canopy than outside the canopy (assuming a bulk density of 1.2kg l\(^{-1}\)).
The high N fixation rates in the harsh California site notwithstanding, there was considerable reticence within the scientific community on whether *Prosopis* fixed N in native range settings since nodules could not be located on *Prosopis* in the field. Given the presence of *Prosopis* on approximately 45 million ha of low N and C containing soils in southwestern U.S.A. and northwestern Mexico (Johnson and Mayeux 1990), and the controversy concerning the encroachment of mesquite (*Prosopis glandulosa* var. *glandulosa* and *P. velutina* principally) onto overgrazed ecosystems, resolution of the importance of *Prosopis* to N cycling in these ecosystems was of considerable importance.

Johnson and Mayeux (1990) provided a fundamental breakthrough on this issue when they examined cores from 65 to 400 cm deep from under the canopies of *Prosopis* and found nodules on 19 trees at five locations in the eastern portion of the range of *Prosopis*. While they were unable to find nodules from some individuals on the drier western portion of the range, *Prosopis* seedlings nodulated when grown in soils from almost all of these sites. These authors concluded that:

> honey mesquite must be a significant contributor to the nitrogen budget of range ecosystems in south-western United States and Mexico and the genus *Prosopis* is likely to play an important role on a global scale.

While Johnson and Mayeux (1990) were able to find nodules on most of the trees on their sites, they did not measure N fixation on these rangeland sites. Due to the deep and extensive root systems, neither acetylene reduction nor $^{15}$N enrichment is possible, leaving the only realistic method of assessment being natural abundance $^{15}$N/$^{14}$N methods pioneered by Shearer and Kohl (Shearer et al. 1983). Villagra-López and Felker (1997) attempted to measure N fixation in natural stands as function of P fertilization and silvicultural management practices, and while they did not observe any treatment effect on N fixation in field settings, they made the serendipitous discovery that the percentage of N derived from biological fixation was inversely proportional to tree size ($r^2 = 0.90, p = 0.0001$). This implied that as the trees grew, they built up N under their canopy and then this increased soil N repressed biological N fixation. Geesing et al. (2000) followed up on this hypothesis by measuring nitrogen fixation using natural abundance methods on seven native stands of *Prosopis* each of which contained small, medium, and large trees. These workers found highly significant correlations between tree diameter and increase in soil C, N and P under vs. outside the canopies with maximum increases of 17.7 Mg ha$^{-1}$ C, 4.4 Mg ha$^{-1}$ N, and 13 kg ha$^{-1}$ P. Moreover they reported highly significant negative regressions between percent of N fixed by the trees and the soil nitrate under the canopies. This physiological response confirmed that the trees were in fact fixing N. These authors reemphasized the classic work of Jenny (1940) on the negative relations between mean annual soil temperature and soil N and C. This was important since arid soils, that contain low water and thus have low heat capacities, have the highest soil temperatures and lowest soil N and C of the world’s ecosystems. Possibly these low
soil C and N contents are what has stimulated the world’s arid ecosystems to have evolved such a high frequency of leguminous trees and shrubs of *Acacia* and *Prosopis*.

**Salt tolerance**

The negative impact of salinity on growth of plants in irrigated and non-irrigated areas of the world’s arid regions continues to be a major problem. Within the family Leguminosae, virtually all of the important annual legumes that belong to the subfamily Papilonoideae such as soybeans, beans, peas, and cowpeas are highly salt sensitive and suffer yield reductions from salinities with conductivities as low as 2 to 3 dS m⁻¹ (Richards et al. 1954; Ayers and Westcott 1985). Alfalfa is the most salt tolerant of the commercial legume species showing yield reductions of 50% at salinities of 9.6 dS m⁻¹ (Ayers and Westcott 1985). In contrast, our work (Felker et al. 1981; Rhodes and Felker 1987; Velarde et al. 2003), as well as others (Ahmad et al. 1994; Baker et al. 1995), has shown that some *Prosopis*, especially *P. pallida*, *P. juliflora*, *P. tamarugo*, and *P. alba* have individual plants with rapid growth at seawater salinity or 45 dS m⁻¹ which is nearly 20 times greater than salinities that can be tolerated by annual temperate legumes. Elite *Prosopis* trees with superior growth in these trials have been cloned by rooting of cuttings (Velarde et al. 2003) and established in seed orchards at the Universidad Católica de Santiago del Estero, Argentina.

It is to be noted that in the same subfamily as *Prosopis*, the Mimosoideae, some *Acacias* had 100% survival at 95 dS m⁻¹ which is more than double the salinity of ocean water (Craig et al. 1991). The nitrogen-fixing woody salt tolerant genus *Casuarina* also has individual trees and species that can grow at salinities of 0.55 M NaCl which is equivalent to seawater (El-Lakany and Luard 1982; Ng 1987). Among these woody salt tolerant species, only *Prosopis* has portions that are highly edible and timber suitable for high quality furniture.

Identification and understanding of the mechanism of salt tolerance in *Prosopis* may have relevance to current commercially important legumes. The majority of the molecular work characterizing salt tolerance has been conducted on *Arabidopsis*, salt-water algae, and yeast mutants (Bohnert et al. 1999; Hasegawa et al. 2000). Although Winicov (1998) has reported a transcriptional regulator for gene expression in salt tolerant alfalfa, *Prosopis* is not a halophyte in that it is not able to grow with facility at 40 to 60 dS m⁻¹ or to absorb and then secrete sodium salts on the leaves. As clonal propagation of *Prosopis pallida* by stem cuttings is moderately easy, this could be a useful model system for salt tolerance in the legume family. It would be interesting to search for cDNAs in highly salt tolerant *Prosopis* clones that were not present in the low salt tolerant clones in hopes that this information would be relevant to common annual legumes.
The tantalizing scenario of growing *Prosopis* in coastal deserts with seawater irrigation as originally suggested by Epstein *et al.* (1979) for other plants appears to be in the realm of possibility since (1) a few *P. alba* and *P. pallida* grew at seawater salinity, (2) only very limited selections from the germplasm base have been examined, and (3) other field management techniques (*e.g.*, provision of divalent cations Ca and Mg, P, and critical micronutrients) may alleviate the stress. Due to the pressing human needs in coastal deserts where *P. pallida* is adapted, *i.e.*, Mauritania, Somalia, Ethiopia, Yemen, India, *etc.*, it seems reasonable to extensively collect *P. pallida* with the objective of finding highly salt tolerant clones also possessing good growth rates and palatable sweet pods as reported by Alban *et al.* (2001).

**High pH tolerance**

Moderately alkaline soils, from pH 7.5 to 8.2 are common on rain fed semi-arid regions of western North America where there is a calcareous parent material. Traditional semi-arid crops such as sorghum and cotton can be grown on these soils taking care to correct macronutrient deficiencies such as phosphorus and trace elements such as Fe, Zn and Cu that have limited availability due to insoluble oxides or carbonates. In areas where irrigation mismanagement or where natural lack of drainage is combined with high evaporation rates, soil pH levels may reach 9.0 to 10.4. Virtually none of the commercial crops and only very few highly adapted plant species can survive on soils of these latter pH values.

Vast areas of the highly alkaline types of soils occur in Argentina (Ragonese 1951) and on about 2.5 million ha in India (Singh *et al.* 1989a, b). Installation of tile drainage systems combined with leaching and treatment with gypsum can be used to reclaim these soils, but this is an expensive option. In India the Central Soil Salinity Research Institute (Grewal and Abrol 1986; Singh *et al.* 1988, 1989a, b; Singh 1995, 1996) has been the world leader in using combinations of trees and grasses to reclaim these high-pH soils. *Prosopis juliflora* was able to grow satisfactorily without amendments up to pH 9.0, but these authors found that when the soil pH was 10.4 it was necessary to plant the trees in augerholes with amendments of 3 kg of gypsum and 8 kg of farmyard manure per hole (Singh 1996). Twenty years after such treatments, the initial soil pH of 10.4 decreased to 9.18 under *Eucalyptus tereticornis*, 9.03 under *Acacia nilotica*, 8.67 under *Albizia lebbek*, 8.15 under *Terminalia arjuna*, and 8.03 under *Prosopis juliflora*. In Argentina, where *P. alba* is being used to reclaim these high pH soils, surface applications of elemental sulfur, micronutrients and K increased growth 42% over the untreated control (Velarde *et al.* 2005).

This author is unaware of trials with Papilionoid legumes on soils with pH in the 8.5 to 10.0 range. It seems likely that analogous to the much higher salinity tolerance of *Prosopis* than annual legumes, this genus also possesses greater tolerance to high pH soils.
Figure 9.2. Comparison of shrinkage values of *Prosopis* lumber to other fine lumbers of the world. The corresponding Latin binomials are algarrobo (*Prosopis alba*), black cherry (*Prunus serotina*), walnut (*Junglans nigra*), teak (*Tectonia grandis*), white oak (*Quercus alba*), Honduran mahogany (*Swietenia macrophylla*), and Indian rosewood (*Dalbergia latifolia*). Values for *Prosopis alba* are from Turc and Cutter (1984) and the others from Chudnoff (1984).

**Economically useful traits**

Apart from environmental benefits such as shade, soil improvement and ornamental value, the two main economically useful traits of *Prosopis* are the pods, some of which are high in sugar and highly palatable to humans, and the lumber, which is excellent for flooring and high quality furniture.

Evidently, during evolution with great seasonal changes in moisture availability and thus water content of the conductive tissue, the wood of *Prosopis* developed a very low coefficient of movement with regard to moisture content. The values for *Prosopis alba* and *P. glandulosa* radial and tangential shrinkage of 1.8% and 2.9% (Turc and Cutter 1984) and of 2.2% and 2.6% (Weldon 1986), respectively, are lower than all the woods listed in the compendium of tropical timbers (Chudnoff 1984), including teak (*Tectona grandis*), mahogany (*Swietenia macrophylla*), Indian rosewood (*Dalbergia latifolia*), and Brazilian rosewood (*Dalbergia nigra*; Fig. 9.2). Because low shrinkage values, and near equal radial and tangential shrinkages, are probably the best measure of wood stability, and because wood stability is one of the most important characteristics in furniture manufacture, *Prosopis* technically ranks with the world’s best furni-
ture species. When this stability is combined with the reddish-brown wood color and above average specific gravity (ca. 0.75) and hardness (770 kg cm\(^{-2}\) for \(P. \text{alba}\) and 1,010 kg cm\(^{-2}\) for \(P. \text{glandulosa var. glandulosa}\)), \(Prosopis\) lumber meets all the requisites to be included in the class of the world finest indoor furniture species. A simple computer search using mesquite and lumber as keywords will illustrate the value and variety of \(Prosopis\) wood products. (In this search it will be instructive to note that the economic analyses of \(Prosopis\) plantations for lumber (Felker and Guevara 2003; see discussion below) assumed a value of $800 per cubic meter which is equal to $2 per board ft). Unfortunately in Argentina, virtually none of the furniture is made from kiln dried wood or has finish and style that would be desirable by U.S. consumers. An example of the logs harvested for \(Prosopis\) furniture and of quality furniture by the company Fiorramonte of Santiago del Estero, Argentina is illustrated in Fig. 9.3A, B.

\(Prosopis\) lumber could provide the basis for substantial value-added industries in arid lands that would indirectly contribute to increased food security, which is one of FAO’s major objectives. To gauge the scale of this potential, it is important to note that North Carolina’s wood furniture industry grosses about $4 billion annually. Furthermore, China has increased its wooden furniture exports to the U.S.A. from zero to almost $4 billion in the last 10 years (Buehlmann et al. 2002). The potential economic impact of new sustainable industries grossing even $100 million per year from countries in Sahelian Africa would be enormous.

Sweet \(Prosopis\) pods were an important component in the diets of indigenous people in North America (Felker 1979), South America (D’Antoni and Solbrig 1977), and the early people in India (Mann and Saxena 1980). A comparison of the protein and sugar content of North and South American species was made for plantation grown trees under various irrigation treatments in Riverside, California (Oduol et al. 1986). The mean sugar and protein concentration under wet, medium, and dry irrigation treatments is presented in Table 9.1 and illustrates great diversity in pod characteristics among \(Prosopis\) species. There was a negative correlation between pod sugar and pod protein concentration \((r = -0.63, p = 0.01)\). This is attributable to the fact that the sugar content is located in the mesocarp while the protein is concentrated in the seeds. Thus a thick pod like \(P. \text{nigra}\) will have a high sugar content, while a pod with almost no mesocarp, such as \(P. \text{articulata}\) has very little sugar. Because the seed sizes are similar between species, the mass of protein per pod is approximately the same, but pods with more mesocarp have a lower percentage protein and vice versa. Given \(P. \text{alba}\) pod sugar concentrations of 37%, it is not surprising that flours based on milling the mesocarp portion of the pods have sucrose concentrations of 48 to 59% (Felker et al. 2003). While in the past \(Prosopis\) pods were a major form of sustenance for indigenous people and their livestock, in today’s world economy it will be difficult to compete on a protein basis with soybean supplements or on an energy basis with molasses from sugar-cane. Thus Felker et al. (2003) have proposed that \(Prosopis\) mesocarp flour will have its greatest potential from the spice type flavor and aroma it lends to baked food products.
Figure 9.3. *Prosopis alba* from Argentina. (A) Logs harvested in the Chaco Province to be used for furniture and flooring. (B) Furniture constructed by Fioramonte in Santiago del Estero.
Table 9.1. Concentrations of protein and sugar in the pods of Prosopis species grown in the University of California Riverside Agricultural Experiment Station (Oduol et al. 1986).

<table>
<thead>
<tr>
<th>Species (Accession)</th>
<th>Entire pod sucrose concentration (%)</th>
<th>Entire pod protein concentration (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. nigra 133</td>
<td>37.5 A</td>
<td>10.4 E</td>
</tr>
<tr>
<td>P. alba 137</td>
<td>37.3 A</td>
<td>11.0 E</td>
</tr>
<tr>
<td>P. alba 039</td>
<td>35.0 B</td>
<td>9.6 E</td>
</tr>
<tr>
<td>P. velutina 032</td>
<td>25.7 B</td>
<td>18.6 A</td>
</tr>
<tr>
<td>P. velutina 020</td>
<td>25.7 B</td>
<td>16.7 ABC</td>
</tr>
<tr>
<td>P. sp. 080</td>
<td>25.4 B</td>
<td>16.5 ABC</td>
</tr>
<tr>
<td>P. velutina 025</td>
<td>24.2 B</td>
<td>15.0 BCD</td>
</tr>
<tr>
<td>P. sp. 074</td>
<td>22.2 BC</td>
<td>13.0 D</td>
</tr>
<tr>
<td>P. glandulosa var.</td>
<td>20.1 BC</td>
<td>14.8 CD</td>
</tr>
<tr>
<td>torreyana 001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. glandulosa var.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>glandulosa 028</td>
<td>17.0 C</td>
<td></td>
</tr>
<tr>
<td>P. articulata 016</td>
<td>5.3 D</td>
<td>17.0 AB</td>
</tr>
</tbody>
</table>

*P. sp. 080 and P. sp. 074 were collected from a region between P. velutina in southern Arizona and P. glandulosa var. glandulosa in west Texas and were intermediate in morphological characters between these species. Means followed by the same letter are not significant at *P* < 0.05.

Unfortunately, a considerable percentage of *P. alba* trees in Argentina (Felker et al. 2001), of *P. pallida* trees in Peru (Alban et al. 2002), and virtually all of the *P. juliflora* trees in Haiti, Sahelian Africa, the Middle East, and the Indian subcontinent, have bitter pods that are not edible. Fortunately an intensive search in Yemen has identified one *P. pallida* tree that produced sweet pods (M. Al Nassiri, Director of Agricultural Research, Govt. of Yemen personal communication). This tree should be clonally multiplied and examined in other similar ecosystems. Preliminary evidence in some bitter *P. alba* suggests that saponins maybe responsible for the bitter flavor (G. Fabiani personal communication). From an evolutionary perspective it would be reasonable that plants would have evolved some anti-insect deterrent compound, such as might be provided by saponins, to avoid predation of high sugar content reproductive organs. Thus *Prosopis* utilization/genetic improvement programs must be cognizant of this limitation.
Potential opportunities and liabilities with *Prosopis* genetic improvement programs

When the extraordinary physiological properties described above such as high levels of photosynthesis and nitrogen fixation at temperatures of 45 °C, growth at seawater salinity and soil pH higher than 9, are combined with economically useful characters such as highly palatable pods with 35% sucrose and lumber of low-shrinkage suitable for high quality furniture, it would appear that all of the requisite genetic traits exist within *Prosopis* to meet the ideotype leguminous food crop tree proposed some 25 years ago (Felker and Bandurski 1979). Unfortunately all of the desirable characters do not yet exist within the same genotype.

Virtually all of the *Prosopis* that currently exists outside its native range was introduced by non-scientists and/or technical officers that evidently were impressed with the vigorous growth of *Prosopis* in its native habitat. These selections were not evaluated in replicated trials in the country of origin or destination prior to their release. After the initial release in the new location, the surviving seedlings were the ones that retained defense and survival components to avoid being eaten by wild and domestic stock or from being harvested (principally for fuelwood). Perhaps, this selection process inadvertently resulted in increased thorn size and lack of single erect stems that would be easy to harvest. As an example to support this hypothesis, *P. alba* almost never survives unprotected in wild in Argentina since its thorns are small and its foliage is highly palatable to goats and sheep, while in Sahelian Africa despite the need for forage, very few animals eat the foliage of *P. juliflora* as the leaves are unpalatable and the spines large.

There is a growing, and very legitimate, worldwide concern against the introduction of plants outside their native range which have the potential to become weedy in the new location. The indiscriminate worldwide introduction of *Prosopis* outside its native range without testing has legitimately contributed to this concern. However, it must be realized that the past exchanges were arranged by political functionaries or casual travelers and not by Ph. D. level geneticists under controlled conditions. Due to the pressing needs for plant species that produce food and/or provide raw materials for manufacturing in harsh arid lands, particularly of Africa, Latin America and south Asia, it would seem important to evaluate new *Prosopis* genetic materials. These materials must be evaluated under very controlled quarantine conditions in the country of destination and priority should be given to genetic materials that have improved characteristics in replicated trials in the country of origin. As a minimum safeguard, the following evaluation procedure is suggested: (a) evaluation of a limited number of elite clones or plants (perhaps 6 to 12 entries) that have resulted from previous field trials, to be compared with about 3 families or clones of the local strain; (b) use of about 6 single tree replicates per introduction; (c) with no more than about 90 trees total, this trial would occupy less than 0.5 ha; (d) location of the trial within the confines of a government or university controlled field.
site with limited access; (e) within the controlled field site, use of an animal proof fence around the trial to prevent the pods, containing the seed, from being taken off-site; (f) during the pod production season, weekly collection of all pods; and (g) quantitative measurements of form, growth, pod production pod quality.

After several years of quantitative data collection and a statistical comparison of the characteristics of the proposed new introductions to the existing germplasm, a national level review committee, with assistance from interested international organizations, would be in the position to make a quantitative risk/benefit analysis. At this time a decision could be made to destroy all or some of the introduced material (for instance using basal triclopyr/clopyralid applications), to release some or all of the material to other organizations for additional evaluation, or to continue evaluations with no release.

In spite of the risks involved with genetic improvement in locations where naturalized *Prosopis* has become a weed, or in locations such as Texas, where the existing native genetic material is often considered to be a weed, genetic improvement programs should be considered to: (a) incorporate specific highly desirable characters from known germplasm (such as erect form, lack of spines, highly palatable pods, resistance to extreme edaphic conditions) and (b) to provide the economic incentive with an agroecosystem of improved strains capable of generating the revenues necessary to control the weedy, non-useful ones.

A survey of the major genetic improvement needs for *Prosopis* around the world is presented in Table 9.2. The first region listed is the African Sahel and similar climates of eastern Africa. Here, the introduced *P. juliiflora* is widely distributed and has been among the species most successful in reforestation for dune stabilization in Sudan (Bristow 1996) and Somalia (Zollner 1986), for fuelwood provision in Senegal (Diagne 1996), and for earlier reforestation efforts in the Sudan (El Houri 1986). In spite of the fact that it was used in the majority of CARE’s (www.CARE.org) reforestation efforts in Niger, due to its long spines and aggressive spreading habit it has not been widely appreciated (Butterfield 1996). These negative perceptions have been increasing with the declaration that *Prosopis* is a weed in Sudan and major institutional complaints on its spread in Kenya. Thanks to the recent definitive taxonomic work of Harris et al. (2003) it has been shown that the naturalized species in the African Sahel is not *P. chilensis* (Molina) Stuntz as it was erroneously known in the Sudan, nor the highly valuable, non-weedy *P. pallida*, but *P. juliiflora*. Field work by this author in Yemen has confirmed that *P. juliiflora* is also the species in Yemen, which is thorny, aggressive, and has pods which are not palatable for human food use.

The very important recognition has been made that like the pods of *P. juliiflora* from India, Pakistan, Haiti, etc., the *Prosopis* pods in Sahelian Africa are bitter and not suitable for the myriad of human use applications described for *P. pallida* in Peru (Grados and Cruz 1996) or for *P. alba* in Argentina (Burkart 1976). Given the extreme poverty in these harsh African
countries, it is a tragedy that the pods that are produced so abundantly are, unlike their *P. pallida* and *P. alba* near relatives, not appropriate for human food use.

Thus it would seem appropriate that a major breeding/genetic initiative be made to replace the *P. juliflora* in Sahelian Africa, which is weedy and thorny, with non-palatable pods with types that are erect, have very small thorns, and have pods highly desirable for human food. As noted in the comparison trials in Haiti (Wojtusik *et al.* 1993), Cape Verde (Harris *et al.* 1996) and India (Harsh *et al.* 1996) genotypes in the *P. pallida* genetic pool seem to be able to offer these advantages. After an intensive search for *Prosopis* trees with sweet pods in Yemen, one tree out of 72 was found with sweet non-bitter pods (M. Al Nassiri personal communication) and would seem to be useful for asexual multiplication.

In a 1996 visit to South Africa, this author observed an incredible variety of *Prosopis* imported from North and South America. The short (height not exceeding 3.5 m), shrubby, thorny, multi-stemmed (often more than 3 stems at ground level), *P. velutina* accessions formed impenetrable stands (often more than 1 stem m$^{-2}$) in stream bed washes and was, by all standards, a very important and difficult problem. This particular phenotype had high pod production at early ages (as California pod production trials had demonstrated; Felker *et al.* 1984) that greatly contributed to the weedy spread. Cankers on the stems of the *P. velutina*, similar to that reported for this species by Lesney and Felker (1995) appeared to further stimulate branching and stunt the growth of this phenotype. On the other hand, tall (15 m), single stemmed *Prosopis alba* with trunk diameters exceeding 50 cm, known as tame mesquite were not reported to spread. The South Africans clearly have a serious problem. What can be learned from this experience is that if 3-to 4-year long replicated field trials had been conducted on the imported species in South Africa prior to release, the *P. velutina* accessions would never have been released, while the *P. alba* tame mesquite accessions might have been. The South Africans are legitimately very sensitive about any new introductions. However, perhaps the existing tame non-invasive *Prosopis alba* could be grafted onto the weedy ones in a type of biocontrol. Perhaps new single-stemmed, erect, non-spiny forms *Prosopis* when cultivated for lumber production would be so valuable (Felker and Guevara 2003) that the cost of eradicating the weedy ones could be absorbed by the new enterprise.

*Prosopis cineraria*, a native species to the deserts of India and Pakistan, has been revered in ancient writings in Sanskrit (Mann and Saxena 1980). This species is omnipresent in farmers’ fields in the Thar desert where the soil fertility is increased below its canopy, where all of the leaves of the trees (up to 10 m tall) are annually harvested for livestock food, and where the pods are consumed for human food. *Prosopis juliflora* a faster growing species was introduced to what is currently India and Pakistan in the late 1800s and early 1900s and has been a mixed blessing as it provides critically needed fuelwood and livestock food on arid, saline, and sodic soils (Singh 1996; Varshney 1996). However, its long spines and its aggressive growth-form often bring complaints from farmers.
<table>
<thead>
<tr>
<th>Region</th>
<th>Species</th>
<th>Genetic improvement needs</th>
<th>Source of material</th>
</tr>
</thead>
<tbody>
<tr>
<td>Senegal, Mauritania, Niger, Chad, Burkina Faso, Mali, Sudan, Ethiopia, Somalia, Kenya, Yemen, Saudi Arabia</td>
<td><em>P. juliflora</em></td>
<td>Pods that are edible by humans, greatly reduced spine size, erect form</td>
<td><em>P. pallida</em> clones Ref: a</td>
</tr>
<tr>
<td>Southern Africa</td>
<td><em>P. velutina,</em> <em>P. glandulosa</em></td>
<td>Non invasive, non shrubby, low pod producing, greatly reduced spines</td>
<td></td>
</tr>
<tr>
<td>South Asia</td>
<td><em>P. juliflora</em></td>
<td>Pods that are edible by humans, greatly reduced spine size, erect form</td>
<td><em>P. pallida</em> clones Refs: a, b</td>
</tr>
<tr>
<td></td>
<td><em>P. cineraria</em></td>
<td>Increased pod production and quality</td>
<td>Native material Ref: c</td>
</tr>
<tr>
<td>U.S.A.</td>
<td><em>P. glandulosa</em></td>
<td>More erect form, smaller spines, pods with greater consumer acceptability</td>
<td>Native material Ref: d Cold hardy <em>P. alba</em> selections</td>
</tr>
<tr>
<td>Mexico</td>
<td><em>P. glandulosa,</em> <em>P. laevigata,</em> <em>and related</em></td>
<td>More erect form, faster growth rate, improved pod quality and production</td>
<td>Native material Ref: e</td>
</tr>
<tr>
<td>Haiti</td>
<td><em>P. juliflora</em></td>
<td>Pods edible by humans, Small spines and erect form</td>
<td><em>P. pallida</em> Ref: f</td>
</tr>
<tr>
<td>Peru</td>
<td><em>P. pallida</em></td>
<td>Increased pod size, flavor and production, more rapid growth, resistance to leaf eating insects</td>
<td>Native material</td>
</tr>
<tr>
<td>Argentina</td>
<td><em>P. alba,</em> <em>P. chilensis,</em> <em>P. flexuosa,</em> <em>P. nigra</em></td>
<td>Straight form for lumber rapid growth to achieve high internal rate of returns for plantations to avoid current overharvest resistance to leaf chewing insects and diseases, increased pod size, flavor, and production</td>
<td>Native material Ref: g</td>
</tr>
</tbody>
</table>

Data are from: a) Alban et al. (2002); b) Harsh et al. (1996); c) Central Institute for Arid Horticulture, Kibaner (Pareek) and Central Arid Zone Research Institute, Jodhpur (Harsh); d) Felker and Ohm (2000); e) Frias Hernández personal communication; f) Wojtusik et al. (1993); g) Felker et al. (2001).
Both the Central Arid Zone Research Institute (CAZRI) in Jodhpur and the Central Institute for Arid Horticulture (CIAH), in Bikaner have been involved in genetic improvement of *P. cineraria* for some time (L. N. Harsh, CAZRI, personal communication; O. P. Pareek, CIAH, personal communication). At CIAH in Bikaner, O. P. Pareek has made numerous selections from the wild for pod characters and has had success in asexual propagation of those superior types.

For the introduced species Goel *et al.* (1997) have made selections and asexually propagated superior types of *P. juliflora* for growth rate and form. However, as occurs for this species in Sahelian Africa, Haiti, and Yemen, the pods of this species are not suitable for human food use due to a bitter, non-palatable flavor. Harsh *et al.* (1996) reported on a trial with more than 200 half-sib families of various South American species and found that the Peruvian *P. pallida* had the greatest overall ranking for erect form, lack of spines and growth rate (Fig. 9.4). These researchers (L. N. Harsh personal communication) also developed mini grafting techniques for 2-mm diameter *Prosopis* capable of converting genetically unimproved selections to improved selections by top working of the coppice regrowth. At the time of evaluation the trees had not produced pods, but as this species has highly palatable pods in Peru (Grados and Cruz 1996) it seems likely that some of them would have edible pods. It appears possible to develop selections or clones from the Peruvian germplasm for use in India that are erect, thornless, fast growing and have highly palatable pods. A very significant portion of the 1 billion people in India live in the semi arid and arid zones and have limited access to fuelwood (Fig. 9.5) and food for humans and livestock. Thus any technique, such as development of *P. pallida* germplasm, with potential to increase ease of fuelwood procurement and livestock and human food supplies needs to be vigorously pursued.

Despite the 20 million ha of *Prosopis* in the U.S.A. there has been little effort for genetic improvement. Form is not important for the growing Texas barbecue industry that harvests unmanaged native stands to produce chips and chunks for the nationwide retail market. The growing mesquite furniture and flooring industry often selects tall erect trees from river bottom sites but these elite trees are being rapidly depleted. With the goal to improve germplasm for trees for the growing mesquite furniture industry in Texas, a tall, straight tree contest was organized (Felker and Ohm 2000). The winning tree was straight and 5.3 m to the first branch. Seeds from these trees were used to establish a seed orchard at Texas A&M University-Kingsville.

A series of fast growing *P. alba* clones were selected for fast growth under heat drought conditions for use as biomass for renewable energy (Felker *et al.* 1983) as *Prosopis alba* was much more rapid growing than the native *P. glandulosa* or *P. velutina* and often thornless. One of these clones (B2V50) had a high productivity of 30 Mg ha\(^{-1}\) in the third year’s growth in a non irrigated trial in Texas (Felker *et al.* 1989). Unfortunately
Figure 9.4. Erect three year old *Prosopis pallida* in progeny trials in Jodhpur, India, with Drs. Harsh and Tewari of CAZRI.

Figure 5. Woman with load of *Prosopis juliflora* firewood collected in Jodhpur, India. Note shrubby, frequently harvested *Prosopis* in the background.
as the Texas winters are more severe than in California and Arizona the *P. alba* types were not adaptable to Texas. Ten year old progeny trials of *P. glandulosa* var. *glandulosa* found the mean annual basal diameter growth rate to vary from 1.45 to 1.81 cm yr\(^{-1}\) but these differences were not significant (Duff *et al.* 1994). In recent years, the U.S. private sector has promoted clones of patented and trademarked *Prosopis alba* and *P. glandulosa* for use in the ornamental nursery trade that are reputed to have superior cold tolerance and form for shade and foliage characteristics. The *Prosopis* Hybrid ‘AZT’ Thornless Hybrid Mesquite was developed by Arid Zone Trees (www.aridzonetrees.com), the *Prosopis* hybrid Phoenix was developed by Mountain State Wholesale (www.mswn.com) whose scion wood was from *P. alba* clone B2V50 mentioned above. This author patented *Prosopis alba* ‘Laurie’ (U.S. patent 9,072) and thornless *Prosopis glandulosa* ‘Beth’ (U.S. Patent 9,256).

A recent comparative economic analysis of *Prosopis* plantations in Argentina and the U.S.A. suggested the use of clones that would shorten the rotation age from 24 to 15 years and would increase the internal rate of return from 11.8 to 18.7% (Felker and Guevara 2003). Thus it would seem important to continue the work on clonal propagation of elite trees in the U.S.A.

Despite the enormous range, variety of species, and economic impact of *Prosopis* on the rural, poor areas of Mexico (Rodríguez-Franco and Maldonado-Aguirre 1996) there are no genetic improvement trials reported in the international literature for *Prosopis* in that country. In northern Mexico, extensive harvests continue for local firewood and for charcoal and mesquite floring production for export into the U.S.A. Near the city of Dolores Hidalgo, State of Guanajuato, this author has observed many small carpenter shops making mesquite furniture and trunks of relic *Prosopis* greater than 1 m in diameter in the midst of 7 to 30 cm diameter trees. Omnipresent mesquite doors and windows in older structures in this area attest to the prior presence of large *Prosopis* that no longer exist. Evidently, since the European arrival there has been an intensive harvest of *Prosopis* for firewood, charcoal, furniture doors, and for use in the mines. With no significant plantings, and evidently little investment into natural regeneration/stand management, the *Prosopis* has been overexploited for centuries. This author believes that range-wide germplasm collections for the most important species, replicated, half-sib field trials, followed by multipurpose selection, cloning of elite individuals, and seed orchard establishment are essential to reverse this decline. Given the low land values and growing U.S. demand for mesquite solid wood products, with selected varieties/clones and plantation management, the internal rate of return should be sufficiently high to attract investors into commercial plantings (Felker and Guevara 2003).

In Haiti, the poorest country in the western hemisphere, *Prosopis* has been the major source of energy (Lee *et al.* 1992; Lea 1996). This is due to the charcoal energy base of the country and the fact that unlike many trees, *Prosopis* has almost no mortality after repeated harvest of the coppice
growth. Unfortunately, the native *P. juliflora* has large spines, not so good form, and the pods are not really palatable for human consumption. Thus a range wide collection was made of the Haitian *Prosopis* resource and compared to a broad range of other species and families in a replicated trial (Lee et al. 1992; Wojtusik et al. 1993). Here it was found that Peruvian *Prosopis* (later found to be *P. pallida*; Harris et al. 2003) was erect, thornless, faster growing than the native *P. juliflora*, and probably produced sweet pods edible by humans. However the trials were not carried out long enough to evaluate this possibility. Clones were made of these elite trees (Wojtusik et al. 1993). The same best half-sib families in the Haitian trial were also the best in trials in Cape Verde (Harris et al. 1996) and in the Rajasthan desert in India (Harsh et al. 1996). Thus there is an immediate possibility for rapidly improving the multipurpose resource of this, the poorest country in the western hemisphere, by genetic improvement based on the Peruvian *Prosopis* genetic material. With the recently described multi purpose Peruvian clones that are easily rooted by cuttings (Alban et al. 2002), this should make for rapid progress.

In the northern coastal deserts of Peru, *Prosopis pallida* is highly revered among the local people for production of 35-40% sucrose pods. A significant cottage industry exists in this region for the preparation of a boiled down concentrate from the *Prosopis* pods, not unlike molasses in consistency, known as algarrobina (Grados and Cruz 1996; Bravo et al. 1998). The principal use of the algarrobina is in the preparation of an alcoholic beverage with pisco sour (a grape brandy), milk, and eggs. However, new products are under development based on the aroma and flavor characteristics of the 45% sucrose flour prepared from the pod mesocarp (Felker et al. 2003). While the technical properties of the wood of *P. pallida* are eminently suitable for fine furniture construction (as is done for *P. alba* and *P. glandulosa*) and while *P. pallida* has some of the best form and growth characteristics of all *Prosopis* species (Lee et al. 1992; Felker unpublished observations), this use is unknown in Peru.

A detailed analysis of form, growth rates, pod production and pod flavor on a 10 ha plantation from mixed *P. pallida* seed on the Universidad de Piura campus, Peru, lead to the cloning of 7 individual trees with superior performance (Alban et al. 2002). It is to be noted that in the final selection which was for pod flavor, 70% of the trees with good form, high pod production and fast growth were rejected due to bitter or very bitter pod flavor. Thus it is not surprising that the bitter *Prosopis* in tropical Africa (as described above) was introduced from a source with bitter, non-palatable pods. A seed orchard of the 7 elite trees was established. Casual observations in northern Peru reveal considerable variation in pod flavor, from mildly bitter to very sweet with out a bitter taste, and size, from about 20 to 35 cm in length. To locate trees with greatest potential for human food use applications in genetic improvement trials, a recent competition was sponsored by the Universidad de Piura and some trees were located that produced 40 cm long pods (L. Alban, G. Cruz, and N. Grados personal communication).
Hydroponic greenhouse trials in Argentina found that Peruvian *P. pallida* germplasm was the most promising for individual trees that could grow rapidly at full seawater (Velarde et al. 2003). It would be most useful to conduct new hydroponic screening trials for growth at high salinity using seeds from the 7 elite clones that were selected for form, growth and pod characters. It is fortunate that *P. pallida* is one of the easiest of the *Prosopis* to root from cuttings, and that when placed on a heated mist bench with hormones, over 90% of cuttings from greenhouse-grown stock plants have roots passing out of an 8 cm diameter pots in 3 weeks (Felker unpublished observations).

It is this author’s firm conviction that the *P. pallida* germplasm pool in northern Peru will be crucial in the resolution of the weedy issue in Sahelian Africa, the Middle East, India and Pakistan that is centered around very thorny *P. juliflora* with pods that are not palatable for human food use. The multi-purpose selection methodology used by Alban et al. (2002) for wood and human pod uses will be fundamentally important in this work. The seven multi-purpose *P. pallida* clones selected by Alban et al. (2002) should be a good starting point in genetic improvement efforts that utilize robust, replicated trials comparing naturalized *P. juliflora* with *P. pallida*. Due to the strategic worldwide importance of this Peruvian *P. pallida* germplasm, intensive germplasm collection for economically important characters and subsequent field evaluation to select further improved clones is urgently needed.

Argentina with more than 20 *Prosopis* species is the world center of biodiversity for the genus, but not of the origin. The four arboreal species *P. alba*, *P. chilensis*, *P. flexulosa*, and *P. nigra* that occur from about 24 to 32° S latitude are the most important economically. In contrast to *P. pallida* that suffers significant damage from temperatures of only –3 °C, these species tolerate freeezes of several hours duration with minimum temperatures of –10 °C with minimal damage. The major cash flow (as opposed to environmental benefits from soil improvement, etc.) is from furniture and flooring. Unfortunately the number of *Prosopis* plantations is minimal (probably less than 500 ha in all of Argentina; Government sources of Provinces of Chaco and Santiago del Estero). With more than 100,000 tons of logs recorded by the Provincial Government of the Chaco as harvested annually for furniture, the current situation is not sustainable. Historically, the high sugar content pods were important for indigenous peoples (Burkart 1976). As of 2003, pressed circular cakes from the ground *Prosopis* pods, known as Patay, were commonly sold in bus stations in interior provinces of Santiago del Estero and Tucuman. More refined ground products of the mesocarp as described by Felker et al. (2003), but without the often insect contaminated seeds, were in the process of being developed for export.

Due to the overwhelming rate of harvesting vs. planting, there is an urgent need to make fast growing selections that will have sufficiently high productivities to make plantations economically attractive. Felker and Guevara (2003) calculated that with good plantation management and improved seed, an internal rate of return of 11.8% would be achieved in a
rotation age of 24 years. However, if the annual growth rate of 2.5 cm diameter yr$^{-1}$ obtained by Felker $et$ $al$. (1989) for clonal plantations in Texas could be achieved, the internal rate of return would increase to 22.8%. This would probably be sufficient to stimulate considerable forestry investment without government subsidies and begin to put Prosopis furniture and flooring industries in Argentina on a sustainable basis.

While Cony (1996) has calculated the heritabilities of various growth characteristics of $P$. $f$lexulosa from half-sibling progeny trials, only Felker $et$ $al$. (2001) have made multipurpose selections based on growth, pod production, and pod quality. A clonal seed orchard of these clones has been established at the Universidad Católica de Santiago del Estero and some of the trees have set pods the second year after planting (M. Ewens personal communication).

This author was continually perplexed at the slow growth rates of $P$. alba in Argentina vs. California and Texas, until Ewens of the Universidad Católica de Santiago del Estero more than doubled growth rates of unselected $P$. alba seedlings, to about 3 cm in diameter per year, with weekly applications of insecticides (Ewens personal communication). Evidently in its native habitat, a suite of chewing and sucking insects has co-evolved with $P$. alba that greatly impacts its growth. As weekly insecticide applications are impossible economically, as well as ecologically, resistance to these insects must be found in genetic improvement trials.

In Burkart’s (1976) second monograph of Prosopis, he decried the overharvest of Prosopis and especially the harvest of taller, straighter trees that were leaving inferior genetically material behind to propagate by seeds. Argentina’s economic crisis from 2000 to 2003 has exacerbated the over-harvest of Prosopis with poor cash flow landowners selling trees far below the cost of production.

This author’s opinion is that Argentina needs both basic genetic studies on Prosopis and goal-oriented genetic improvement programs to rapidly achieve improved seeds, grafted seedlings or rooted cuttings that can make plantations sufficiently attractive to reverse the over harvest of native stands. It is important that the basic genetic studies include full-sib interspecific crosses, such as between $P$. alba and $P$. nigra so that the genetics of important characters such as the leaf insect resistance in $P$. nigra (but not $P$. alba), the stem boring resistance in $P$. alba (but not $P$. nigra), form and pod flavor traits can be mapped.

Genetics, new clones, and asexual reproduction

There is a critical need for some form of economically viable asexual propagation within Prosopis due to the high variability resulting from its self incompatible breeding mechanism. Due to this breeding mechanism, a “plus tree” in the forest will have at least as much genetic variation as an F1 seedling. Thus seeds from these superior “plus” trees will have at least as much variability as F2 seedlings. This variation manifests itself in the 2-to 3-fold range in the 95% confidence intervals for biomass production within
half-sib families of *Prosopis* (Felker *et al.* 2001). Despite numerous attempts, there is no report of a tissue culture system for *Prosopis* with shoot subculture and subsequent multiplication from explants of field grown trees. Rooting of cuttings techniques have been reported for *Prosopis* (Leakey *et al.* 1984; Klass *et al.* 1990) but really are only viable for large scale plantations in *Prosopis pallida* and *P. juliflora* due to the much easier rooting in these species (Alban *et al.* 2002). Techniques have been developed to graft North and South American *Prosopis* species using moderately sized rootstock (Wojtusik and Felker 1993). Following the suggestion of L.N. Harsh in Jodhpur, India, we reexamined mini grafting of *Prosopis* and found that we could reliably graft 35-day old, 2-mm diameter seedlings of *P. alba* with about 75% success (Ewens and Felker 2003). At this time this is the only commercially viable method to asexually reproduce *P. alba* clones. Unfortunately, this eliminates the possibility of asexually propagating salt tolerant rootstock. However some research suggests that by continually regrafting the desired scions on young rootstock, higher rooting of cutting percentages can be obtained. Due to this constraint, separate clonal seed orchards have been established for highly salt tolerant and for multipurpose *P. alba* clones in Argentina (M. Ewens personal communication) and for multipurpose *P. pallida* clones in Piura, Peru. Hopefully due to the self incompatible nature of these clones, the resulting hybrid seed will be mixtures of both elite male and female parents.

**Potential for combining economic development and management of the weediness**

With the combination of nitrogen fixation, economically valuable products, heat-, drought-, salinity-tolerance, and genetic diversity, *Prosopis* offers an unparalleled opportunity for arid lands. Unfortunately, these properties, in combination with non-holistic management, also have led to weediness. While some genetic combinations in *Prosopis* have led to very weedy strains, there is no reason why the ideotype of a deep rooted N fixing tree with edible pods that is resistant to extreme temperatures and edaphic conditions is not a useful goal for arid lands.

It is important to mention three important ecological factors that influence this weediness (a) the role of *Prosopis* in the N cycle of overgrazed ecosystems; (b) the dynamics of forest stand population/automortality/stem diameter relationships in forest succession; and (c) the natural tendency for some species to be much less weedy than others.

From a steady state assessment of N fluxes in arid ecosystems, Felker (1998) and Geesing *et al.* (2000) noted that current livestock stocking rates were equal to the equilibrium point where the N inputs and outputs balanced. Further, this stocking rate was about 10-fold lower than could be supported on the basis of transpiration water use efficiency for C$_3$ or C$_4$ plants. The nearly 50% ecosystem loss of the N ingested by herbivores, due to volatilization from urine and feces, was suggested to be the major N loss to the system and the major steady state constraint to sustainable livestock.
production. Moreover this 50% elimination of the aboveground N in the ecosystem with each grazing cycle was probably a major contributor in the conversion of grasslands to the encroachment of N fixing Prosopis on arid ecosystems (Felker 1998). The management of multiple use, semi-arid ecosystems should recognize the drain on the ecosystem from volatilization of excreted N from grazing animals and incorporate tree legumes to balance N input/output ratios.

It is important to understand the relationships between tree spacing and stem diameter that occur as recently colonized dense stands of most tree species mature. Both hardwood and conifer stands may initially occur as closely spaced (< 1m) small trees (< 2m tall) on recently colonized sites. However as natural mortality or self thinning occurs, the stands thin-out and the trees achieve the large diameters and heights typical of commercially harvestable forests. When the stands mature and reach large diameters, very rarely do dense stands of small trees reoccur beneath their canopies. This type of self thinning control strategy has been proposed for Prosopis (Felker et al. 1990) to help in both achieving desirable diameters for lumber production and in preventing the re-encroachment of dense stands impenetrable to livestock or humans.

There is no doubt that some Prosopis species are much more weedy than others. For example P. ruscifolia in Argentina, P. glandulosa and P. velutina in some parts of southwestern U.S.A., and P. juliflora in some areas of the arid tropics have many undesirable characteristics and stands. As mentioned above, fungal pathogens that further stimulated multiple low branching in P. velutina in South Africa have made this species worse than this author has viewed in its native habitat. On the other hand P. alba which is in danger of being over harvested for lumber, has small thorns, leaves that are highly palatable to domestic stock and wildlife, and in its native Argentina is almost never found in open rangeland unprotected from livestock. Thus in addition to ecological considerations of N cycling and self thinning, genetics plays a role in the Prosopis weedy issue.

Typical net returns from arid lands are so low (ca. $5 ha⁻¹ yr⁻¹; Felker and Guevara 2003) that it is difficult to finance expenditures necessary for out-of-control, weedy dense Prosopis stands. Felker and Guevara (2003) made a comparison of the rate of internal return provided by various Prosopis products (logs, lumber, pods), wildlife and grazing. These authors found that the only scenario that could provide an internal rate of return sufficiently high to attract commercial investors (ca. 10%) was that of growing trees for furniture quality Prosopis lumber that is currently valued about $850 m⁻³ ($2 board ft⁻¹). As the trees in this analysis were on 10 m by 10 m spacings, this scenario would be compatible with cattle, wildlife, and intercropping (in the first few years) and also prevent the encroachment of weedy stands. Thus it would seem important to include a lumber component in these ecosystems (1) to provide an attractive return on the investment, (2) to provide the financial means to convert weedy stands to a productive system, and (3) to provide an economically sustainable agricultural ecosystem on wide spacings compatible with multiple uses such as grazing and wildlife.
Conclusions

A comparison between the common Papilionoid cultivated legumes, such as soybeans, beans, cowpeas, and alfalfa and *Prosopis* from the Mimosoideae, reveals nearly an order of magnitude greater resistance in most of the fundamental physiological processes related to heat/drought and salinity in the latter genus. As noted above photosynthetic rates of 18 µmol m$^{-2}$ s$^{-1}$ at 45 °C, with leaf water potentials of –4.5 MPa, the ability to fix nitrogen at leaf air temperatures of 43 °C and water potentials of –3.8 MPa, the ability to grow in seawater 45 dS m$^{-1}$ and at pH values of 10.4, all place *Prosopis* in a class apart from the Papilionoid legumes. The small size of its diploid genome (392 to 490 Mbp) and the ability to make wide interspecific crosses would facilitate the mapping of these traits and the possible utilization in more common annual legumes.

Perhaps no other species has the potential to create economic development in the most poverty stricken, and environmentally difficult areas of Sahelian Africa, the middle East and the deserts of India and Pakistan. These areas are characterized by daily summer maximum temperatures of approximately 42 °C, some with 6-month-long dry seasons, yearly potential evapotranspiration of about 2,000 mm and rainfalls less than 500 mm per year. In these areas *Prosopis* can grow and reproduce if there are favorable microsites, such as water courses, or permanent underground water that is within 4 m of the soil surface. As of this writing, *P. juliflora* has become naturalized to all of these areas where it is sometimes perceived as a weed. Thus there is no doubt as to its adaptability.

Unfortunately, unlike some of the North and South American *Prosopis* that have highly palatable sweet pods, through all this range the introduced naturalized species have pods that are not palatable for human use. Genetic improvement trials in Haiti, Cape Verde, and India found the same half-sibling families of Peruvian *Prosopis* to be more erect, faster growing, with much less thorniness than the naturalized *P. juliflora*. Recent trials in Peru found that less than 30% of the trees had pods that could be classified as sweet or very sweet, while the remaining 70% of the trees were classified as bitter or very bitter.

No other gene pool in the plant kingdom possesses the combination of:

1. Genes for heat, drought, high pH, and salinity stress to permit routine active physiological functioning of critical processes such as photosynthesis and nitrogen fixation at temperatures higher than 40 °C typical of the African Sahel, India, etc.

2. Many interbreeding species native to two continents capable of providing the reservoir of genes for disease and pest resistance.

3. Economically useful traits such as highly edible, high sugar pods, and highly dimensionally stable lumber suitable for fine furniture.

The presence of unselected weedy species of this genus should not prevent scientists from taking a broad perspective of this genus to examine the potential of using these genes in conventional legumes and in deliberately creating, testing and clonally multiplying elite individuals for the world’s harshest arid ecosystems.
Acknowledgements

The financial support of the Universidad Católica de Santiago del Estero, while the author was in Argentina, was gratefully appreciated.

Literature cited


