Forest Ecology and Management, 59 (1993) 329–340
Elsevier Science Publishers B.V., Amsterdam

Interspecific graft incompatibility in *Prosopis*

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(Accepted 18 November 1992)

Abstract

Tree species in the genus *Prosopis* have been recognized as valuable for reforestation in the world's semi-arid regions. Self-incompatibility and the mandatory outcrossing of *Prosopis* species results in a high degree of genetic variability, resulting in a need for asexual propagation of trees with desirable characteristics. Five species from *Prosopis* section *Algarobia* (*Prosopis articulata, Prosopis chilensis, Prosopis juliflora, Prosopis glandulosa* var. *torreyana* and *Prosopis alba*) and one species from the section *Strombocarpa* (*Prosopis tamarugo*) were reciprocally grafted to each other to determine their graft compatibility. All species from *Prosopis* section *Algarobia* were graft compatible with each other. Graft compatibility barriers apparently exist between *P. tamarugo* from the section *Strombocarpa* and the species from section *Algarobia*. A simple and effective method for grafting *Prosopis* has been identified.

Introduction

The need for effective means of reforestation in the semi-arid regions of the world is acute. The demand for wood and charcoal has caused the destruction of natural forests and vegetative cover. Fuel wood and charcoal satisfy much of the energy needs in under-developed countries (Eckholm, 1975; De Troyer, 1986). Many reforestation programs have been attempted in the semi-arid regions of the world but the success of these programs has been far below what was expected (Weber, 1982; The World Bank, 1985).

Seedling establishment in semi-arid regions is difficult due to low moisture, high winds, infertile soil, dangers of livestock grazing, and thievery. In many of these locations weedy, unimproved *Prosopis* exist that could serve as root-stock onto which superior genetic material could be grafted, thus avoiding the difficulties associated with seedling establishment.

Prosopis species are well suited to the purpose of semi-arid land reforesta-

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tion. Drought tolerance and nitrogen-fixing rhizobial associations give these species the ability to survive where others cannot. The wood is hard and dense, with a high caloric value when burned (Felker, 1991) and trees are able to resprout after being harvested.

There is a large amount of phenotypic variation of morphological characteristics within the species of the genus *Prosopis*, at least partially a result of their self-incompatibility (Simpson, 1977; Hunziker et al., 1986). For example, *Prosopis alba* (Accession 0285) had a range of dry weight production per tree of 0.1–56.3 kg for 2-year-old trees (Felker et al., 1983) and *Prosopis* seed pods varied from 10 to 17% protein and 10 to 44% sugar (Oduol et al., 1986). There are also spineless and spiny varieties in the same species. This high degree of variability suggests a need for asexual propagation. *Prosopis* has been asexually propagated by rooting cuttings (Felker and Clark, 1981; Klass et al., 1985; Leakey et al., 1990), air-layering (Solanki et al., 1986) and tissue culture (Goyal and Arya, 1984).

Grafting would appear to be a useful complement to rooting cuttings for several reasons. The precise control of light and other environmental factors necessary for producing rooted cuttings of *Prosopis* (Klass et al., 1985; Arce and Balboa, 1991) may make it impractical in developing countries. There has been speculation that root systems of cuttings may not be as good as those of seed-grown stock because of the lack of a strong taproot. It has been our experience that less than 1% of cuttings root from mature, elite field trees as opposed to 70–100% rooting from the same clones when aggressively managed in a greenhouse. Arce and Balboa (1991) have also encountered difficulty in rooting cuttings from mature field trees. Thus, there is a major rate-limiting step in the genetic improvement process due to the difficulty in quickly obtaining large numbers of asexual propagules from mature field trees.

The grafting of *Prosopis* has not yet been extensively explored. Our purpose was first to identify the most useful types of grafts for *Prosopis*, and second to examine the genetic barriers to grafting within the genus. The genus has Asian, African and New World species. The New World species are divided into several sections, the larger of which are further divided into series (Burkart, 1976). We chose the most diverse species available to us to examine their graft compatibility. Unfortunately, we did not have the Asian *Prosopis cineraria* to serve as stock plants. Within the series *Chilensis*, section *Algarobia*, we compared the Chilean/Argentinian species *P. alba* and *Prosopis chilensis* to North American species *Prosopis glandulosa* and the truly tropical species *Prosopis juliflora*. Also examined was *Prosopis articulata* from Series *Pallidae*, section *Algarobia*, from Baja, Mexico. Since there was only a limited amount of stock plants of *Prosopis tamarugo*, Series *Cavenicarpae*, section *Strombocarpa* available, we decided to examine the compatibility of *P. tamarugo* with *P. glandulosa*, a North American species, and *P. alba*, a South American species.

Materials and methods

The *Prosopis* trees were about 5 years old and were grown in 19-l plastic pots in a greenhouse, whose temperature ranged from 27 to 35 °C. The plants were watered daily by a drip-irrigation system. The stock plants used for scions and rootstock were actively growing during these experiments. The *P. alba* trees used were all B_2V_{50} clones of a high biomass producing individual tree from Imperial Valley, California, USA (Felker et al., 1983). Three accessions of *P. articulata* originally from Verde Bay in Baja, Mexico were used. Accession 0593 was grown from the seed of a high biomass producing *P. articulata* (0016) tree in Imperial Valley, California. *Prosopis articulata* Accessions 1142 and 1143 were cloned from a high biomass producing tree of Accession 0593. The *P. chilensis* Accessions 1150, 1152, 1153, 1154, 1160 and 1165 were selected from individual trees of *P. chilensis* Accession 0009 that grew in the same salinity as seawater (3.2% NaCl) (Rhodes and Felker, 1987). The original *P. chilensis* seed source was Buenos Aires, Argentina. *Prosopis glandulosa* var. *torreyana* Accessions 0199 and 0301 were from a cold hardy individual tree from Needles, California (USA), and from Warner Springs, California (USA), respectively (Felker et al., 1981). *Prosopis juliflora* Accessions 1129 and 1130 were from Petrolina, Brazil. *Prosopis juliflora* Accessions 1179 and 1184 were selected from individual trees of Accession 0044 from Ross-Bethio, Senegal that survived 3.2% NaCl for 6 weeks. The three *P. tamarugo* trees (Accession 0317) were from La Huayca, in Region I of Chile.

A preliminary experiment was conducted to determine the best type of grafting for *Prosopis*. One *P. alba* clone B_2V_{50} was used as scion and rootstock for each graft. We examined T-budding, whip and tongue, cleft and a modification of side-veneer graft types as described by Hartmann et al. (1990). Each of the four graft types was randomly assigned to a different stem on the same stock plant on nine separate occasions with nine different stock plants, for a total of 36 grafts. Percentage survival was based on the number of living scions for each graft type after 6 weeks of growth.

Stems of *P. alba* B_2V_{50} stock plants ranging in diameter from 0.4 to 0.8 cm were used as rootstocks. Scions with diameters equal to or smaller than their corresponding rootstocks were also cut from *P. alba* B_2V_{50} stock plants.

Single-edged razor blades were used for cutting the plant material. An individual blade was used for no more than two grafts to ensure sharpness. The completed graft unions and the scions were wrapped with stretchable, non-adhesive grafting tape (outdoor vinyl, 0.1 mm×12.7 mm) from Forestry Suppliers Inc., Jackson, Mississippi. They were left covered for 21 days after grafting to prevent desiccation. All subsequent grafts were made and wrapped in the same manner.

Three weeks after grafting the tape was removed and the condition of the graft union and the scion inspected. Subsequent inspections of each graft were also made 4, 5, and 6 weeks after grafting.

Two experiments with split-plot designs were conducted to determine interspecific graft compatibility. The overall design had stock plants 'nested' within rootstock species (whole plot), and scions randomly assigned to rootstocks (subplot). It was necessary to do two experiments since there was an uneven number of stock plants.

In the first experiment the species *P. alba, P. articulata, P. chilensis, P. glandulosa* var. *torreyana* and *P. juliflora* were examined with each species serving both as scion and rootstock. Each tree had five scions randomly assigned to separate stems approximately 0.5 cm in diameter, one from each of the other four species and one from the same species. There were six stock plants of each species serving as rootstocks for a total of 30 trees and 150 grafts.

Since there were only three *P. tamarugo* stock plants available, a second experiment was conducted to compare the graft compatibility of *P. alba, P. glandulosa* var. *torreyana* and *P. tamarugo. Prosopis alba* and *P. glandulosa* var. *torreyana* were chosen because they represent examples of South American and North American *Algarobia* species, respectively. As in the first experiment, each tree had three scions randomly assigned to separate stems approximately 0.5 cm in diameter, one from each of the other two species and one from the same species. There were three stock plants of each species serving as rootstocks for a total of nine trees and 27 grafts.

The cleft graft method described by Hartmann et al. (1990) was used for all inter-species grafting (Fig. 1). Budwood was used immediately after being

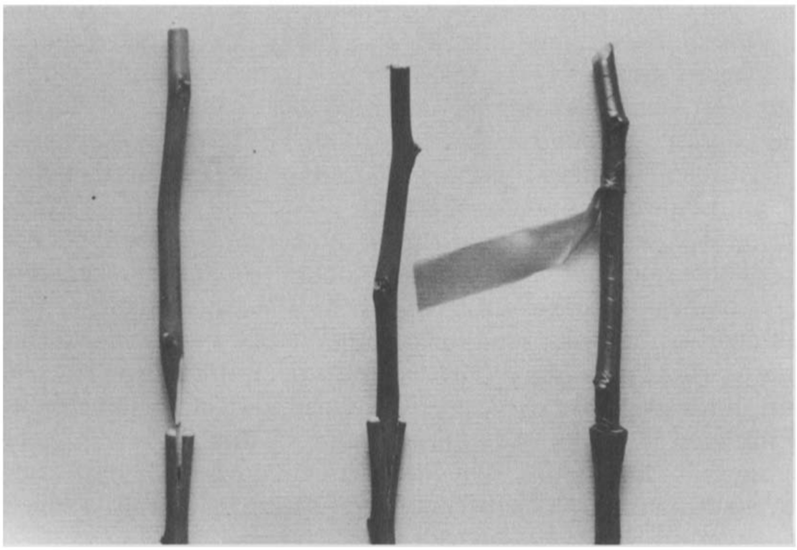

Fig. 1. Stages of cleft graph shown from left to right.

cut from the parent plant or stored in a towel soaked in distilled water. Budwood that was not used within an hour of being cut from the parent plant was discarded.

The grafting tape was either removed 21 days after grafting or earlier if the buds of the scion began to grow. Weekly measurements of scion shoot growth were made for 8 weeks following grafting. After the final growth measurements were made, the scion material was cut from the rootstock just above the graft union and weighed.

These interspecific grafting procedures were conducted from 5 April to 7 April, and from 20 September to 22 September 1991. Harvest measurements were made on 2 June and 18 November 1991, respectively.

Results

In the preliminary experiment the T-bud graft type was 0% successful, the side-veneer graft type 47% successful, and both the cleft and whip and tongue graft types were 67% successful.

Duncan's multiple range test showed that only the T-bud graft type had a significantly ($P<0.05$) different percent of success than the other three methods. Even though the whip and tongue and the cleft methods proved equally successful for grafting *Prosopis*, the cleft method was chosen for all

Table 1
Analysis of variance of graft survival and scion fresh weight for inter-species grafting of *Algarobia* species: *P. alba, P. articulata, P. chilensis, P. glandulosa* var. *torreyana* and *P. juliflora*

Source	DF	Survival (%)		Fresh weight (g) of scion	
		MS	*P*	MS	*P*
Rootstock	4	0.19	0.229	6010	0.001
Tree (rootstock)[1]	25	0.12		162	
Time	1	2.45	0.001	9	0.860
Time × rootstock	4	0.097	0.576	1376	0.005
Time × tree (rootstock)[2]	25	0.13		282	
Scion	4	0.36	0.003	2695	0.001
Time × scion	4	0.34	0.005	2803	0.001
Rootstock × scion	16	0.07	0.656	308	0.514
Time × rootstock × scion	16	0.16	0.028	176	0.921
Error[3]	200	0.09		324	

[1]Error term for *F*-test for rootstock effect.
[2]Error term for *F*-tests for time effect and time × rootstock interaction.
[3]Error term for all *F*-tests involving scion.

Table 2
Survival and mean fresh weight results for *Prosopis* section *Algarobia* species graft combinations. Values are based on 12 replications of each combination that are pooled results from the spring and fall experiment

Rootstock	Scions				
	P.alba	*P. articulata*	*P. chilensis*	*P. glandulosa*	*P. juliflora*
P. alba					
% Survival	92	83	100	100	75
MFRWT[1] (g) (SD)	46.5 (12.0)	28.7 (6.7)	44.2 (6.7)	19.3 (4.4)	41.1 (8.7)
P. articulata					
% Survival	100	83	75	100	75
MFRWT (g) (SD)	13.8 (1.9)	11.4 (2.5)	17.0 (3.9)	12.8 (4.3)	21.6 (4.5)
P. chilensis					
% Survival	100	100	92	92	83
MFRWT (g) (SD)	35.3 (3.4)	21.0 (4.2)	33.1 (8.8)	12.4 (2.7)	39.3 (9.2)
P. glandulosa					
% Survival	83	83	67	92	67
MFRWT (g) SD)	18.2 (4.1)	12.8 (2.7)	13.5 (3.7)	9.7 (1.9)	19.6 (4.9)
P. juliflora					
% Survival	100	92	75	83	83
MFRWT (g) SD)	14.6 (2.9)	16.1 (4.5)	12.0 (3.3)	4.3 (0.9)	20.8 (4.9)

[1]MFRWT, mean fresh weight.
[2]SD, standard deviation.

subsequent grafting due to the relative ease with which it can be made and the uniformity that can be achieved with large numbers of grafts.

An analysis of variance of inter-species grafting within section *Algarobia* (Table 1) revealed a significant ($P<0.05$) effect of rootstock species on scion fresh weight, but no significant effect on scion survival. The scion species had a significant ($P<0.05$) effect on both scion fresh weight and survival. However, there was a significant ($P<0.05$) interaction between both scion and rootstock species, and time, for scion fresh weight. There was also a significant ($P<0.05$) interaction between time and scion species for survival (Table 1).

In the interspecific graft compatibility experiment, high percentages of graft survival were observed for all possible scion/rootstock combinations for the five *Prosopis* species within section *Algarobia* (Table 2). The lowest survival rate was 67% for the scion/rootstock combinations of *P. chilensis/P. glandulosa* var. *torreyana* and *P. juliflora/P. glandulosa* var. *torreyana*. Of the 25 possible species combinations, 76% had better than 80% survival and 28% of the combinations had 100% survival.

Scions of *P. alba, P. chilensis*, and *P. juliflora* grafted onto *P. alba* and *P. chilensis* rootstocks had a faster growth rate than scions grafted onto the other three species and produced up to twice the fresh weight.

There were sizable differences between scion fresh weights resulting from scion/rootstock species interaction. In the 2 month growth period, scions of *P. juliflora* grafted onto *P. alba* and *P. chilensis* rootstocks developed roughly twice the fresh weight as they did when grafted onto rootstocks of *P. articulata, P. glandulosa* var. *torreyana*, or even *P. juliflora* itself. This seems to be the tendency for all five species of scions grafted onto these rootstock species. In general, scions of a given species developed the greatest fresh weights when grafted onto *P. alba* rootstocks, closely followed by *P. chilensis* rootstocks, with *P. articulata, P. glandulosa* var. *torreyana*, and *P. juliflora* rootstocks resulting in variable, lesser weights.

Statistical analysis of the *P. alba/P. glandulosa* var. *torreyana/P. tamarugo* interspecific grafting results revealed a significant ($P<0.05$) effect of both scion and rootstock species on both scion fresh weight and survival. However, there was a significant ($P<0.05$) interaction between scion and rootstock species and time for survival, and a significant ($P<0.05$) interaction between rootstock species and time for scion fresh weight (Table 3).

Table 3

Analysis of variance of graft survival and scion fresh weight for inter-species grafting of *P. alba, P. glandulosa* var. *torreyana* and *P. tamarugo*. The death of a *P. glandulosa* var. *torreyana* rootstock plant during the fall replication resulted in an unbalanced data set

Source	DF	Survival (%)		Fresh weight (g) of scion	
		MS	*P*	MS	*P*
Rootstock	2	1.15	0.001	2554	0.014
Tree (rootstock)[1]	6	0.02		269	
Time	1	0.27	0.017	352	0.018
Time × rootstock	2	0.28	0.011	581	0.004
Time × tree (rootstock)[2]	5	0.02		29	
Scion	2	3.40	0.001	2361	0.001
Time × scion	2	0.12	0.009	34	0.622
Rootstock × scion	4	0.34	0.001	897	0.001
Time × rootstock × scion	4	0.13	0.002	99	0.262
Error[3]	22	0.02		70	

[1]Error term for *F*-test for rootstock effect.
[2]Error term for *F*-tests for time effect and time × rootstock interaction.
[3]Error term for all *F*-tests involving scions.

Table 4
Survival and mean fresh weight results for *P. tamarugo, P. alba* and *P. glandulosa* var. *torreyana* graft combinations. Values are based on six replications of each combination that are pooled results from the spring and fall replications

Rootstock	Scions		
	P. alba	*P. glandulosa*	*P. tamarugo*
P. alba			
% Survival	100	100	0
MFRWT[1] (g) (SD)[2]	47.0 (6.1)	24.7 (3.3)	0 (0)
P. glandulosa			
% Survival	100	100	0
MFRWT (g) (SD)	24.2 (6.9)	25.8 (10.0)	0 (0)
P. tamarugo			
% Survival	17	50	0
MFRWT (g) (SD)	0.2 (0.2)	0.3 (0.1)	0 (0)

[1]MFRWT, mean fresh weight.
[2]SD, standard deviation.

In contrast to the high degree of graft compatibility observed for Section *Algarobia* species combinations, combinations which included *P. tamarugo* had little graft survival (Table 4). None of the *P. tamarugo* scions survived, regardless of the rootstock species. Only the *P. glandulosa* var. *torreyana* scions grafted to *P. tamarugo* rootstock in the fall replication survived, but the graft unions were weak and after 8 weeks little scion growth had developed. Leaves formed on the *P. glandulosa* var. *torreyana* scions, but no new shoots developed. Only one of the six *P. alba* scions grafted to *P. tamarugo* rootstock, also in the fall replication, had survived at the end of 8 weeks' growth and it also displayed a weak graft union and little scion growth. In contrast to the low survival with *P. tamarugo*, the scion/rootstock combinations involving the species *P. alba* and *P. glandulosa* var. *torreyana* had 100% graft survival.

Discussion

The 44 species of *Prosopis* occur in North, Central and South America, Asia and Africa. South America has the highest concentration of species and Argentina is the center of greatest species diversity, with about 27 species (Burkart, 1976). It would seem reasonable to expect that more closely related species from the same geographical region would have greater graft compatibility than less closely related species that are geographically isolated.

No significant differences were found between survival rates for all graft combinations of species in the section *Algarobia*. Differences in survival probably resulted from varying conditions of some stock plants and human error in grafting. It is our belief that in a standardized grafting system only minimal losses will be incurred.

Apparently there are no graft compatibility problems between North and South American species of section *Algarobia*. There might be a graft compatibility barrier between *P. tamarugo* and section *Algarobia*. Alternatively, the low success in grafting *P. tamarugo* to other species may be attributable to the low grafting potential of *P. tamarugo* and not necessarily an indication of graft compatibility between species. We were unsuccessful in our attempts to graft *P. tamarugo* scions to any species of rootstock, including *P. tamarugo*. It should be noted that in some species graft incompatibility is expressed many years after a successful graft was made. Thus, it will be necessary to continue to examine graft compatibility as the trees reach maturity.

There appears to be a correlation between these graft compatibility results and sexual hybridization of *Prosopis* species. Interspecific hybridization is frequent between species of *Algarobia* but no known hybrids between *Algarobia* and *Strombocarpa* species have been documented (Hunziker et al., 1986).

Many species of section *Algarobia* are understood to be self-incompatible (Simpson, 1977; Palacios and Bravo, 1981), but their barriers of reproductive isolation are weak and there is wide genetic variation in populations (Hunziker et al., 1986). *Prosopis tamarugo*, on the other hand, has been observed to be self-compatible and populations of the species have low genetic variation (Hunziker et al., 1986). This information suggests a possible genetic explanation for the graft compatibility results. It would be useful to extend the study of graft compatibility to include tree species from the Old World sections *Prosopis* (syn. sect. *Adenopis*) and *Anonychium*, such as *P. cineraria* and *P. africana*.

The variable growth rates of scions on different rootstock species may be due to metabolic differences between rootstock species. Under favorable greenhouse conditions perhaps *P. alba* and *P. chilensis* rootstocks have the advantage over the other rootstocks and can impart the benefits of their higher metabolic rates to the scions grafted onto them, regardless of the species of the scion. There is the possibility that under harsh conditions *P. articulata, P. glandulosa* var. *torreyana* or *P. juliflora* rootstocks would have an advantage over the other rootstock species and fresh weight production of scions grafted onto that advantaged rootstock species would be the greatest.

In the interspecific grafting of *Algarobia* species, the differences in the seasonal growth tendencies of the various species resulted in a time interaction for scion fresh weight data. For instance, *P. alba* scions had consistently higher fresh weight values in the spring replication, regardless of rootstock species. In contrast, *P. juliflora* scions had consistently higher fresh weight values in the fall replication, regardless of rootstock species.

Although the *Algarobia* graft survival percentages were high for the spring replication, they were even higher for the fall replication. Nevertheless, two scion/rootstock graft combinations had lower survival percentages in the fall replication than in the spring replication. These variations resulted in a significant ($P<0.05$) interaction between time and the rootstock and scion species. Improved skill of the grafter can explain the overall graft survival percentage increase and differences in stock plant condition and human error resulted in variations.

The time and rootstock species interaction was significant ($P<0.05$) for both graft survival and scion fresh weight growth in the analysis of variance of the data involving *P. tamarugo*. The time and scion species interaction was significant ($P<0.05$) for graft survival. Seasonal variations in growth of the three species and the *P. glandulosa* var. *torreyana* scions, and the *P. alba* scion that survived on *P. tamarugo* rootstocks in the fall replication, may have resulted in these significant interactions between species and time. Although these four grafts survived they produced almost no new growth and their graft unions were not sound after 8 weeks of growth. The sample size for this second split-plot experiment was small; therefore caution should be exercised in drawing conclusions based on these results.

Criteria could be developed for the selection of species and varieties of *Prosopis* to be used for rootstocks and scions. The criteria for rootstock selection would be based on the planting site while the scion selection would be based on the desired end-product. Climatic considerations are necessary in making both choices.

Prosopis varieties have been identified that are able to tolerate extremes in soil conditions. Rhodes and Felker (1987) identified four accessions, *P. articulata* 0016, *P. juliflora* 0044, *P. nigra/flexuosa* 1012, and *P. alba/nigra* 1117 that were able to survive in water containing 3.3% NaCl, equivalent in salinity to seawater. Singh et al. (1991) grew *P. juliflora* in association with forage grasses in soils with pH 10.4 and 90% exchangeable sodium. These tolerant varieties could be employed as rootstock, onto which material from superior production varieties could be grafted. Such grafting techniques could be utilized to produce trees for reforestation of harsh sites which otherwise have little potential.

When selecting a scion variety, resistance to insects, fungi and other pests must also be considered. For example, *P. alba* has more resistance to psyllid insects than *P. glandulosa* (P. Felker, unpublished observation, 1980). Production of seed pods, forage and wood are the main considerations for scion selection. Oduol et al. (1986) found that seed pods of *Prosopis velutina* (Accession 032) had an average protein content of 18.6% and seed pods of *P. glandulosa* var. *glandulosa* (Accession 028) had an average sugar content of 38.3%. The absence or presence of thorns is a consideration for final choice of variety.

The grafting of *Prosopis* can be used for topworking existing plantations or native stands. This would be especially advantageous since well-adapted, elite individual trees usually exist in plantations. Scions from these elite, proven individual trees could then be used to upgrade the remainder of the plantation. This can be done to increase the production of wood or forage pods in addition to changing the variety to produce superior quality seed pods. One can take advantage of existing rootsystems by grafting onto established trees that are already accustomed to the site. Grafting of new stock onto these root systems should significantly increase early growth and survival over other stand improvement techniques. The tops removed from the existing trees can be used for fuel wood or the production of charcoal.

We have developed a technique for inter-species grafting of *Prosopis* that has proved effective for use with the majority of important *Prosopis* tree species. There were no apparent graft compatibility problems between species in *Prosopis* section *Algarobia*. This technique needs to be evaluated for reforestation in areas where naturalized *Prosopis* exists such as Sudan, Haiti and India. Research is needed to combine exceptional rootstock characteristics of salinity and alkalinity tolerances with fast-growing, thornless, high seed pod producing scion material.

Acknowledgments

The financial assistance of the General Service Foundation, Robert Musser, President, and of the US Agency for International Development Grant no. DAN-5542-G-SS-2099-03 is gratefully acknowledged.

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