Cactus Pear (*Opuntia* spp. Cactaceae) Breeding for Fruit Production

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INTRODUCTION

Cactus pears are members of the Cactaceae family, native to Central Mexico and the Caribbean region. They are reported to belong to *O. albicarpa* s. n., *O. ficus-indica* (L.) Mill, and *O. robusta* Wendl var. *larreyi* (Web.) Bravo (Scheinvar, 1995). It is a perennial plant, characterized by its jointed flattened stem, cylindrical or conical succulent and ephemeral leaves on young stems; the presence of glochids; areoles (the equivalent of a complex buds with glochids and spines arranged in clusters); fruits with thick rinds; and comparatively large seeds covered by hard, bony, light-colored arils (Weniger, 1984). It is reported as polyploid. Cultivated varieties and forms have the highest chromosome number (2n=6x=66 and 2n=8x=88), contrasting with the wild ones, which normally have 2n=2x=22 and 2n=2x=44 (Pinkava et al., 1992; Pimienta, 1995; Munoz et al., 1995).

It is cultivated mainly for its fruits and tender pads, which are consumed as a vegetable. Wild populations are a source of maintenance forage for livestock in dry areas of northern Mexico and Texas. The plant has also been recognized as an important food for several wildlife species, mainly mammalian herbivores and birds (Hellgren, 1994).

Vegetative reproduction based on whole pads or branches is the most common means of propagation. There are no specialized nurseries; cuttings are obtained from productive orchards, selecting from pruning residues.

Mexico and Italy are the main producing countries and consumers. Chile and South Africa as well as Israel have also started planting commercial orchards. In the US, California is the leading state with 300 ha. It has been estimated that there are approximately 59,000 ha worldwide, Mexico accounts for 70% and Italy 3.3% (Inglese et al., 1993; Nobel, 1994).

Reports of the use of cactus pear date back to the ancient groups which inhabited Mesoamerica. Evidence from fossilized human feces indicates that agave and cacti have been part of the human diet for over 9000 years (Nobel 1994). In this regard, Hoffman (1995) reported that gathering activity of fresh as well as dried fruits and early domestication of wild plants could have taken place before 6000 BC.

This paper reviews the background of breeding cactus pear for fruit production. Vegetable and forage production are not addressed here because the information available is limited and its cultivation as a vegetable is less widespread than fruit production.

ORIGIN AND EARLY DEVELOPMENT

This plant was domesticated in Central Mexico where it still represents an important product in the semiarid areas. It is consumed on a regular basis, both as a fresh fruit and as a vegetable. Extensive use of the plant as a perennial crop, current exploitation of wild populations, and its common widespread use as human and animal food support this view.

According to Hoffman (1995), a crucial step was the transition from use as a wild plant to that of the planned cultivation of the *Opuntias*. While some traditionally used species (e.g. *Steneocereus stellatus)* are only now being cultivated, cactus pear has been farmed for thousands of years. They are, together with corn, beans, and agave, the oldest cultivated plants in Mexico.

Cactus pears were brought to Europe by the Spanish conquerors in the late 15^{th} and early 16^{th} centuries. They were attractive due to the unusual morphology and to the importance that the Aztecs attached to the prickly pear in the economic, social, and religious life (Barbera et al., 1992). Later events account for the actual wild populations observed in North Africa, especially the Italian influence on its neighboring countries. The plant spread along the Mediterranean coast as birds ate its fruits, and to North Africa with the Moors' return from Spain. The use of cactus as an antiscurvy food on long ship voyages and the ability of cladodes to easily tolerate long journeys without losing their ability to take root further spread cactus around the world (Barbera, 1995).

The plant moved as far south as Australia. It is reported that in the 17^{th} century a governor of this country envisioned that the cochineal industry would be suitable for the Australian economy. Therefore, he picked up some cacti and insects from Rio de Janeiro and carried them to Australia. Unfortunately, whereas the cactus flourished, the cochineal insect did not, and the industry was a failure. However, cactus pear became one of the worst pests of the country, dominating large areas of grazing land (Baker, 1970). The pest was ultimately controlled by the introduction from Mexico of cactus parasites as a biological control (Dodd, 1949).

The plant evolved as a formal crop in the current century, moving from collection of outstanding wild plants to few selected individuals in the farmers' backyards. The need for drought-resistant species in dry areas, gave it special advantage on governmental drought-relief programs in Mexico, which provided the basis for the first commercial orchards in the 1960s. In Italy it is also found in the driest areas, where it out competes other annual and fruit crops. Modern cultivation of *Opuntia* has also been attempted in both countries on irrigated prime agricultural land with notable success.

GENETIC RESOURCES

The Cultivated Gene Pool

Modern cultivars of cactus pear are the product of selection by growers. The number of cultivars varies according to the intensity of usage and the variability available in each of the countries that grow cactus pear. The most important cultivars have been described by Mondragon and Perez (1993), Pimienta and Munoz (1995), and Mondragon (1996). The names of the varieties reflect some specific peel or flesh features and, in some cases, the response to stress and resistance to handling. Mexico accounts for six or seven popular cultivars, some with white-greenish pulp: 'Reyna', 'Cristalina', 'Esmeralda', 'Chapeada', and 'Burrona'. 'Reyna' sets the standard of quality and is widely accepted at the national level (Mondragon, 1996). With orange pulp: 'Naranjona' and 'Amarilla Montesa'. Finally, the spineless red-purple 'Roja Lisa'. The abundance of less-known accessions available in regional markets with local acceptance is remarkable. Most of them are either grown in small orchards or collected from the wild.

The cultivars available in the Sicilian area of Italy are 'Gialla' (yellow), 'Bianca' (white) and 'Rossa' (red). 'Gialla' is the most abundant in the plantations and is thought to be the most productive, able to be handled, and well liked by consumers (Barbera et al., 1992). A seedless variety is also known but its commercial cultivation has never been attempted because of the poor quality of the fruits.

In Chile a cultivar of *O. ficus-indica* known as 'Verde' (green) (Sudzuki, 1993) or 'Blanca' (white), (Pimienta, 1995) is the most common cultivar. It is consumed in the central dry areas of the country. Exports to the US market have been reported since 1982, taking advantage of the fact that the spring harvest season in the southern hemisphere matches the lowest availability of fresh fruits in the northern hemisphere.

Production in Israel is based mostly on the cultivar known as 'Ofer', which has yellow pulp. In the US, a red cultivar marketed as 'Andy Boy' is currently available in chain stores from November through April. It is produced in California, where the availability of irrigation and the presence of mild winters allow for out-of-season production.

In South Africa, the varieties now present originated from the introduction of 21 spineless types imported from the Burbank nursery of California in 1914. All known types currently grown developed from the original material, either as clones or as artificial or natural hybrids. At present there are three groups of cactus pear types with specific climatic requirements: five types for hot frost-free areas; one for intermediate climatic areas; two types for areas with a cold winter. The most common taxonomic species is *O. ficus-indica* (Pimienta, 1995).

The Wild Gene Pool

Traditionally, cactus pear plantings are found on small family properties in dry regions. *Opuntia* hedges surround whole villages or stand concentrated close to the farmsteads. They also carry out the function of protecting farm families' fruit and vegetable gardens. The individuals present represent the transition from wild plants to types used in modern commercial farming. Their genetic variety means that they are important for guaranteeing the subsistence and for the cultivation of new types of this irreplaceable resource. Therefore, they can be described as mini gene banks (Hoffman, 1995).

The concentration of outstanding accessions in mixed populations in family orchards can provide an interesting source of new individuals, derived by chance from free natural out crossings. Finally, the last reservoir of interesting individuals are the wild populations. Several efforts to collect them have been attempted. Mexico accounts for two or three reliable germplasm banks, with the number of accessions varying from 50 to about 150. Italy and South Africa also have germplasm banks. The US has 130 accessions selected primarily for cold hardiness (Felker, 1995). Considerable exchange has taken place after 1992, when international cooperation formally began, so the numbers mentioned are rather dynamic. However, collecting plant material by relying on common names leads to the existence of duplicated accessions. The likelihood of replicated clones is high in a plant like cactus pear which has only subtle differences, even to the expert's eye. *Opuntias* are also highly plastic plants that react to differences in their environments more quickly and with more drastic growth-form changes than do other cacti. Cladode spininess, and shape and the size of cladodes as well as fruits are a few examples, (Weniger, 1984).

BREEDING OBJECTIVES

The following traits seem to be of considerable importance to breeders: fruit size and seed content. The flesh of the fruit of cactus pear is constituted of tightly packed tiny pieces, with the seeds acting as their core. The enlarged portion corresponds to the funiculus; botanically, the fruit is recognized as a fleshy berry. Every single seed has the capacity to form pulp even if it is not completely developed. Normal, nonfertilized as well as aborted seeds are able to bear flesh. Seeds are intended to be swallowed along with the pulp, a well known fact in the native places of cactus pear, but a barrier to attracting new consumers in the US and other nations. The seed count ranges from 80 to more than 300 (Barbera et al., 1991; Pimienta, 1990), which means from 2.8 to 7.5 grams of seeds per fruit according to the fruit size and the cultivar (Mondragon and Perez, 1995). The ratio between empty and normal seeds is higher in the Italian (0.44) than in the Mexican cultivars (0.11) (Barbera et al., 1992b; Pimienta and Leguizamo, 1989). Seed content is correlated positively with fruit size. In this regard, the ideal fruit should have a large number of seeds to attain good size, but a high ratio of aborted to normal seeds.

These two traits have to be worked out together because large fruits bring a premium price on the market and fruit size is a quality trait. Natural parthenocarpy has been mentioned as a solution to this problem. Vegetative parthenocarpy was reported in BS1, a yellow-fleshed accession native of Israel, a clone of *O. ficus-indica* that bears fruits containing only degenerated seeds, but the fruits are similar in size and color to the yellow fruits of *O. ficus-indica* cultivars. A study conducted to elucidate the mechanism involved in the development of this seedless fruit indicated that BS1 is a vegetative parthenocarpic clone, i.e., pollination is not required for fruit seed and development; however, its overall quality was not acceptable (Weiss et al., 1993; Nerd and Mizrahi, 1994).

There is wide variability for both traits in the actual germplasm. Differences in fruit size are more evident in Mexican accessions, with the green-clear fruits being larger than the South African or Italian ones (Inglese, 1995). The average fruit size of native cultivars of cactus pear ranged from 67 g to 216 g (Mondragon, 1996).

Several attempts have been made to reduce the size of the seeds by applying gibberellin, but with poor results, (Gil and Espinoza, 1980; Aguilar, 1987; Ortiz, 1988). Selection on available germplasm can provide limited results on a short-term basis. Crosses between the accessions having the desired traits is a long-term goal.

Novel Fruit Colors

The most appreciated fruits on the international market are yellow-orange (peel and flesh) and red-purple (Inglese et al., 1993). National markets show specific preferences. In Mexico, green-clear or white cultivars are predominant; Italian and northern European consumers prefer yellow-orange cultivars. In the US, the color of fruits available depends on the season and the exporting country. Clearly, the trend is toward yellow and red cultivars.

In order to appeal to a wider market, new yellow and red cultivars with improved quality (lower seed content) are to be developed. The broad gene pool available insures that it is an accomplishable goal, but not in the short term. Green-clear cultivars also have to be improved in terms of seed content as well.

Cladode Spininess and Glochids in Fruits

Spines and glochids represent modified leaves that help the cactus pear withstand drought. Thus, the most drought-hardy accessions also are most spiny. In regard to crop management, spines represent an inconvenience, especially at harvest time. There are different levels of spininess on cactus pears; density and thorn size vary among accessions. Commercial cultivars in Mexico are spiny (except for 'Roja Lisa'). All other producing countries rely on spineless clones. Efforts to develop new cultivars should be focused on spineless cultivars.

The presence of glochids or spicules (essentially, spine-like hairs) on the fruit is also a constraint to increased consumption. Glochids can be removed after harvest, but technologies must be improved and consumers educated. Eventually, selection and breeding for glochid-free varieties should be encouraged (Barbera, 1995). Another possibility is the induction of early shedding of glochids. Genes for low number of areolas and short glochids are present in *O. robusta*, a species that also is the earliest ripening in the season (available in May in the northern hemisphere). But it has limited acceptance due to its low sugar content and highly water-soluble purple dye in the pulp.

Out-of-Season Production

According to the market trend for fresh fruits, early varieties command a premium price. For the northern hemisphere, any fruit that is ripe at the end of May and June, in general, has no marketing problems. In the southern hemisphere, harvest season is less restricted because it is intended for exports to the northern markets in winter. Actual germplasm is adapted to produce from the end of June to September; the most preferred ones are concentrated in July and August.

Manipulation through fertilization and irrigation as well as plastic covers have been reported to modify harvest season (Barbera, 1993; Nerd et al., 1989). Certainly, a definitive and affordable solution for growers is the availability of new cultivars with the ability to produce out of season, valuable mostly for the northern hemisphere.

High Soluble-Sugar Content

More than 13°Brix (a measure of sugar concentration based on viscosity) total soluble sugars is a desirable level. Actual cultivars have from 13°Brix to 17°Brix. This trait is highly influenced by the environment and crop management. Fruit obtained in dry years or in dry areas are sweeter than those produced in humid conditions. A similar effect has been observed in out-of-season production (Mondragon et al., 1995), late fruits growing in cool temperatures with cloudy days are less tasty than those produced in the hot, sunny days of summer. This is also and important trait for some value-added by-products, such as jams and candies. For some markets fruits with higher acid content were favored in sensory tests (Saenz and Sepulveda, 1990).

Flesh Juiciness

Fruits with juicy pulp are favored over the dry-pulp ones. There are almost all combinations of this trait and flesh color in the available germplasm.

Cold Tolerance

Agronomically important cactus pear are usually irreversibly injured at temperatures of –5°C to –10°C (14°F to 23°F) (Nobel, 1993). Indeed, susceptibility to freezing is the primary factor limiting the expansion of prickly pear as fodder and forage in cattle-producing areas of the US. Reduced water content and accumulation of organic solutes (mucilage, among others) have been mentioned as partially responsible for cold acclimation (Goldstein and Nobel, 1991).

Cold tolerance is an important feature for cactus pear production (fruit as well as forage) in the southern US where freezing temperatures occur from time to time. Germplasm collected in northern Mexico from a few areas in the highlands currently exposed to late frosts and light snow cover are assembled and are being tested in Kingsville, Texas.

Disease and Pest Resistance

A number of pests and diseases afflict cactus pear. So far, the most difficult pests to control are those that thrive inside the cladodes, affecting the inner succulent tissues. However, to date, pruning has proven to be an effective means of control.

In regard to diseases, the accessions of the actual germplasm needs to be screened in search of tolerance or resistance to black soft rot (*Erwinia carotovora*) (Fucikovsky and Luna, 1988), as well as excessive budding and cladode swelling, both of unknown origin. Suspicions of mycoplasmal involvement have been reported in both problems (Pimienta, 1974; Gutierrez, 1992).

Handling and Packing

It has been observed that some cultivars, e.g., 'Cristalina' and 'Burrona', can be handled better than others. Peel thickness, as well as peel toughness, could be involved in improved resistance to handling. In regard to fruit shape, oval or barrel-shaped fruits are easier to harvest than elongated fruits and, therefore, suffer less harvest damage to the stem end (Cantwell, 1991). Higher resistance of the peel to handling (Wessels, 1988), especially on the fruit base, is desirable in order to reduce damage. This is extremely important because cactus pear is harvested by hand and some twisting of the fruit is involved.

BREEDING TECHNIQUES

Floral Structure and Biology

About 90% of the flower buds are on the top story of pads, which normally are six months to one year old. They are present on the crown of the cladode but they can also be on the sides if the first flush is damaged. The reproductive potential varies with species and cultivar. Mature (six to eight years old) well-tended plants of 'Reyna' carry as many as 6 fruits (40 flowers), all of them can reach the ripe phase and produce seeds. Since almost all flower buds set fruits, the number of fruits produced per plant is a function of the number of fertile cladodes and the average number of flower buds per cladode (Pimienta, 1990). Flowering season varies with cultivar and management. Under normal conditions, flowering occurs in March and April in the northern hemisphere and in September and October in the southern hemisphere (Nerd and Mizrahi, 1995).

Budding flushes are spread over several weeks, and plants can bear newly initiated buds, flowers, and young cladodes (Nerd et al., 1989; Wessels and Stuart, 1990) and even ripe fruits at the same time. The plant is able to withstand the loss of the first flush, bearing a new one after 50 to 70 days. This unique feature is used in out-of-season production by employing manual bud removal (scozzolatura).

Many characteristics make the cactus flower unique: a number of perianth segments weakly differentiated as petals, numerous spirally arranged stamens, a pistil of four or more fused carpels enclosed in the floral cup, and a unilocular ovary with parietal placentation that appears to be embedded in the end of a modified branch (Boke, 1980, cited by Sudzuki, 1995). Furthermore, cacti are among the few plants in which the exterior of an inferior ovary, the receptacle, displays leaves and perfect areoles; this structure later becomes the peel of the fruit. Floral differentiation occurs 50 to 60 days after the meristem starts to be active till anthesis. This is in contrast to other temperate-climate fruit trees where floral differentiation occurs the year before. The flower blooms in the daytime, is hermaphroditic and actinomorphic.

According to Pimienta (1990), most flowers open late in the morning (type A); although some open in the afternoon (type B). All flowers close in the evening, marking the end of the anthesis phase in type-A flowers. In type B, anthesis resumes the following morning and the flowers close the final time in the evening. However, it was observed that both types of flowers reopened for an additional day during the morning hours. The flowers of *O. lindheimeri*, a wild species, open for one day; early in the day, the anthers dehisce and expose the yellow pollen (Grant et al., 1979).

Flower color is variable from yellow to reddish. In some green-clear cultivars, such as 'Reyna', flowers of different hues can be present on the same plant. Pollinated flowers fade and present a pink color. They have been reported as self-pollinating (Nerd and Mizrahi, 1994). Bagged flowers are able to set fruit, but once the flower opens, pollination by insects (mainly bees) insures a higher number of seeds. Similar response was reported by (Grant et al., 1979) for *O. lindheimeri*, they also found that bagged flowers alone did not produce fruits. Thus the plants are self-compatible but nonautogamous. The protandry explains the autogamic process (cleistogamy). Sicilian cultivars have been shown to be self-compatible, since problems of fruit-set are seldom encountered in vegetatively propagated plantations composed of a single cultivar or in single plants grown in backyards (Damigella, 1958, cited by Nerd and Mizrahi, 1995).

At the beginning of anthesis the stamens are close to the style and the anthers are in contact with the base of the pistil (Pimienta, 1990). The stamens are thigmotropically sensitive and bend toward the style when touched (Grant et al., 1979). It has been proposed that this nastic response may promote insect, self-, or cross-pollination. Pollen tubes grow rapidly; 24 hours after flower opening they reach the base of the style. The first flower tubes to reach the micropyle of the ovule were observed three days after the flower opening. A high percentage of ovules are viable and most of them are fertilized by the pollen tubes that enter the locule (Rosas and Pimienta, 1986).

The flowers have an inferior ovary that contains numerous ovules. Nerd and Mizrahi (1994) reported that the cultivar 'Ofer' averaged 270 ovules, which are in the outer ovary wall (parietal placentation). The edible tissue develops from the funiculi and the funicular envelopes of the seeds. The peel develops from the receptacular tissue. The fruits contain both viable and aborted seeds and the funicular envelopes of both seed types are equally capable of contributing to the pulp tissue (Pimienta, 1990).

Pollen Collection, Storage, and Testing

Short-term storage (less than a week) can be accomplished by collecting buds just before flowering and placing them in a bed of moist sand in a cool and shaded location. Before use, the buds are exposed to full sun for a few hours in order to promote flowering. Nonopen buds can be used also, but their pollen yield is lower. Long-term storage has not been reported. Germination tests of pollen can be conducted in vitro using the technique reported by (Brewbaker and Kwack, 1963). Five milligrams of pollen are suspended in 5 ml of germination medium made up of 100 ppm of H_3BO_4, 300 ppm of $Ca(NO_3)_2{\bullet}4H_2O$, 200 ppm $MgSO_4$, and 100 ppm KNO_3 in 40% sucrose solution.

Emasculation and Controlled Pollination

The emasculation of a cactus pear flower resembles that of a surgical operation and, as such, should be performed carefully. The material needed for emasculation includes rubber gloves, brush, a sharp knife or razor blade, small scissors with a bent tip, rinsing bottle, paper towels, glassine bags, and rubber bands. The following steps are taken when emasculating cactus pear flowers:

1. Clean the buds with the brush to allow easy handling.

2. Excise the corolla, using as few strokes as possible. Avoid wounding and mechanical damage to the style.

3. Shave carefully the stamens and anthers, cutting close to the base.

4. Rinse thoroughly with clean water, to get rid of pollen residues and anthers.

5. Clean the wounded surface with a paper towel.

6. Allow 15 to 20 minutes to promote drying of the wounded tissues.

7. Cover the flower with a glassine bag and seal it with a rubber band.

8. Label.

A special concern is the extent of damage the flowers can withstand. In this regard, it has been observed that the flowers are able to recover from considerable damage (as long as the stigma remain intact) without harming significantly its reproductive potential. With this method damage to the flower is extensive; however, the plant is able to withstand it due to the abundance of mucilage which slowly flows from the wounds. Mucilages are complex, polymeric carbohydrates, soluble in water (Whistler, 1982). Among other functions, mucilages have also been implicated in wound healing (Ting, 1994). As the mucilage is exposed to the air it dries quickly, covering the wound, reducing the water loss and the possibility of infection.

After emasculation the receptivity of the stigma can be observed in 3 to 4 days. However, under warm (about 35°C) conditions, they are ready in two days. At this time the tip of the stigma is shiny and sticky with the lobes wide open. It has been observed that even young flowers can be emasculated without appreciable loss of fertility, Handling very young buds is difficult because the stamens tend to be less exposed, and the risk of mechanical damage or wounding the stigma is greater.

The most efficient way to pollinate is by means of a detached, fresh, fully open flower devoid of its style and corolla, in order to allow close rubbing of the stamens with the stigma of the female flower. Buds that are not fully open can be used also, taking advantage of the protandric nature of cactus-pear pollination. The difficulty involved in emasculation and the high number of seeds that can be expected from a single fruit, (about 100 to 250 normal seeds from a single fruit, depending on the cultivar) stresses the point of having a few carefully performed crosses rather than numerous trials.

Longer availability of flowers for crossing can be accomplished by eliminating the first flowering flush, which insures that after 50 to 70 days a new round of crosses could be available. In general, the later the flowering season the lower the number of normal seeds expected.

SEED EXTRACTION AND GERMINATION

Seeds should be extracted from ripe and healthy fruits. Fruits are peeled and processed in a blender at low speed. Seed disinfection is accomplished by soaking the seeds in commercial bleach (5–6% sodium hypochlorite) for 10 minutes. Then the seeds are dried in a oven for 2–3 hours. Cactus pear seeds do not present dormancy. Seeds obtained in the same season are able to germinate after scarification. Seed viability is reduced after long term storage. Muratalla et al., (1990), reported out that nine-year-old seed lots attained germination percentages close to 50%.

Cactus pears have a hard seed coat that hinders germination. Several treatments have been reported to overcome this barrier. In our experience, scarifying seeds for 20–40 minutes in concentrated sulfuric acid (the longer time is suggested for larger seeds that normally are associated with thicker seed cover), thoroughly rinsing with water, then soaking in distilled water for 24 hours has been enough to germinate seed under greenhouse conditions in about 12–17 days.

Additional advantage is provided by bottom heat. Vulcanized rubber mats can be used for this purpose, with the temperature set to 90°F–100°F until the seeds start to germinate. It has been observed that bottom heat reduces the time needed for germination by about 20%–30%. Temperature is the most important variable for cactus seed germination. Nobel (1988) reported that for 19 species of cacti the optimal temperature for seed germination ranges from 17°C to 34°C with a mean of 25°C. *O. lindheimeri* and *O. phaeacantha* needed 30°C and 28°C, respectively. Differences attributed to cultivar and seed condition have also been observed. Under greenhouse conditions, cactus-pear seeds need to be watered every other day if planted in standard germination trays.

HANDLING OF SEEDLINGS

Seedlings are kept in germination trays until the first cladode is recognizable (30–45 days), then transplanted to medium-sized pots (1 kg). Prior to transplanting, the tap root is excised (followed by a short dehydration of 5–6 days to promote suberization of wounded tissue) to stimulate formation of adventitious roots, thus enhancing aerial growth and root anchoring.

Cactus, in general, are known to be slow-growing plants. This is a well-known fact for columnar and spherical forms under natural conditions. However, fast growth of seedlings is accomplished through intensive management practices. Almost all types of cacti, including the spherical and columnar, have been reported to respond to optimal conditions of water and nutrients (Nobel, 1988). Several factors influence this response. As reported by Sanderson et al. (1986), photoperiod length is an important factor for cacti growth. They found that for *Chamaecerus silvestri* Britton & Rose and *Opuntia mycrodasys* plants produced more shoots when grown on the long photoperiod (8 h plus 4 h supplementary light applied from 10:00 p.m. to 2:00 a.m.) than when grown in the short photoperiod.

Atmospheric CO_2 concentration has been recognized as an important factor that affects growth in cacti and succulents, especially under greenhouse conditions. The CO_2 range occurring in a well-controlled greenhouse cultivation varies roughly from 200 to 1200 ppm. It may drop below the normal outside concentration; recommended levels are 700 to 900 ppm (Nederhoff, 1994). Net uptake and biomass accumulation by the CAM plant *O. ficus-indica* were substantially enhanced when the CO_2 level was doubled when growing in open-top chambers. (Cui et al., 1993; Nobel and Israel, 1994).

Six-month-old seedlings grown in a greenhouse can be transplanted to a definitive site in the field. At this age they bear 2 or 3 slender pads. They can be managed as adult plants or used as a source of vegetative material for grafting.

It has been observed that plants derived from seeds tend to grow in an upright slender shape, branching only in the upper part. Branching can be promoted by pinching the seedlings in the one-cladode stage. This practice encourages thickening of the basal cladode as well as branching, thus increasing photosynthetic area and improving anchorage and vigor. Pinching also allows for an early expression of adult cladode shape.

SHORTENING OF JUVENILITY

Grafting has been reported as a standard practice to maintain rare forms of cacti, such as those that do not posses chlorophyll and have strange shapes (Haage, 1963; Pizzeti, 1985; Pilbeam, 1987), as well as to propagate endangered species. However, the information available regards mostly those cacti of spherical forms, such as *Echinocactus*, as scions onto cylindrical forms of *Myrtyllocactus geometrizans*, *Hylocereus* spp, *Cereus*, *Trichocereus*, *Pereskia*, and *Rhipsalis* as "a" stocks (Pizzeti, 1985). Grafting platyopuntias is a little more complicated issue. The main concern is the size and shape of the cuttings and scions.

Seedlings three to four months old are soft enough to get a clean cut. At this stage the young cladodes have tender thorns and glochids. It has been observed that buds 6–10 cm long can be placed onto mature pads without much difficulty. Comparisons between age of the shoot as well as stock and its relationships with dry-matter accumulation and differentiation are worthwhile to try. The best species to perform as stocks are from *O. ficus-indica*, which are almost spineless, allowing easy handling, and also are fast growing. Cultivars such as 'Seleccion Pabellon', available in Mexico for vegetable and forage production, and 'Gialla' of Italy are also well suited for this purpose.

Corkborers 1–1.5 cm in diameter can be used to punch holes on top of mature cladodes. A slightly larger corkborer is used to give shape to the base of the scion as well to expose the chlorenchyma. Close contact between both tissues should be insured by scraping slightly the contour of the wound made by the corkborer, until the chlorenchyma is exposed, increasing the surface contact between the scion and the stock. After placing the scion in position the wound can be sealed with pruning and graft dressing. The coating will dry up and harden enough to keep the scion in place. Special care should be taken in selecting the spot in which the graft will be performed. The top of the pad is the most active growing part. The hole to place the graft should be located between two glochids. Removal of any young cladodes already present reduces apical dominance, which is advantageous for the scion.

Grafting can also be performed with young but fully grown cladodes. The scion is prepared by cutting and matching pieces of the same size, shape, and thickness as possible in both the scion and the stock. This is accomplished by using an aluminum can with one edge sharpened as a knife and template at the same time, and punching all the way through the donor cladode, keeping the upper part complete. The same operation is performed in the rootstock. The scion will be placed carefully trying to match as close as possible the tissues. The scion can be maintained in place using rubber bands.

With the aforementioned system at least one flowering cladode can be expected in the next two growing seasons compared to 4 to 6 years needed by seedlings transplanted to the field straight from the greenhouse.

BREEDING SYSTEMS

Species Crossability

Self-pollination of cactus pear is possible due to the early shedding of pollen before the flower opens (protandry) as reported in the floral biology review. Therefore, partial as well as total cross breeding are likely to be found in cultivated accessions.

All Mexican cultivars are reported to be the products of hybridization of *O. ficus-indica* with different wild cactus pear forms (Pimienta, 1995). Some of the South African selections are also reported as produced by hybridization and selection (Dreyer, 1985). This fact accounts for the possibility of hybridization and selection as a means of generation of new cultivars.

Polyploidy

The differences in fruit and cladode sizes found in wild and cultivated populations are undoubtedly due to differences in ploidy levels. Previous cytogenetic studies revealed the existence of different levels (2x, 3x, 4x, 5x, 6x, 8x, 10x, 11x, 12x, 13x, 19x, and 20x). It has been mentioned (Pinkava et al., 1992) that about 63 percent of the species of the subfamily Opuntioidea are polyploids. An interesting conclusion that emerged from this study is that the cactus pear cultivated varieties and forms with the highest number of chromosomes are commonly found in cultivated populations (2n=66 and 2n=88). In contrast, the lowest numbers are found in wild populations (2n=2x=22 and 2n=4x=44); although, in a few cases, forms with the higher number of chromosomes (2n=8x=88) are found in wild populations, as in the case of *O. streptacantha*. (Pimienta, 1995). However, the cultivars reported as 'Charola' and 'Cardona' by Mondragon and Perez (1996) belong to this species, in which certainly the plant vigor is high, as well as productivity, but polyploidy is not expressed in fruit size because its average fruit weight is only 67 g and 83 g, respectively.

It also has been hypothesized that the actual octoploid cultivars are autopolyploids originated by three rounds of chromosome duplication of the original (2n=22) wild ancestor (Pimienta, 1990).

Apomixis

Embryos derived from asexual reproduction have been reported in *Opuntia*. Richards, (1986) indicated that they originated by adventitious embryony. In this process, the sexual embryo and one of the apomictic embryos coexist, sharing the same endosperm. Thus, the mature seed may have one sexual embryo, and one or more apomictic embryos.

Apomictic embryos are fairly easy to recognize during germination. The sexually derived seedling germinates first, pushing the seed cover. After a few days (15 to 25), depending upon the cultivar, a new seedling arises from the base of the older one. Normally, a single root is observed. The number of extra seedlings varies from 1 to 3. In germination trials conducted using the cultivar 'Andy Boy' it was found that polyembryony ranged from 15% to 22% (Mondragon, unpublished data).

BREEDING ACHIEVEMENTS

As with other perennial plants, cactus pear has a long juvenile period. It has been estimated that 6 to 8 years are needed in order to have a fully mature plant originated from seed. Widespread interest on this plant is also a recent issue, starting around the 1980s. So far, it has been considered among the recent trend of "new" tropical and subtropical crops. These are some of the reasons for the scant information about breeding.

Hybridization of cactus pears was first claimed by Luther Burbank at the beginning of the century, which, in turn, led to the development of the so called "spineless" cactus. Its creator saw it as having immense potential as cattle forage in desert areas. Several varieties were formed, five of them were advantageously marketed by Burbank's company. They were said to be the products of extensive crossings and selections among accessions shipped from Mexico, South Africa, and other countries. These accessions were assiduously collected until one finally turned up that was without the usual spines on the "stalks" and another lacked spicules on the "pads" (Dreyer, 1985). The lack of registers and formal publications, a typical criticism of Burbank's work, weakens the accuracy of this accomplishment. Today four of the aforementioned cultivars are still included in the South African collection.

During the 1970s attempts at breeding started in Mexico. Dr. F. Barrientos of the Colegio de Postgraduados de Chapingo pioneered the first hybridizations of cactus pear in Mexico. Using a limited stock of white-fleshed selections from the central region of Mexico, he developed several cultivars (the COPENA series) which had only modest success among growers. The most probable reason is that they did not represent a clear advantage over the native white-fleshed cultivars. However, this effort settled the basis for the actual interest in these remarkable cacti species.

Selection of outstanding cultivars by growers can be regarded as a great accomplishment. Fruit quality, productivity, drought, and late-frost tolerance, as well as rusticity, were the main selection criteria. The outcome of this long-term activity can be appraised by the importance of the commercial varieties and the market they sustain. Six to eight commercial accessions are the basic stock for the Mexican and Italian markets, so far the most important producers and consumers worldwide.

After the aforementioned, the efforts have not been sustained. The main interest in the last 10 years has been collection of wild and semidomesticated accessions, evaluating them in several environments in hope of finding something better. Efforts at crossings are underway in the US, South Africa, Israel, and Mexico, but results have not been reported.

BREEDING PROSPECTS

Cactus pear research generated global interest in the last 10 years due to its potential as an alternative fruit and fodder crop in semiarid areas of the world. Basic information on horticultural aspects of the cactus pear culture is available to the farmers and investigators. However, in regard to breeding, progress is still limited. Germplasm studies represent the most active field. Plant exploration has been conducted several times in Mexico, the proposed country of origin and export rather than exchange with other countries has been very active. So far, no new cultivars have been released to farmers and commercial stock is supported by accessions generated by selection.

The following aspects of germplasm assessment remain to be solved:

- Accurate description of accessions.
- Assessing collection gaps and redundancies.
- Identification of clones true to type.
- Elucidation of genetic relationships.
- Occurrence of natural apomixis.

In regard to breeding, the need for studies on mode of inheritance of basic traits, such as fruit color, size and shape, and seediness, along with cladode spininess, are imperative. Additional interesting traits were mentioned in this paper. They basically are concerns of regional programs.

Relying on phenotypic traits to describe individuals poses special difficulties due to close similarities between accessions as a result of the high plasticity found in cactus pear. The challenge and, at the same time, the opportunity is to incorporate a fairly undeveloped crop, such as cactus pear, into the modern molecular techniques of germplasm assessment in order to improve the chances of breeding.

Molecular techniques of germplasm assessment have proven to be useful in a number of fruit species. Cultivar identification has been accomplished with DNA fingerprints in grape (Bowers et al., 1993), kiwi (Crowhurst et al., 1990), and avocado (Levi et al., 1991), among others. New studies keep adding crops to the list.

Genetic markers can also be used as an aid in designing sampling strategies, core subsets with minimal redundancy, characterization of newly acquired germplasm, and maintenance of trueness-to-type as well as quick identification of plants with desirable traits (Bretting and Widrlechner, 1995).

Due to the long juvenile period the feasibility of traditional inheritance studies is greatly reduced. The challenge is to identify DNA markers related to seedling phenotypic features in order to allow for early screening. We are currently interested in seedling coloration and cladode spininess and shape. They are to be correlated with peel and flesh color, adult cladode spininess and shape in adult plants.

In the fruit industry in general, the development of new fruit cultivars through gene transfer is not yet in reach (Sansavini, 1996). Perennial species with their large size, slow growth, and huge genomes have been poor prospects for gene transfer methods that are proving so useful for improving small crop plants such as canola or tomato. However, on-going research is revealing that cactus pear can be infected by *Agrobacterium rhizogenes* (Phillips, G., 1996 pers. comm.), which represents another possibility of gene transfer besides the classical genetic approach, thus speeding up the process of generation of new improved varieties. Recent accomplishments on handling juvenility in the European aspen by transferring the LEAFY gene, which controls flower development in *Arabidopsis thaliana,* flowering was expressed in the first year of growth, a process that normally takes a decade or two (Simon, 1996; Weigel and Nilsson, 1996) are only two examples of interesting discoveries worth trying in cactus-pear breeding.

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