

Cactus ecosystem goods and services

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INTRODUCTION

The Cactaceae family includes about 1 600 species native to America but disseminated worldwide. *Opuntia* is the most widely known genus in this family and *O. ficus-indica* (L.) Mill. is cultivated in more than 20 countries (Nefzaoui *et al.*, 2014). Cacti are cultivated on 2.6 million ha across the world, and mostly used for forage or fodder: in Tunisia (600 000 ha), Mexico (230 000 ha) and Algeria (150 000 ha) (Nefzaoui and Ben Salem, 2006); in South Africa (525 000 ha) and Ethiopia (355 000 ha) (Reveles Hernández *et al.*, 2010); in Brazil (> 600 000 ha) (Torres Sales, 2010); and in southern Morocco (90 000 ha) (Anegay and Boutoba, 2010). In Argentina, the cultivated area of cactus is estimated at 10 000 ha for forage and fruit production, with syrup as a secondary product (Dubeux *et al.*, 2013); the area cultivated with *Opuntia* solely for fruit production was 2 000 ha in 2003 (Ochoa, 2006).

Cold winter temperatures are the principal limitation to cactus cultivation in parts of Argentina and northern Mexico (Borrego Escalante *et al.*, 1990), the Mediterranean Basin (Le Houérou, 1996a), the arid highland steppes of western Asia (Le Houérou, 1996b) and the southwestern United States of America (Parish and Felker, 1997). Under a range of climatic conditions, the thermal limit for frost-sensitive species such as *O. ficus-indica* is indicated by a mean daily minimum temperature in the coldest month of 1.5-2.0 °C (Le Houérou, 1995). Cactus and other drought-tolerant and water-efficient fodder shrubs can survive with as little as 50 mm rainfall in a given year, but with neither growth nor production. Mean annual rainfall of 100-150 mm is the minimum requirement for the successful establishment of rainfed cactus plantations (Le Houérou, 1994), provided soils are sandy and deep (Le Houérou, 1996a). Plantations of drought-tolerant and water-efficient fodder shrubs, especially *Opuntia* species, have been established as buffer feed reserves as a strategy to mitigate the effects of drought in animal production systems in various arid and semi-arid areas of the world (Le Houérou, 1991). Cacti have good water-use efficiency, thanks to the crassulacean acid metabolism (CAM) photosynthetic pathway (Han and Felker, 1997; Nobel, 1991, 1994); for this reason, they are especially suited for forage production in arid land.

Opuntia spp. can withstand prolonged drought, high temperatures, and wind and water erosion. This ability,

plus the wide range of economic uses, makes them ideal for agricultural development in areas affected by the world's two biggest environmental problems: desertification and climate change (Nefzaoui and El Mourid, 2008).

"Humble", "aggressive", "gold green", "green jewel", "fruit of the poor", "fruit of thorns and delights", "priceless treasure", "treasure under the thorns", "dromedary of the vegetal world", "plant of the future" and "monstrous tree" are just some of the many epithets used to describe the plant and fruit of cactus pear (*Opuntia* spp.). They reflect what "tuna" means to those who work or live with a plant appreciated and loved by many, but feared and hated by others. In any case, this "humble" plant continues quietly but firmly, to earn a leading place in programmes aimed at the agricultural development of arid and semi-arid areas in many countries.

Cacti, endemic to America, were incorporated into many Native American cultures. For example, the nopal (*Opuntia* spp.) is one of the most important resources in arid and semi-arid areas of Mexico, where it has influenced culture, history and traditions. In the social, economic and religious life of the Aztecs, the plant played a very important role and the symbol of Great Tenochtitlan (now Mexico City) was an eagle on a cactus devouring a snake. This symbol is now incorporated in the Mexican national emblem. *Opuntia* is also linked with feelings of national unity in Mexico and is frequently associated with the Virgin of Guadalupe and the Indian Saint Juan Diego.

Tuna is now part of the natural environment, and has been integrated into the culture of many countries where it is well adapted to zones characterized by drought, erratic rainfall and poor soils exposed to erosion. It is naturalized in the landscape as part of the local flora, as can be seen in postcards and tourist advertisements in Italy, Spain, Morocco, Israel, Kenya, Yemen and Saudi Arabia. Notably, Lorenzo Bernini (1598-1680) included the cactus in the Fountain of the Four Rivers in Piazza Navona in Rome where the Río de la Plata is represented.

The controversy over whether it is a helpful or harmful plant depends on the species, where, when and how it is grown, and to whom it applies. There are contradictory assessments, true in one case and not in another, based on experiences under different ecological, eco-

conomic and social conditions. Different situations evolve depending on the individual reality. For example, in Australia and South Africa, biological control was used to stop its expansion and even exterminate it in certain areas. In Ethiopia and Eritrea, on the other hand, where the climate is suitable and no natural enemies exist, nopal effectively invaded thousands of hectares after it was introduced > 150 years ago. In any case, while it may affect local plant genetic resources, the current reality is that after so many years, people have an economic dependency on cactus food and products, regardless of whether the introduction of nopal was a curse or a blessing. Its potential for adaptability and rapid expansion in wilderness areas or in areas previously disturbed by human intervention is another matter requiring examination. Cactus pear is more than useful: it is a vital plant that has been called “a crop that saves lives of humans and animals”, especially in times of severe drought (Arias Jimenez, 2013b).

There are numerous reasons behind the diffusion of *Opuntia* spp. around the world, particularly of *O. ficus-indica*, including:

- simple cultivation practices required to grow the crop;
- rapid establishment soon after introduction in a new area;
- easy multiplication practices that favour rapid diffusion and exchange of material among users;
- ability to grow in very harsh conditions characterized by high temperature, lack of water and poor soil;
- generation of income from the sale of much-valued and appreciated fruits;
- use of stems in the human diet and as forage for livestock;
- useful deployment of plants for fencing farms;
- nutritional value of juicy fruits;
- long shelf-life of fruit; and
- production of a wide range of industrial derivatives from fruit.

These and other factors have contributed to such a wide distribution, from the regions of origin in Latin America to remote areas, spanning continents, cultures and traditions.

Main objective of this chapter

Despite its ecological, economic and social importance, *Opuntia* (cactus pear) continues to receive limited scientific, political and media attention. Well-maintained cactus plantations generate positive externalities and environmental goods and services: they can play a major role, not only in terms of biodiversity enhancement and carbon sequestration, but with regard to

landscape and nature conservation, mitigation of soil erosion, water protection and cultural heritage. However, these public services do not have a market price, are difficult to disaggregate, are highly interrelated in complex dynamic ways and are difficult to measure. The strong links between cactus pear production and the provision of diverse ecosystem goods and services, especially in marginal areas, need to be considered and integrated into a standard evaluation framework for environmental impacts of agricultural production. **The main objective of this chapter is to highlight the benefits generated from cactus pear.**

RANGELAND IMPROVEMENT

Rangeland improvement using spineless cactus has been practised since the early 1930-1940s, principally in North Africa. Le Houérou (2002) reported that fodder plantations were systematically developed, especially in Tunisia, following the research conducted by Griffiths and collaborators in Texas, United States of America. Griffiths was invited by the Government of Tunisia in 1932 and his 30 years' experience with the use of cactus as fodder has since been applied in central Tunisia to mitigate the effects of drought on livestock. The development of cactus for fodder was strongly supported by the Government. Conditional land allotments were authorized in central Tunisia on condition that the contracting beneficiaries planted 10% of the allocated land with spineless cactus. This was to serve as an emergency standing fodder crop reserve, which would stand as a buffer in times of fodder shortages. This was a strategic move as the country faced 3 years of severe droughts from 1946-1948, during which livestock were decimated by 70-75%. Livestock losses were lower for those who had cactus plantations (Le Houérou, 2002).

The plantation of cactus is applicable in many settings, particularly where the environment is too limited or challenging for traditional agricultural crops or where the land is in need of rehabilitation. Cactus is recommended wherever soils are too shallow, too stony, too steep or too sandy, or when the climate is too dry for practical farming. As a result, they have a key role in rehabilitation strategies to improve rangeland, shrubland, bushland or poor farming areas. For rehabilitation, the planting density is 1 000-2 000 single or double pads per ha, with a spacing of 5-7 m between rows and 1-2 m within rows. Fertilization, pruning and pest/disease treatment are not generally applied, but they can be in order to improve productivity. Occasionally, if the first year is too dry, supplemental irrigation is applied during establishment. Plantations are exploitable after 3-4 years and fully grown after 7-10 years; they can remain productive for > 50 years when managed well. Since

Opuntia can survive with minimal management, it is recommended in rehabilitation programmes.

Intensive management is not a prerequisite for cactus survival, but a plantation can reach high productivity levels if appropriation practices are applied. The productivity of rangelands planted with cactus can be increased by a factor of 1 to 10 when rangelands are very degraded and by 1 to 5 when rangelands are in good condition (Le Houérou *et al.*, 1991). Nefzaoui and El Mourid (2009) compared the productivity of rangelands in central Tunisia when they were rehabilitated with cactus (*Opuntia ficus-indica*) and fast-growing shrubs (*Acacia cyanophylla*). Rehabilitation with cactus (*O. ficus-indica*) yielded higher productivity rates than rehabilitation with fast-growing shrubs (*A. cyanophylla*) (Table 1).

Few plant species are able to increase land productivity at the high rate mentioned above, particularly in the case of marginal lands. Cacti can – because of their rain-use efficiency (RUE). Indeed, degraded Mediterranean rangelands have a RUE of 1-3 kg DM ha⁻¹ year⁻¹ mm⁻¹, rangelands in good condition exhibit a RUE of 4-6, and degraded rangelands may have a RUE as low as 0.1–0.5 (Le Houérou, 1984). In contrast, rangelands rehabilitated with *Opuntia ficus-indica* exhibit a RUE of 10-20 kg of above-ground DM ha⁻¹ year⁻¹ mm⁻¹ in arid areas with annual rainfall of 200-400 mm.

ALLEVIATION OF SOIL EROSION

Land degradation occurs in all continents and affects the livelihoods of millions of people, including a large proportion of the poor in the drylands (Nefzaoui *et al.*, 2014). Dry zones with annual moisture deficits of > 50% cover approximately 40% of the earth's land surface. More than 70% of all dry areas suffer from desertification, currently accounting for 36 million km² (Winckler, 2002). Water and soil are the most precious

renewable natural resources. Drought avoidance and coping strategies are imperative: for example, choose drought-tolerant crops, maintain low plant densities, and apply water conservation and water harvesting. However, only a small fraction of rainfall becomes usable soil moisture: 1-10% of the rain that falls in the drylands ends up in the tissue of natural vegetation and crops of economic significance (El Beltagy, 1999). Water erosion is accelerated by tillage on slopes and gully margins. Soil productivity is rapidly declining.

Soils of arid and semi-arid zones are very susceptible to water erosion (Cornelis, 2006), mostly due to the scarce vegetation cover, low organic matter content and poor resistance to erosion forces. The magnitude of water erosion also depends on texture, water content, evaporation, percolation and leaching. These soil characteristics are not favourable to the resistance of soil to water erosion (D'Odorico and Porporato, 2006). In arid and semi-arid areas, soils with little or no vegetation cover are exposed to torrential precipitation events, characterized by short duration and high intensity, and are prone to physical and chemical processes that change the surface layer conditions, such as surface sealing and crusting. When the surface is dry, a hard layer is formed (crust). Crusting soils are typical of dry areas, where soil degradation is induced by diminishing infiltration rates and increasing runoff and erosion rates (Ries and Hirt, 2008). Arid and semi-arid areas are fragile environments where vegetation cover is scarce and soil erosion processes occur rapidly and severely after rainfall events. However, even under such conditions, native vegetation has a very important role in the regulation of surface hydrological processes (Vásquez Méndez *et al.*, 2011).

Erosion control is another important use of cactus pear (*Opuntia* spp.), as it grows quickly and has small roots that regrow each year from the main root during times of rain. In dry periods, the small roots die, adding organic matter to the soil. With an increased

TABLE 1 Productivity (forage units per hectare) of natural and improved rangelands in Tunisia (Nefzaoui and El Mourid, 2009)

Rangeland type	Productivity (forage unit per hectare) ^a
Natural rangeland in Dhahar Tataouine, Tunisia (100 mm rainfall)	35-100
Private rangeland improved by cactus crop in Ouled Farhane, Tunisia (250 mm rainfall)	00-1 000
Cooperative rangeland improved through <i>Acacia cyanophylla</i> , Guettis, Tunisia (200 mm rainfall)	400-500

^a One forage unit is equivalent to 1 kg barley grain metabolizable energy.

organic matter content, it is easier for the soil to absorb rainwater. *Opuntia* spp. are utilized in programmes to prevent soil erosion and combat desertification; they are very adaptable, growing in severely degraded soil which is inadequate for other crops, and are ideal for responding to increases in atmospheric carbon dioxide (CO₂) levels. *Opuntia* is also important as cover in arid and semi-arid areas, because it can survive and spread under conditions of scarce and erratic rainfall and high temperatures (Reynolds and Arias, 2001).

Tests involving the planting of cactus for water harvesting strips, contour ridges, gully check structures and biological control of rills and small gullies have had good results. Contour ridges consist of parallel stone ridges built 5-10 m apart to stop runoff water (and the soil it carries) from damaging downstream areas. Each ridge collects runoff from the area immediately upstream/uphill, which is channelled to a small plantation of fodder shrubs or cactus. With a combination of well-designed ridges and cactus, farmers can meet a large proportion of their fodder requirements. In North Africa, particularly Tunisia, cactus is successfully associated with water-harvesting structures. Planted according to contour lines, cactus hedges play a major role in erosion control (**Figure 1**). Soil physical properties and organic matter content are considerably improved under these hedges and in the immediate adjacent areas, with an improvement in organic matter and nitrogen compared with non-treated fields. There have been reports of rates of 40-200% increase in organic matter and nitrogen. Topsoil structural stability is enhanced, sensitivity to surface crusting, runoff and erosion are reduced, and permeability and water storage capability are increased. Marginal lands have been rehabilitated at low cost in Tunisia and Algeria by contour planting of cacti (Nefzaoui *et al.*, 2011).



Figure 1
Management in Tunisia
for the protection of
watershed

In a comparison of different cultivation systems, such as downhill planting, contour planting, reduced weeding, and intercropping with contour hedges, it was found that soil losses (0.13-0.26 tonnes ha⁻¹ year⁻¹) are lowest with contour hedges. Cactus planting in contour hedges may help retain ≤ 100 tonnes of soil ha⁻¹ year⁻¹. Experiments conducted in Brazil and Tunisia show clearly that planting cactus in an agroforestry system is more efficient for soil and water conservation than conventional land use (**Table 2**) (Margolis *et al.*, 1985).

The eruption of massive dust storms in the Sahara can move 66-220 million tonnes of fine sediment each year. Wind erosion is a major cause of soil degradation on agricultural land in arid and semi-arid areas throughout the world. Wind damages soil by removing the lighter, more fertile and less dense soil components, such as organic matter, clay and silt. Reduced soil productivity

TABLE 2 Comparison of soil loss (tonnes ha⁻¹ year⁻¹) under different crops in semi-arid northeast Brazil (Margolis *et al.*, 1985)

Crop type	Soil preparation phase	Cultivation phase	Harvest until next growing season	Total soil losses	C factor
Bare soil	7.19	8.2	13.71	29.1	1
Cotton	2.42	1.77	6.72	10.91	0.392
Maize	1.51	0.68	3.75	5.94	0.199
Maize + beans	1.36	0.55	2.02	3.93	0.119
<i>Opuntia ficus-indica</i>	0.48	0.02	1.48	1.98	0.072
Perennial grass	0	0.02	0.01	0.03	0.001

is not the only agricultural impact of wind erosion. Blowing sediment cuts and abrades plants, reduces seedling survival and growth, lowers crop yields, and can increase susceptibility to diseases and the spread of plant pathogens (Northcutt, 2001). In arid lands subject to wind erosion, cactus planted alone as a biological barrier or together with physical barriers is an easy, cheap and efficient way to prevent and control topsoil loss, and it facilitates the accumulation of wind-borne deposits.

The somewhat scattered results obtained to date are testimony to the lack of research in this domain. Development actions are mainly based on assumptions and observations gathered by practitioners (Nefzaoui and El Mourid, 2010).

Many Cactaceae species live in arid environments and are extremely drought-tolerant. One survival technique of *O. microdasys* (Lehm.) Pfeiff., which originates in the Chihuahua Desert, lies in its unique and efficient fog collection system, attributed to the integration of its multilevel surface structures (Ju *et al.*, 2012; Bai *et al.*, 2015). This system comprises well-distributed clusters of conical spines and trichomes on the cactus stem; each spine contains three integrated parts, each with a different role in fog collection depending on their surface structural features. The gradient of Laplace pressure, the gradient of surface-free energy and multifunction integration provide efficient fog collection. There is also evidence that some cactus species can harvest dew on their stems and spines (Malik *et al.*, 2015).

Opuntia can tolerate drought in open spaces by increasing and moving chloroplasts and avoiding drastic decreases in their osmotic potential (Delgado Sánchez *et al.*, 2013). *O. ellisiana* Griffiths is a CAM plant, and its conversion efficiency of water to dry matter is several times greater than either C3 or C4 plants. A significant quantity of water (17 mm = 170 000 kg ha⁻¹) can be stored in this cactus and used for animal drinking water (Han and Felker, 1997). Cactus can take advantage of the lightest rainfall, because its roots are close to the soil surface. The water is quickly collected by the roots and stored in thick, expandable stems. The fleshy stems of the barrel cactus (*Ferocactus wislizeni* Britton & Rose) are pleated like an accordion and they shrink as moisture is used up. The green stems produce the plant's food, but they lose less water than leaves do, thanks to their sunken pores and a waxy coating on the surface of the stem. The pores close during the day and open at night and, therefore, only release a small amount of moisture. The price paid by cactus for these water-saving adaptations is slow growth (Zemon, 2015).

There is an urgent need to enhance ongoing research activities with a sound research initiative to investigate all possible benefits and the efficiency of new technol-

ogies using cacti as a keystone species to help control desertification and adapt to global warming (Nefzaoui and El Mourid, 2010).

BIOLOGICAL FENCING/VEGETATIVE BARRIERS

Cactus pear can be grown as hedges and fences by planting them around 30 cm apart. Within several years, the plants grow together to form a wall of spiny pads protruding at all angles. Plantings can also be established for erosion control in deforested areas. In time, cacti such as *O. ficus-indica* may grow into freely branching plants 3-6 m high (University of California Cooperative Extension, 1989). The use of various species of cactus for fencing has great benefits which reach well beyond the savings made by not having to use expensive resources such as iron. Once created, a living fence provides fruit and excellent security for crops and homes, while providing home or habitat for wild fauna species. Deer and its main predators can jump over it or crawl through natural tunnels. Also, if given reasonable amounts of water, cactus can grow quickly and – since most farms and homes have water – a fence can be established in as little as 1 year. The closer pads are planted, the quicker the fence fills in, but a difficult pruning job later becomes necessary. Once established, a cactus border provides security, beautiful flowers (bees and other insects are attracted to them) and fruit. Each variety should be sampled for ease of handling and flavour, as some are too seedy. A spiny variety of standard cactus pear *Opuntia* makes a good fence; and spineless varieties will not keep humans away if the lack of spines can be seen from a distance. The bluish *O. violacea* Engelm var. *santa-rita* (Griffiths & Hare) L. D. Benson makes an excellent fence – the fruit is beet red, packed with seeds and has almost no edible pulp; it also has thick spines clustered on the fruit. To make a fence, cut the thickest pads from a plant, allow the scar to heal for about a week and then plant the pads at a 1.3 m spacing. However, if there is little time available, place the pads flat on the ground on the same day and leave for a year or two; they form a cup-shape and retain rainwater. If this latter method is adopted, very thick or woody pads are best (White Dove Farm, 2015).

Thorny cacti *O. ficus-indica* var. *amyclaea* (Ten.) A. Berger and var. *elongata* Shelle are often used as defensive hedges for the protection of gardens, orchards and olive groves throughout North Africa and in parts of Italy and Spain. These hedges demarcate boundaries while helping to control erosion. However, in regions where winters are temperate to mild (mean daily minimum temperature in January > 3° C), the fruits of *Opuntia* hedges may host the fruit fly, *Ceratitis capitata*



L. Fruit-bearing cacti may, therefore, need to be treated against fruit fly or eliminated from other fruit crop areas. In the case of fodder cacti, however, if harvested every 2-3 years, they do not produce fruit and cannot, therefore, host fruit fly. Not only do these hedges have a very efficient defensive role (particularly when established in double rows), they also play an important part in landscape organization and the local socio-economy, defining land rights and land ownership in countries or regions where no land registry exists. Cactus hedges are often planted as testimony of land ownership, because in some countries, tradition dictates that tribal land may become the property of whoever among the rightful users has established a permanent crop on it. This is a strong motivation for planting cactus hedges (and olive groves) on communal lands, and explains their popularity in countries such as Tunisia. Cactus hedges also play a major role in erosion control and land-slope partitioning, particularly when established along contours. Soil physical properties and organic matter content are considerably improved under hedges and in the immediately adjacent areas (Monjauze and Le Hou  rou, 1965b). The aggregates in the topsoil become more stable and less sensitive to surface crusting, runoff and erosion; permeability and water storage capacity increase. Moreover, hedges are a physical obstacle to runoff: they help accumulate temporary local runoff and silting and prevent regressive erosion. Some badlands, developed in outcrops of shale and stony/rocky slopes, have been rehabilitated at low cost in Tunisia and Algeria with contour planting of cacti. In arid lands subject to wind erosion, cactus hedges are an easy, cheap and efficient way to prevent and control topsoil loss and aid accumulation of wind-borne deposits (Le Hou  rou, 1996a).

The costs of establishing a fence depends on the material used. A metallic fence (four strands of barbed wire) costs about US\$1 m⁻¹, i.e. US\$150 ha⁻¹ in Tunisia for plantations of about 10 ha. A fence made of a double row of spiny cactus costs less than US\$60 ha⁻¹, but needs to be established for at least 2 years before it begins to function (Le Hou  rou, 1989).

CARBON SEQUESTRATION POTENTIAL

Over the last four decades, it has become evident that rising atmospheric CO₂ from fossil fuel consumption is causing increased climate variability. This leads to important issues associated with global warming and modified continental patterns of precipitation that are already having significant effects on species distribution and function in the plant biosphere (Walther *et al.*, 2002; Root *et al.*, 2003). Research has focused on evaluating the potential of biological CO₂ sequestration

for various types of plants. In comparison with C₃ and C₄ plants, CAM plants (agaves and cacti) can use water much more efficiently with regard to CO₂ uptake and productivity (Nobel, 2009). Biomass generation per unit of water is on an average 5-10 times greater than in C₄ and C₃ plants (**Table 3**). The potential of CAM systems to accumulate high biomass depends on their capacity to partition more carbohydrates to growth than to nocturnal acid metabolism (Borland and Dodd, 2002).

The role of cactus plantations in the carbon cycle is extremely important. They help complete the cycle of life by recycling building block nutrients to the plants and carbon (CO₂) to the atmosphere (Doran, 2002). This is important in the soil decomposition process and is often mediated by organisms in the soil. Various experiments in different regions have been carried out to quantify the carbon sequestration potential of *Opuntia*. Measurements of gas exchange in *O. ficus-indica* began in the early 1980s, when Nobel and Hartssock (1983) measured CO₂ uptake on single cladodes, using portable infrared gas analysers with cuvettes adapted to fit cladode morphology. At optimal temperature and intercepted radiation, instantaneous values of net CO₂ uptake of 1-year cladodes may reach 18 mmol m⁻² s⁻¹, with a total daily CO₂ uptake of 680 mmol m⁻² (Nobel and Bobich, 2002). In a similar study – evaluating the effects of seasonal variations in temperature, irradiation and soil moisture content on the photosynthetic rates of *O. ficus-indica* – the total daily net CO₂ uptake was 393 mmol m⁻² averaged over five measurement dates, and annual CO₂ uptake was 144 mol m⁻² (Pimienta Barrios *et al.*, 2000).

Opuntia has greater water-use efficiency than C₄ or C₃ plants due to the CAM photosynthetic pathway, which is more efficient in converting water and CO₂ to plant dry matter (Nobel, 1991, 1994; Han and Felker, 1997; Nobel, 2009). As stated by Nobel (2009), the consequences of nocturnal gas exchange depend on temperature. Temperatures are lower at night, which reduces the internal water vapour concentrations in CAM plants, and results in better water-use efficiency. This is the key reason for which CAM species are the most suited plants for arid and semi-arid habitats. The importance of nocturnal opening and diurnal closure of stomata in CAM species for water conservation has long been recognized (Black and Osmond, 2003). In addition to the advantages of being a CAM species, *Opuntia* plants are also known for their ability to regenerate and grow easily. They act as carbon sinks and can be grown on a large scale in areas where precipitation is inadequate or unreliable. They can grow where evaporation is so great that rainfall is ineffective for crop growth (Osmond *et al.*, 2008). C₃ and C₄ plants suffer irreparable damage once they lose 30% of their water content, while many cacti can survive an 80-90%



loss of their hydrated water content and still survive. This is due to the ability of CAM plants to store large quantities of water; to shift water around among cells and keep crucial metabolism active; and to tolerate extreme cellular dehydration (Nobel, 2009). These abilities, in turn, stem from the cactus characteristics: extra thickness of the cuticles providing an efficient barrier for water loss; presence of mucilage; and daytime stomatal closing. In addition, cacti are characterized by asynchronous development of various plant organs, so that even under the worst conditions, some part of the plant remains unaffected. It is well known that cacti grow in the desert where temperatures are extremely high. Many authors (e.g. Nobel, 2009) report that many agaves and cacti can tolerate high temperatures of 60-70° C.

This aspect is covered in detail by Nobel (2009). In view of the specific phenological, physiological and structural adaptations of cacti described above, they may be considered well positioned to cope with future global climate change. *Opuntia ficus-indica*, for example, can generate a carbon sequestration of 20 tonnes of dry matter (equivalent to 30 tonnes of CO₂) per ha and per year under suboptimal growing conditions similar to those in the arid regions of North Africa.

One *Opuntia* species is known to occupy open and abandoned farmland and to invade open scrubland and forest. This occurs especially in the unpredictable but frequently wet habitats of central eastern Australia that have non-effective rainfall for the growth of agricultural crops (Leeper, 1960; Osmond *et al.*, 1979). The plant has succeeded in its adopted habitat for multiple reasons: in part, because it is a CAM plant with exceptional water-conserving potential; in part, because its extraordinarily low root-to-shoot ratio, dominated by above-ground cladode biomass, can focus on photosynthetic activity; but most of all, because it is characterized by extraordinary vegetative and sexual reproductive activities.

Increased atmospheric CO₂ stimulates further growth and carbon sequestration of *O. ficus-indica* (Gomez Casanovas *et al.*, 2007). Drennan and Nobel (2000) reported that doubling atmospheric CO₂ stimulated the total CO₂ uptake by an average of 31% for six large cacti, and stimulated growth and biomass by 33%. These responses were unexpected because elevated CO₂ was not expected to stimulate CO₂ assimilation in the presence of closed stomata in the light; further, it was expected that CO₂ assimilation in the dark by phosphoenolpyruvate carboxylase would be saturated at internal CO₂. However, these responses are in good agreement with what is now known of the diffusion limitations of CO₂ fixation in all growth states of CAM species (Rascher *et al.*, 2001; Nelson *et al.*, 2005; Griffiths *et al.*, 2007). Wang and Nobel (1996) found that

the growth of *O. ficus-indica* in elevated CO₂ for 3 months showed little evidence for downregulation of photosynthesis commonly found in herbaceous plants. Herbaceous plants usually experience sink limitations and feedback effects of sugar on CO₂ assimilation and gene expression. However, in *O. ficus-indica*, higher CO₂ assimilation (source capacity) was found with greater sucrose transport in the phloem and stronger sink strength. Drennan and Nobel (2000) concluded that high-biomass CAM communities offer potential as a low-input system for atmospheric CO₂ sequestration in arid habitats. Although more research is needed, long-lived CAM plants in arid ecosystems may present effective regional carbon sequestration systems on time scales of decades to centuries.

Limited data are available on cladode net CO₂ uptake according to cladode age. Liguori *et al.* (2013a) used an open gas exchange chamber to measure whole plant or single organ net CO₂ uptake in cactus pear, particularly to understand the response of the whole plant to environmental stress. Unlike with single cladode measurements, after 60 days of drought the whole plant maintained the same level of net CO₂ uptake, although there was substantial water loss in the parenchyma of the most photosynthetically active cladodes. Future research on individual cladode CO₂ uptake is required to understand the best pruning practices needed to increase CO₂ uptake, particularly for cultivated fields of *O. ficus-indica*.

ALLEY CROPPING

Expansion of cereal cropping into rangelands, combined with not allowing lands to go fallow, is one of the major reasons for declining soil fertility and wind erosion. One way of combating degradation resulting from cereal monocropping is the introduction of adapted forage legumes, shrubs/fodder trees and cactus in the cropping system (Nefzaoui *et al.*, 2011). Alley cropping is an agroforestry practice where perennial crops are grown simultaneously with an arable crop. Shrubs, trees or cactus are grown in wide rows and the crop is grown in the interspace. Alley cropping is a form of hedgerow intercropping. Leguminous and fast-growing tree/shrub species are preferred because of their soil-improving attributes, i.e. their capacity to recycle nutrients, suppress weeds and control erosion on sloping land. This technology enables the farmer to continue cultivating the land while the trees/shrubs planted in intermittent rows help maintain the quality of the soil. Cactus can function in this system as a windbreak, resulting in improved grass/cereal yields. The wide alleys allow animals to graze biomass strata or cereal stubble during summer; cactus pads can be



harvested, chopped and given directly to grazing animals as an energy supplement to low-quality stubbles (Nefzaoui *et al.*, 2011).

Although cacti are well known as the best plants for reforestation of arid and semi-arid areas because of their resistance to scarce and erratic rainfall and high temperatures, alley-cropping systems in Tunisia are a largely new phenomenon. When properly managed, alley cropping can provide income at different time intervals for different markets in a sustainable, conservation-orientated manner. Alley designs can also optimize the space available between trees, adding protection and diversity to agricultural fields.

The practice of planting only shrubs is not widely adopted for various reasons, including the technical design of the plantation, mismanagement, and competition for land often dedicated to cereal crops. Some of these disadvantages can be overcome by **alley cropping**, which:

- improves soil;
- increases crop yield;
- reduces weeds; and
- improves animal performance.

Properly managed alley cropping allows diversification and the farmer can benefit from several markets. It also promotes sustainability in both crop and livestock production. The benefits of cactus-barley alley cropping were evaluated in Tunisia (Alary *et al.*, 2007; Shideed *et al.*, 2007). Compared with barley alone, the total biomass (straw plus grain) of barley cultivated between rows of spineless cactus increased from 4.24 to 6.65 tonnes ha⁻¹, while the grain yield increased from 0.82 to 2.32 tonnes ha⁻¹ (**Table 3, Figure 2**). These figures are the result of the micro-environment created by alley cropping with cactus, which creates a beneficial “windbreak”, reducing water loss and increasing soil moisture. The barley crop



Figure 2
Alley cropping using *Opuntia ficus-indica* and barley crop

stimulated an increase in the number of cactus cladodes and fruits, while the cactus increased the amount of root material contributing to the soil organic matter.

BIODIVERSITY CONSERVATION

The intensification of agricultural practices in a context of climate change is cause for concern, as it dramatically alters soil characteristics and affects the local flora and fauna communities (Ouled Belgacem and Louhaichi, 2013). These disturbances affect biodiversity, the most important factor affecting the stability of ecosystems and agro-ecosystems (Fontaine *et al.*, 2011). Stopping or reversing the decline in biodiversity is a major challenge for the maintenance of biodiversity and wider ecosystem services.

Cactus pears are prominent in many arid and semi-arid habitats. They have an important role

TABLE 3 Total biomass changes and barley crop yields (tonnes ha⁻¹) in Sidi Bouzid (Tunisia)^a (Alary *et al.*, 2007)

Treatment	Natural rangeland	Barley crop (alone)	Cactus crop (alone)	Alley cropping (cactus + barley)
Above-ground biomass (tonnes ha ⁻¹)	0.51	0.53	1.87	7.11
Underground biomass (tonnes ha ⁻¹)	0.33	0.11	1.8	1.98
Barley grain yield (tonnes ha ⁻¹)	1.51	0.82		2.32
Barley grain + straw + weeds (tonnes ha ⁻¹)	1.36	4.24		6.65

^a Average rainfall in Sidi Bouzid is 250 mm year⁻¹. All treatments were without fertilizers.

in the ecology and are important for the fauna and flora sharing their habitat. Padilla and Pugnaire (2006) report that some plants benefit from closely associated neighbours, a phenomenon known as facilitation. Cacti often act as “nurse plants” in hot climates: their shade, and sometimes nutrients associated with their presence, help seedlings of other species to become established, which they might otherwise not be able to do in hot or poor soil. Cacti can be an attractive source of shelter for wildlife and their shade is very important for animals, as well as for other plant species. Cactus species provide significant nesting sites for birds, rodents and other animals. Birds perch on their branches to examine their surroundings. Bird droppings often contain seeds of other plants and the shade of the cacti can provide a microclimate that promotes other plant life.

Cacti provide fruits and flowers for a range of animals – many species of bird, bat and insect, including bees. Cacti survive in the natural environment without artificial watering and they produce most of their flowers and fruits during the dry season, when very few other resources are available for wildlife; moreover, their flowers attract butterflies and other pollinating insects. Some *Opuntia* species produce juicy fruit in summer, appreciated by many birds. The succulent fruits containing many seeds are particularly attractive to passerine birds; for this reason, it is not uncommon to find plants developing to maturity in rocky outcrops, on wooden fence posts or along wire fence lines. Prickly pear cactus offer good escape cover for birds. For instance, the cactus wren (*Campylorhynchus brunneicapillus* Lafresnaye) is native in the southwestern United States of America and southwards to central Mexico. It is found in deserts and arid foothills characterized by cactus, mesquite, yucca and other types of desert scrub. It nests in cactus plants – sometimes in a hole in a saguaro and or where it is protected by the prickly leaves of a cholla or yucca. Building the nest in cactus provides some protection for the young, but the wrens also use these nests throughout the year to roost. They eat mainly insects, occasionally seeds or fruits, but they rarely drink water, getting moisture from their food.

Hundreds of species of ants use cacti for food and – together with other insects – are important cactus pollinators. While other predators find the spines daunting, ants forage along cactus stems, capturing small fauna and feeding from extra-floral nectaries, which provide a sugar mixture often high in amino acid content. Furthermore, ants and other insects feed on cactus seeds and play a role in seed dispersal. Cacti provide a habitat for many different types of insects. The bee assassin, *Apiomerus crassipes* Fabricius, lies in wait in

cactus flowers and preys upon its bee or ant victims by injecting a paralyzing enzyme with its hypodermic-like beak. The cochineal insect, *Dactylopius coccus* Costa, is a cryptic species (a taxon that uses anatomy or behaviour to elude predators) and the females spend their entire lives in colonies on the stems of prickly pear. This insect species is noted for the secretion of carminic acid, used by the ancient Aztecs to produce a crimson dye. Hundreds of butterfly, moth and skipper species are known pollinators of Cactaceae (Hogan, 2015). The flowers contain large amounts of nectar and the fruits are rich in water.

Cacti are also important for many desert animals. Nectar-feeding bats, *Leptonycteris curasoae curasoae* Mill. and *Glossophaga longirostris elongata* Petit and Pors, are valuable for the pollination of many important plants in Curacao, and they depend on columnar cacti for their survival. Their diet consists mainly of cactus nectar, pollen and fruits when available. Larger mammals, such as white-tailed deer (*Odocoileus virginianus* Zimmerman), actually consume the pads of prickly pears, despite the formidable spiny armour (Ramawat, 2010). The cactus pads are filled with water, used by several animals including prikichi (brown-throated parakeet, *Aratinga pertinax* L.) and the white-tailed deer. Coyotes (*Canis latrans* Say) feed in a semi-desert grass shrub habitat and consume a variety of foodstuffs throughout the year. Many cactus species in the Sonoran Desert bear fruit during summer – an important food source in drier months. Coyotes feed on cactus fruits when they are ripe, as shown by the analysis of scats collected in autumn (Short, 1979). In Arizona, packrats, also known as the American rat, live primarily in the desert beneath fallen cactus and debris piles. They burrow under a cactus (usually cactus pear), killing the roots and causing the cactus to collapse over them. This creates a prickly armoured home relatively safe from mammal and bird predators. Some species use the base of a prickly cactus pear as the site for their home, utilizing cactus spines for protection from predators.

Unfortunately, the habitat provided by cactus is not always beneficial or agreeable to humans. As a result, during the summer months many ranchers burn cactus to eliminate them from their fields. While cacti are often considered invasive weeds in much of the southern United States of America, the presence of many *Opuntia* species was actually documented by the first settlers to the area. Also in Mexico, the plant is often regarded as a weed, but it is an important food source in Mexican culture. Cactus pads have recently become a health trend and they are sold as a vegetable in many supermarkets in the United States of America. It is hoped that its use as a food will highlight the impor-



tance of the plant; however, many have yet to realize its ecological importance for biodiversity.

CONCLUSION AND RECOMMENDATIONS

Human societies derive many essential goods and services from natural ecosystems. This chapter focuses on the importance of cactus pear and its significant role in the livelihood of farmers. The goods and services provided by cactus pear include: soil and water erosion control; regulation of climate through carbon sequestration; biodiversity conservation; habitat for wildlife; pharmaceutical and industrial benefits – in addition to their aesthetic beauty as evergreen plants. Despite their ecological, economic and social importance, cacti receive limited scientific and media attention and there

is insufficient focus on their conservation merits. This is largely due to limited knowledge and a narrow vision focusing on cacti for forage and fruit production. A major shift in the role of cactus and its production is required, towards a much broader concept of ecosystem goods and services. A **holistic approach** is needed, with a balance among environmental conservation, farming system production and socio-economic development. It would be of great benefit to promote the ecological, economic and social benefits of cacti and strengthen the technical capacity of human resources dedicated to these species. In addition to the analysis of current trends in research, it is vital to present new discoveries and plans for future research in all areas concerning cacti. Public policies and credit are essential in order to increase cultivation of this important plant in the arid and semi-arid regions of the world.

