

Recent Ecophysiological Advances for *Opuntia ficus-indica* and Other Cacti

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OVERVIEW

Cacti are increasingly cultivated for the production of fruits as well as use as vegetables and fodder, especially platyopuntias such as *Opuntia ficus-indica* (Russell and Felker, 1987a; Nobel, 1994). Currently, *O. ficus-indica* is cultivated in about 20 countries for "cactus pears", which are sold fresh as well as processed, the latter especially in Mexico. Young stem segments (cladodes) are cooked as vegetables known as "nopalitos", again especially in Mexico. Use of mature stem segments for cattle forage and fodder is prevalent in Brazil, Mexico, Tunisia, and various other countries, such as the United States, where the spines are burned off before feeding to cattle. In addition to cactus pears, tasty fruits known as "pitayas" can be produced by columnar cacti such as *Cereus peruvianus* and *Stenocereus queretaroensis* as well as vine-like cacti such as *Hylocereus undatus* and *Selenicereus megalanthus* (Pimienta-Barrios and Nobel, 1994; Mizrahi, Nerd, and Nobel, 1996).

Net CO₂ uptake and water loss by various cacti has been investigated in the field as well as under controlled laboratory conditions (Nobel, 1988). Because stomatal opening for such Crassulacean acid metabolism (CAM) plants occurs predominantly at night when air and plant temperatures are lower, water loss tends to be less for CAM plants than for the majority of plants (C₃ and C₄) whose stomates open during the daytime. The resulting water-use efficiency (CO₂ uptake per water loss) is 3 to 7 times greater for cacti than for C₃ and C₄ crops. Certain cacti are not only efficient crops with respect to water utilization but also can be highly productive, especially when irrigated (Nobel, 1991a). Yet little effort has gone into the systematic study of cacti, so the effects of the timing of water supply on fruit production and other management aspects have not been well researched (Inglese, Barbera, and La Mantia, 1995). Cacti that are highly productive also tend to be sensitive to freezing temperatures. Again, mechanisms of low temperature damage and their genetic control have received little research attention.

BIOMASS PRODUCTIVITY

Biomass productivity depends on the environmental conditions. Daily net CO₂ uptake by the shoots is generally higher when soil water is readily available, is greatest at a particular regime of day/night air temperatures, and increases with the daily photon flux absorbed by photosynthetic pigments, usually reaching a maximum at light levels characteristic of the native habitat of the species under consideration. Responses of net CO₂ uptake by *O. ficus-indica* to rainfall, temperature, and light determined in the laboratory can be evaluated with respect to local climatic conditions to help indicate where this species should be cultivated. Future considerations must include the effects of global climate change induced by elevated atmospheric levels of CO₂ and other greenhouse gases.

Environmental Productivity Index

To understand the effect of environmental conditions on net CO₂ uptake by shoots and hence on plant productivity, gas exchange (net CO₂ uptake and water loss) by CAM plants generally is studied over 24-h periods. In contrast, gas exchange by C₃ and C₄ plants usually is measured only during the daytime when the stomates are open, thus their total nighttime respiration is difficult to quantify accurately. Yet, net CO₂ uptake over 24-h periods is crucial for understanding the productivity of any plant and has become embodied in an environmental productivity index (EPI) (Nobel, 1984, 1988). EPI indicates the relative daily net CO₂ uptake based on the fraction of maximal net CO₂ uptake caused by limitations of specific environmental factors:

$$\text{EPI} = \text{Water Index} \times \text{Temperature Index} \times \text{Light Index} \quad (1)$$

A component index is unity (1.00) when that factor is optimal for net CO₂ uptake, and it is zero (0.00) when that factor completely eliminates net CO₂ uptake. Therefore, if prolonged drought precludes net CO₂ uptake, reducing the Water Index to zero, the temperature and light levels are irrelevant with respect to net CO₂ uptake.

An important use of EPI is for planning specific agricultural management practices. Although temperature is an important parameter for plant growth, essentially, it cannot be controlled under field conditions. Water availability can be controlled by irrigation, and the consequences for net CO₂ uptake can be evaluated using EPI. Interplant spacing determines the interception of radiation and hence the Light Index, so considerable modeling effort has gone into assessing the optimal spacing for *O. ficus-indica* with respect to biomass productivity (Garcia de Cortázar and Nobel, 1986, 1991).

Nutrients and Elevated CO₂

Net CO₂ uptake and productivity by cacti can also be influenced by soil element levels and atmospheric CO₂ concentrations (Nobel, 1989, 1991b). For cacti, nitrogen is the most important soil element, as it is for nearly all cultivated species; phosphorus and potassium are also important. Of 25 other elements considered (Nobel, 1988), the two most important are sodium, whose presence in the soil adversely affects net CO₂ uptake and growth of cacti, and boron, which can limit productivity of cacti under natural conditions in the Chihuahuan Desert but which is usually present in sufficient amounts (Nobel, 1989).

When sufficient soil volume is available for root growth, raising the CO₂ concentration from the current atmospheric value to double that value greatly enhances net CO₂ uptake over 24-h periods for *O. ficus-indica* (when soil volume is limiting, enhancements are much less; Cui and Nobel, 1994; Nobel *et al.*, 1994). In particular, for plants in open-top chambers in the field, cladode daily net CO₂ uptake averaged 70% higher after 5 months (Cui, Miller, and Nobel, 1993) and 35% higher after 12 months (Nobel and Israel, 1994). For plants under controlled conditions in environmental chambers, doubling the CO₂ concentration enhances daily net CO₂ uptake by 70% after 3 months (Nobel and Israel, 1994). Such enhancements in daily net CO₂ uptake translate into increased biomass productivity, as the shoot dry weight of *O. ficus-indica* in open-top chambers under the doubled CO₂ concentration is 55% higher after 5 months (Cui *et al.*, 1993) and 38% higher after 12 months (Nobel and Israel, 1994). The climbing cactus *Hylocereus undatms* has 34% more daily net CO₂ uptake when the atmospheric CO₂ concentration is doubled (Raveh, Gersani, and Nobel, 1995). The greater net CO₂ uptake under the doubled CO₂ concentration mainly reflects the higher substrate level for the two carboxylation enzymes, CO₂ for ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO, active in the daytime) and

HCO₃⁻ for phosphoenolpyruvate carboxylase (PEPCase, active mainly at night; Israel and Nobel, 1994). In any case, a higher atmospheric CO₂ concentration will mean greater net CO₂ uptake and productivity for *O. ficus-indica*, a highly productive and important CAM species (Nobel, 1991b, 1995).

Magnitudes under Optimal Conditions

CAM species such as cacti often grow slowly, e.g., species of *Mammillaria* can be only 10 cm tall when over 50 years old. However, slow growth is not a necessary corollary of the CAM pathway, as *O. ficus-indica* can exceed 120 cm in height within 2 years of placing detached cladodes in the ground. Using EPI (Eq. 1) to predict net CO₂ uptake by individual cladodes and summing over all cladodes on hypothetical plants of various architectures, the spacing that maximizes biomass productivity for *O. ficus-indica* has been predicted (Garcia de Cortázar and Nobel, 1986, 1991). Field trials then tested the predictions that close spacing of the plants to maintain a stem area index (total area of the cladodes per unit ground area) of 4.2 to 5.8, for which very little radiation was incident on the ground, could lead to high productivities (Garcia de Cortázar and Nobel, 1992; Nobel, Garcia-Moya, and Quero, 1992). Productivity was also maximized by using irrigation to raise the Water Index (Eq. 1) to unity and by fertilization. The resulting biomass harvests of 45 to 50 tons hectare⁻¹ year⁻¹ are some of the highest ever recorded for any species (Table 1).

Table 1. Maximal annual aboveground dry weight productivities of various plant groups. Data are for relatively optimal conditions, which include close spacing and irrigation for the Opuntias (Nobel, 1991a; Nobel *et al.*, 1992; Garcia de Cortázar and Nobel, 1992).

Group	Annual Productivity (tons hectare ⁻¹ year ⁻¹)
Opuntias (<i>Opuntia amyoclea</i> , <i>O. ficus-indica</i>)	45 – 50
Other CAM species (<i>Agave mapisaga</i> , <i>A. salmiana</i> , <i>A. tequilana</i> , <i>Ananas cosmosus</i>)	35
C3 crops (<i>Beta vulgaris</i> , <i>Elaeis guineensis</i> , <i>Lolium perenne</i> , <i>Manihot esculenta</i> , <i>Medicago sativa</i> , <i>Triticum aestivum</i>)	35
C3 trees (<i>Cryptomeria japonica</i> , <i>Eucalyptus globulus</i> , <i>E. grandis</i> , <i>Pinus radiata</i> , <i>Salix purpurea</i> , <i>Tsuga heterophylla</i>)	39
C4 crops (<i>Cynodon dactylon</i> , <i>C. plectostachyus</i> , <i>Pennisetum purpureum</i> , <i>Saccharum officinarum</i> , <i>Sorghum bicolor</i> , <i>Zea mays</i>)	49

The basis for the extremely high productivity for certain CAM plants has been examined at the level of net CO₂ uptake by the leaves or stems and at the cellular level (Nobel, 1991a). When supplied with sufficient water, some CAM plants can take up appreciable amounts of CO₂ during the daytime, especially early in the morning and late in the afternoon. On the other hand, C₃ and C₄ plants do not take up any CO₂ at night, but instead release respired CO₂ then. Thus even though the maximal CO₂ uptake rates are lower for CAM plants, they can take up CO₂ over a larger portion of the 24-h cycle than do C₃ or C₄ plants. RuBisCO acts both as a carboxylase, fixing CO₂, and as an oxygenase, incorporating O₂ into a photosynthetic substrate (ribulose-1,5-bisphosphate), eventually releasing some CO₂ and thereby partially undoing the work of the carboxylase. Moreover, the biochemical pathway beginning with O₂ incorporation,

an overall process known as photorespiration, requires an input of energy, further undoing photosynthetic energy storage. C₄ and CAM plants greatly diminish the doubly wasteful photorespiration by raising the CO₂ level near RuBisCO to such a high level that the carboxylase activity overwhelms the oxygenase activity (in C₄ plants using an intercellular biochemical shuttle and in CAM plants by decarboxylating massive amounts of organic acids during the daytime when their stomates are closed). In any case, the high biomass productivities for *Opuntias* and other CAM plants under the proper conditions (Table 1) augurs well for the future increase in use of such plants.

EXTREME TEMPERATURES

Temperature not only affects net CO₂ uptake and productivity of plants (Eq. 1) but also their survival. In particular, episodic extreme temperatures limit the distribution of natural populations and cause major damage for certain agricultural crops. Succulent CAM plants, including cacti, are relatively sensitive to low temperatures and most of the species studied are relatively tolerant of high temperatures, such as those occurring at the soil surface in deserts.

Low Temperature

The most important environmental factor limiting the cultivation of cacti in the United States and many other countries is low temperature (Nobel, 1988, 1994). Most commercial cultivars of *Opuntia* are damaged at -5 to -10°C (Russell and Felker, 1987b; Nobel, 1990; Goldstein and Nobel, 1994). *Hylocereus undatus* and *Selenicereus megalanthus*, tropical vine-like cacti now cultivated for their fruits, are apparently even more sensitive to freezing temperatures. Yet certain cacti can tolerate much lower temperatures, e.g., *Opuntia humifusa*, which is native to southern Canada and the eastern United States, can tolerate -24°C when properly acclimated and *O. fragilis* is native to western United States and Canada, including up to 58° N latitude in northern Alberta where temperatures can drop to -40°C (Loik and Nobel, 1993a; Nobel, 1994). Thus the potential exists within the genus *Opuntia* for the toleration of extremely low temperatures, indicating that breeding efforts may be successful to introduce genes from the wild species into cultivated ones (Nobel, 1995). Yet the genus *Opuntia*, with 160 to 200 species (Gibson and Nobel, 1986; Nobel, 1994), is exceedingly diverse, so crosses with the desired characteristics may be difficult to obtain.

Some progress has been made in understanding the cellular events underlying the influence of freezing temperatures on cacti. For instance, when the tissue temperature is progressively reduced below zero, the initial ice formation occurs extracellularly (Nobel, 1981, 1988). Water is then distilled from inside the cells, causing the extracellular ice crystals to grow. Eventually, the intracellular loss of water leads to the death of a cell, similar to cellular death caused by prolonged desiccation by drought. Cacti are not as susceptible to freezing damage if their water content is reduced by drought. Also, exposure to low but nonlethal temperatures causes various solutes, e.g., glucose, fructose, and sucrose, to increase in the cells, raising their osmotic pressure and thus helping to retain water intracellularly (Goldstein and Nobel, 1994; Nobel *et al.*, 1995). Apparently the protection offered by such metalizable solutes is nonspecific, because injection of glucose into cladodes of *O. ficus-indica* and *O. humifusa* gave essentially the same protection from low-temperature damage as injecting the nonmetalizable 3-O-methylglucose. Spraying the plant hormone abscisic on cladodes of *O. ficus-indica* and *O. fragilis* increases the tolerance of both species to lower temperatures; the time for the increase in tolerance is similar to the time for acclimation induced by lowering the ambient temperatures, with half times of about 3 days (Loik and Nobel, 1993b). Although mechanisms are not fully understood for the low-temperature acclimation by *Opuntias* and other cacti, clearly properties of cellular water are involved.

High Temperature

Cacti are extremely tolerant of high temperature. Of 18 species tested that had been maintained at relatively high air temperatures, all could tolerate a 1-hour exposure to 60°C and four species could tolerate 70°C (Nobel, 1988), temperatures that are lethal for nearly all other vascular plants. Both RuBisCO and PEPCase from *O. ficus-indica* tolerate higher temperatures than these enzymes do from other vascular plants; enzyme activity is not substantially reduced until the 1-hour treatment temperatures exceed 55°C, and some activity of its PEPCase remains after a 1-hour treatment at 65°C (Israel and Nobel, 1995). Thus toleration of high temperatures is rarely a problem for *O. ficus-indica* and most other cultivated cacti, although net CO₂ uptake is greatly reduced when moderate temperatures are exceeded. For instance, a day/night air temperature of 40°C/30°C reduces net CO₂ uptake over 24-hour periods by 88% compared with the optimal temperatures of 25°C/15°C (Nobel, 1988), a matter quantified by the Temperature Index (Eq. 1).

WATER AND SOLUTE TRANSPORT

Water transpired by the stems of cacti enters from the soil and moves through the plants in the xylem. The phloem moves organic solutes produced by photosynthesis in the stems to developing organs. Compared with C₃ and C₄ plants, relatively little is known about these circulatory systems for CAM plants in general and cacti in particular.

Roots – Water Uptake and Loss

Roots of cacti tend to be shallow, most occurring in the upper 20 cm of the soil, and generally represent only 7% to 14% of the plant dry weight (Nobel, 1988). The relatively small root dry weights compared with C₃ and C₄ plants reflect the high water-use efficiency of CAM plants, so less root tissue is necessary for water acquisition (Nobel, 1994). Although roots take up water from a wet soil, water has a thermodynamic tendency to leave roots to a drying soil whose water potential (ψ) is less than that of the shoot. The same dilemma is faced by all plants but is particularly apparent for succulent species with their high water-storage capacities.

The rate of water movement into plants can be represented by the volumetric flux density (J_v , m³ m⁻² s⁻¹), which depends on a drop in water potential from the root surface to the root xylem ($\psi_{\text{surface}} - \psi_{\text{xylem}}$):

$$J_v = L_p(\psi_{\text{surface}} - \psi_{\text{xylem}}) \quad (2)$$

where L_p (m s⁻¹ MPa⁻¹) is the root hydraulic conductivity. In wet soil, L_p is the main limiter to water uptake. As the soil dries, the soil water potential (ψ_{soil}) steadily decreases, and water is lost from the root once (ψ_{soil}) is less than (ψ_{surface}) (Eq. 2). The water loss rate could become excessive during such drought were it not for four possible changes.

First, roots of cacti can die and be shed during drought, especially the finer lateral roots (Nobel, 1988). This reduces the surface area across which water can be lost. Second, L_p (Eq. 2) can decrease. For 3-month-old roots of the barrel cactus *Ferocactus acanthodes* and *O. ficus-indica*, 30 days of drought decreases L_p three- to five-fold, partly because of lacunae developing as root cortical cells collapse (North and Nobel, 1992). Such drought for 12-month-old roots of these species reduces L_p by two- to three-fold, which is accompanied by a dehydration of suberized peridermal root layers. Actually, most of the decrease in L_p in both cases is caused by the introduction of air into the xylem, a process called embolism, which interrupts water continuity and hence flow in the xylem. Upon rewetting, such embolism is reversed and new roots can be induced, restoring the water uptake ability of the root system (Huang and Nobel, 1993).

The third event that helps prevent water loss to a drying soil is the development of a root-soil gap filled with air, which is relatively nonconducting. In particular, 6-week-old roots of *F. acanthodes* and *O. ficus-indica* reversibly decrease 15% to 18% in diameter in 4 to 5 days when ψ_{soil} is reduced from -0.1 to -10 MPa (Nobel and Cui, 1992a). For *O. ficus-indica*, root shrinkage ranges from 43% at 3 weeks of age to 6% at 12 months (Nobel and Cui, 1992b). Yet the most important event in preventing water loss during prolonged drought from cacti and other plants is changes in the soil hydraulic conductivity (L_{soil}). In particular, L_{soil} decreases by a factor of 10^6 as ψ_{soil} for sandy desert soil decreases from -0.1 MPa to -10 MPa (Young and Nobel, 1986). The decrease reflects the lower soil water content and consequently the more tortuous pathway for water movement, with its inherently lower L_{soil} . The predominant factor limiting water movement out of roots of *F. acanthodes* and *O. ficus-indica* during drought is thus changes in L_p during the first 7 days, the root-soil air gap for the next 13 days, and L_{soil} and some root shedding thereafter (Nobel and Cui, 1992a, b).

Phloem

Because of the small diameter of the conducting cells of the phloem, generally less than 0.04 mm, obtaining uncontaminated phloem sap is difficult. For many C_3 and C_4 plants, aphids penetrate leaf tissue to the phloem with their stylets, so removing their bodies provides a conducting channel from the phloem to the leaf surface. Although aphids could not be induced to feed on *O. ficus-indica*, the scale insect *Dactylopius opuntiae*, a natural predator of this species used for the production of carminic acid (the cochineal dye produced by the females), has a longer stylet that penetrates to and feeds upon the phloem solution (Wang and Nobel, 1995). Sucrose, total aminoacids, and potassium account for 56%, 21%, and 9%, respectively, of the relatively dilute phloem sap of *O. ficus-indica*, which has an osmotic pressure of only 0.9 MPa compared with over 2 MPa for essentially all other species studied.

Fruit

Developing fruits of *O. ficus-indica* can have a water potential that is 0.17 MPa higher than the cladodes bearing them after 4 weeks and 0.07 MPa higher after 10 weeks (Nobel *et al.*, 1994). Because water flows energetically downhill (toward lower water potentials) in the xylem (Nobel, 1991c), this conducting pathway does not account for the water importation accompanying fruit growth. Net photosynthesis by the fruits of *O. ficus-indica* supplies only about 9% of their organic carbon need over the first 30 days, declining to 1% at 75 days (Inglese, Israel, and Nobel, 1994). Thus organic compounds such as sucrose must be imported via the phloem, which is relatively dilute, so the phloem also supplies a considerable amount of water to the developing fruit. Indeed, the phloem supplied all the water necessary for the fresh weight growth of fruits and for their transpiration (Nobel *et al.*, 1994).

CONCLUSIONS AND FUTURE PROSPECTS

EPI (Eq. 1) can help evaluate the cultivation of *O. ficus-indica* in new regions. For instance, instead of correlating growth of prickly pear and other cacti with annual rainfall, which is relatively imprecise, actual rainfall events can be interpreted on a daily basis with respect to their impact on the Water Index (Eq. 1; Garcia de Cortázar and Nobel, 1986, 1991), which directly reflects the net CO_2 uptake ability of *O. ficus-indica* and other species. Much remains to be learned about the nutrient responses of cacti, from the effect of specific elements on plant growth and productivity (Nobel, 1989) to the effects of mycorrhizal fungi (Cui and Nobel, 1992). For instance, dry weight

of roots of *O. ficus-indica* is reduced 30% by 30 mM NaCl and 93% by 100 mM NaCl, indicating the great sensitivity of this species to salinity stress (Gersani, Graham, and Nobel, 1993). Indeed, a Nutrient Index involving five elements (N, P, K, Na, B) can be incorporated into EPI (Eq. 1) for cacti (Nobel, 1989).

The influences of global climate change induced primarily by increases in atmospheric CO₂ concentrations should benefit the cultivation of *O. ficus-indica* and other cacti (Garcia de Cortazar and Nobel, 1990; Nobel and Garcia de Cortázar, 1991; Nobel, 1995). Specifically, daily net CO₂ uptake when the roots are not in constricted volumes increases 1.0% to 1.6% as the atmospheric CO₂ concentration increases by 10 μmol mol⁻¹ (10 ppm by volume; Cui *et al.*, 1993; Nobel and Israel, 1994). Changes in rainfall patterns with global climate change tend to favor CAM plants, which have high water-use efficiencies, as they are more competitive at low rainfall and yet their productivity can be stimulated by high rainfall. Increased temperatures near the equator will tend to decrease net CO₂ uptake by cacti. On the other hand, increased temperatures at midlatitudes will reduce the damage caused by freezing temperatures on commercially important cacti. Indeed, understanding and controlling for freezing damage can greatly extend the cultivation of cacti in the United States and other countries (Nobel, 1994, 1995).

Although cactus pears of *O. ficus-indica* have so far received the most worldwide attention, the market for “pitayas” may represent the cactus-fruit growth industry of the future (Nobel, 1994; Mizrahi *et al.*, 1996). Fruits of *Stenocereus queretaroensis*, which unfortunately have a shelf-life of only a few days, are initiated before the June–September rainy season, whereas its major stem extension tends to occur in October (Nobel and Pimienta-Barrios, 1995), so resource acquisition predicted by EPI (Eq. 1) is not contemporaneous with reproductive or vegetative growth (Pimienta-Barrios and Nobel, 1995). Irrigation during the winter-time dry season increases fruit size and seed germination but did not affect reproductive demography, another area requiring further investigation (Inglese *et al.*, 1995).

Growth and maintenance respiration for roots of *F. acanthodes* and *O. ficus-indica* of various ages has been measured (Palta and Nobel, 1989; Nobel, Lopez, and Alm, 1991; Nobel, Alm, and Cavelier, 1992), as has L_p and hence the water uptake ability (Nobel *et al.*, 1991; North and Nobel, 1992). Such studies should be integrated into a comprehensive model predicting optimal root deployment with respect to the carbohydrate costs for water uptake. Cladodes and cladode-cladode junctions of platyopuntias such as *O. ficus-indica* also offer interesting objects for study. Such rigid structures are deflected relatively little by wind or the cladodes mass, even though the contact between sequential cladodes corresponds to less than 4% of their peripheral area (Nobel and Meyer, 1991).

Inter-organ partitioning of carbohydrates for *O. ficus-indica* and other cacti is just being investigated. For instance, basal cladodes incorporate about 65% of their own photosynthetic products whereas young daughter cladodes incorporate about 96% (Luo and Nobel, 1992). When daughter cladodes are shaded, they import more carbohydrate, and when unshaded they become photosynthetically self-sufficient after about 4 weeks (Luo and Nobel, 1993). Cladodes of *O. ficus-indica* do not produce fruits unless their dry weight is at least 32 g above the minimum value expected for cladodes of that surface area (Garcia de Cortázar and Nobel, 1992; Inglese *et al.*, 1994). A certain minimum of stored carbohydrates is apparently necessary for fruit initiation and growth, yet hormonal and other controls must surely also be involved, another matter to be resolved

by future research.

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