Recent Ecophysiological Findings for Opuntia ficus-indica

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ABSTRACT

Recent research concerning *Opuntia ficus-indica* from our laboratory is reviewed. A root-soil air gap that develops as the roots of *O. ficus-indica* shrink in response to drying conditions helps retard water loss to the soil in the initial phases of drought, with cellular changes affecting the root hydraulic conductivity playing a secondary role and decreases in soil hydraulic conductivity becoming dominant after a few weeks of drought. The xylem is the vascular system typically supplying water to plant parts, for which flow occurs toward regions of lower water potential. However, both fruits and young daughter cladodes of *O. ficus-indica* have higher water potentials than the supporting cladodes, which they depend on for organic compounds. These compounds are transported in the phloem in a relatively dilute sap that also supplies the water needed for growth of the new organs. Detached unrooted cladodes of *O. ficus-indica* form a model system for studying environmental and solute responses of the stem. Shading and injection of gibberellic acid can inhibit new organ initiation but injection of indole-acetic-acid and kinetin accelerates it. New organ initiation is greatest when the cladodes are detached in the winter. Low day/night air temperatures favor the initiation of flowers, whereas high temperatures favor initiation of daughter cladodes.

INTRODUCTION

Various responses of *Opuntia ficus-indica* (L.) Miller and other platyopuntias to the environment have become better understood over the last decade. For instance, cultivated prickly pear cacti are not very tolerant of freezing temperatures, with damage being evident for various species at S5°C to S12°C (Russell and Felker, 1987; Nobel, 1990; Gregory et al., 1993). However, various short-statured wild species such as *Opuntia fragilis* and *O. humifusa* from cold habitats in Canada can tolerate S25°C to S40°C when properly acclimated by exposure to low day/night air temperatures (Loik and Nobel, 1993; Nobel, 1996a). The low-temperature sensitivity, which mainly reflects a poor ability for low-temperature acclimation, severely limits the regions for commercial exploitation of prickly pear cacti, although such regions are predicted to expand as air temperatures rise accompanying global climate change (Nobel, 1996a). On the other hand, prickly pear cacti are relatively tolerant of high temperatures. For instance, *Opuntia basilaris, O. chlorotica*, and *O. ficus-indica* all can tolerate tissue temperatures over 60°C for 1 hour when properly acclimated (Nobel, 1988), a high-temperature tolerance that surpasses that of nearly all other vascular plants.

Many wild species of prickly pear cacti are relatively slow growing, but this is certainly not the case for various cultivated species. For instance, *Opuntia amyclea* and *O. ficus-indica*, when closely spaced and irrigated, can produce 47 tons (Mg) of dry matter per hectare per year (García de Cortázar and Nobel, 1991; Nobel et al., 1992). This is a higher productivity than for

nearly all other agricultural plants and trees (Nobel, 1991a), which also bodes well for the increased cultivation of prickly pear cacti in the future (Nobel, 1994).

The present article is a review of three other areas of physiological and environmental responses of *O. ficus-indica* that have recently received research attention in our laboratory. Because most of the methodological details can be found in the literature cited, emphasis is on the major findings and certain implications for understanding the behavior of commercial prickly pear cacti in the field. First, air gaps that can develop around the roots of *O. ficus-indica* as the soil dries are described and the influence of such gaps on plant water relations is presented. Second, the role of the main water transport system in plants (the xylem) versus the system responsible for distributing photosynthetic products in plants (the phloem) in supplying water to the developing cladodes and fruits is discussed. Third, the use of detached unrooted cladodes as a model system for investigating environmental and physiological responses of stems is presented.

ROOT-SOIL AIR GAPS AND WATER CONDUCTANCES

As occurs for other species, roots of *Opuntia ficus-indica* shrink radially when exposed to desiccating conditions, such as prolonged drought. This can lead to the development of an air gap between the root surface and soil particles across which water must move as a vapor. Because soil water moves more readily as a liquid than as a vapor, air gaps can retard water flow into or out of roots. In particular, the rate of water movement to or from a root depends linearly on the soil hydraulic conductivity coefficient (L_{soil}), the distance across any root-soil air gap, and the hydraulic conductivity coefficient of the root (L_P) (defined in Table 1). Analytical equations have been developed for the effective conductances of each of these parts of the pathway (Nobel and Cui, 1992a).

Table 1. Components of Hydraulic Conductivity.

The volumetric rate of water flow into a root (J_v) depends on the overall hydraulic conductivity (L_{verall}) and the drop in water potential from the soil to the root xylem ($Δψ$): $J_v = L_{overall} \, Δψ$.

Component	Symbol	Description for Opuntia ficus-indica
Soil decreases	L_{soil}	Very high (not limiting) for water uptake from wet soil; greatly as soil dries; very low (limiting) for dry soil
Root-soil air gap	L_{gap}	Gap develops as roots shrink radially in a drying soil; main limiter for water uptake or loss for young roots during the initial phases of drought
Root	L_P	Main limiter of plant water uptake from wet soil; decreases somewhat during drought
Overall	L_{verall}	$1/L_{verall} = 1/L_{soil} + 1/L_{gap} + 1/L_P$

Diameters of 6-week-old roots of *O. ficus-indica* have been determined under wet soil conditions (water potentials of S0.01 MPa), moderately dry conditions (S1.0 MPa), and also very dry conditions (S10 MPa). Roots initially 2 mm in diameter shrink 18% in the radial

direction over a 4-day period at S10 MPa and recover to the initial diameter 5 days after being placed back at S0.01 MPa (Nobel and Cui, 1992a). When transferred from S0.01 MPa to S1.0 MPa, root shrinkage is less and more gradual, amounting to 11% over a 10-day period. Water movement is predominantly limited by L_P for the first 7 days of soil drying, the root-soil air gap for the next 13 days, and L_{soil} thereafter (Nobel and Cui, 1992a). Compared with the conductance of the water uptake pathway in wet soil, the decrease in the overall conductance by a factor of 3000 during 30 days of soil drying greatly reduces the water loss from the plant to the drying soil. The root-soil air gap is the primary limiter during a crucial early phase of drought, whereas the conductance of water through a dry soil becomes the major limiting factor near the end of the first month of drought (Table 1).

Root shrinkage, which mainly reflects water loss from the cortical cells between the epidermis and the endodermis surrounding the vascular tissue, varies with root age. Three-week-old roots of *O. ficus-indica* shrink 43% when exposed to the very dry conditions of S10 MPa, whereas 12-month-old roots shrink only 6% (Nobel and Cui, 1992b). Very little shrinkage occurs until the soil water potential becomes less than S0.3 MPa, which is essentially the initial water potential of the roots (Nobel and Cui, 1992b). As the soil water potential decreases below S0.3 MPa, the root-soil air gap initially becomes the main limiter of water loss. Water uptake from wet soil is controlled mainly by root properties as described by L_P , but because L_{soil} decreases by a factor of one million as the soil goes from wet (-0.01 MPa) to very dry (-10 MPa), the soil is the ultimate limiter of water loss (Table 1). Equations have also been developed that quantify eccentric locations of roots in the air gaps created by root shrinkage under desiccating conditions (Nobel and Cui, 1992c).

Morphological and anatomical changes in a root of *O. ficus-indica* and its root-soil air gap in the initial stages of drought are important for water movement. Drying in initially moist soil for 30 days causes little change in L_P or anatomy for 1-month-old roots, primarily because of the formation of soil sheaths around the root bound together by root exudates and root hairs (North and Nobel, 1992). For 3-month-old roots, L_P declines 3- to 5-fold during 30 days of drying, partly due to lacunae that develop in the cortex as cells collapse. The dehydration of suberized peridermal layers during 30 days of drying for 12-month-old roots decreases L_P by 2- to 3-fold. Air embolism in the xylem during the 30-day drought greatly decreases axial conductance along the root, further decreasing L_P ; such embolism can be fully reversed by 7 days of rewetting (North and Nobel, 1992). These changes help limit water loss to a drying soil. Under wet soil conditions, the living cells of the cortex are the greatest limiter of water flow from the soil to the root xylem in the young distal part of a root of *O. ficus-indica* with rhizosheaths, whereas at the bare midroot and the proximal part, the cortical cells are dead, and the radial conductance of the cortex is relatively higher compared with other tissues (North and Nobel, 1996). During drought the conductance of the endodermis in the distal region and the periderm at midroot decreases. The radial shrinkage for young roots of *O. ficus-indica* can cause the soil contact in the bare-root region to decrease from 81% to 31% of the root periphery during 21 days of drought (North and Nobel, 1997). Such decreasing root-soil contact as roots shrink and air gaps develop can be visualized in resin-embedded sections of roots in soil and can be reduced by daily vibration of the soil, which increases water flow from roots to a drying soil by reducing the root-soil air gap. Again, the root-soil air gap limits water loss from the cactus to the drying soil in the initial phases of drought.

XYLEM VERSUS PHLOEM WATER FLOW TO DEVELOPING ORGANS

The primary pathway for water movement in plants is the hollow conduits of the xylem. Once water enters a vessel member or a tracheid, both of which are dead cells with thick cell walls, flow occurs down a hydrostatic pressure gradient toward lower water potentials from the root to the stem to the transpiring leaves or other organs (Table 2). Because the flow is in hollow dead cells, no membranes need to be crossed along the xylem, greatly facilitating the flow of water and dissolved inorganic nutrients. The other vascular tissue in plants, the phloem, has living conducting cells surrounded by membranes and is primarily involved with the redistribution of carbohydrates and other organic compounds. Because the conducting lumens of the phloem are surrounded by membranes across which active transport of solutes such as sucrose most likely occurs, flow does not occur passively to regions of lower water potential and can be in the direction of higher tissue water potentials (Nobel, 1991b).

A puzzling observation was that fruits of *O. ficus-indica* have higher water potentials than the cladodes on which they develop (J. L. Andrade and P. S. Nobel, unpublished observations), which contradicts the belief that water moves from the cladodes to the fruits in the xylem. The initial observations were confirmed by more detailed studies, which show that 4-week-old fruits have a water potential that is 0.17 MPa higher than the cladodes on which they develop and 10-week-old fruits have a water potential that is 0.07 MPa higher (Nobel et al., 1994). Thus water is not entering via the xylem (Table 2). By using the stylets (mouth parts) of the cochineal scale insect Dactylopius opuntiae as conduits from the phloem to the cladode surface, the phloem sap was sampled and was found to have an osmotic pressure of only 0.90 to 0.98 MPa (2- to 3-fold less than for most other vascular plants). Thus the phloem supplies a relatively dilute solution to the developing flowers and fruits, which must import essentially all of the carbohydrates needed for their growth. In particular, photosynthesis by flowers and young fruits contributes only 9% of their net carbon gain over the first 30 days, decreasing to 3% at 75 days when the fruits reach maturity (Inglese et al., 1994). The daily dry-weight gain indicates the carbohydrate input via the phloem, which, along with the phloem sap concentration, can be used to calculate the amount of water delivered. Such water entry exceeds the daily water gain of the fruits by about 50%. Some of the excess water returns to the underlying cladodes by flowing energetically downhill toward lower water potentials in the xylem and the rest is lost by transpiration. Thus, the dilute phloem sap supplies both the organic compounds and the water needed to support the growth of the fruits.

Table 2. Relative Water Flow into Developing Organs of *O. ficus-indica*.
Water entering developing organs of plants can be supplied by the xylem flowing toward regions of lower water potential (usual method) or by the phloem in concert with photosynthetic products needed for growth (accompanying dry-weight increases).

Organ	Water Supplied	Description
Daughter cladodes	Phloem up to about 4 weeks, xylem	Are sink organs for the first 4 weeks of development when thereafter they require daily inputs of dry weight.
Fruits which	Phloem	Fruits always have a higher water potential than the cladode on they develop; photosynthesis by the fruit never matches its need for daily dry-weight increases.

In contrast to fruits, which are constantly a sink organ and always require an input of organic compounds from the underlying cladode, daughter cladodes of *O. ficus-indica* are dependent on the underlying mother cladodes for only approximately 4 weeks (Table 2; Luo and Nobel, 1992). For instance, a 14-day-old daughter cladode is a sink organ with a negative daily net CO_2 uptake. The water potential of such a daughter cladode is higher than that of the underlying cladode, again implicating the phloem as the tissue that delivers water as well as organic compounds (Wang et al., 1997). In particular, the relatively dilute phloem sap (dry weight of 7.4%) of the underlying cladode supplies all the water (7.1 g per day) along with photosynthate needed for the growth of a 14-day-old cladode. About 3% of the water imported into the daughter cladode flows back to the underlying cladode in the xylem (Wang et al., 1997). This is one of the first demonstrations that the phloem can be the water supply pathway for a developing vegetative organ. In another study, the maximal growth rate of daughter cladodes occurs sooner as the conditions for net CO_2 uptake improve, e.g., maximal growth of new cladodes occurs at 20 days under a relatively low light level, 15 days when that light level is doubled, and 12 days when the light level and the ambient CO_2 concentration are both doubled (North et al., 1995).

ORGAN INITIATION ON UNROOTED CLADODES

Detached cladodes of *O. ficus-indica* and other platyopuntias, which can remain alive for over 12 months and readily form new roots when placed in moist soil, can be a valuable model system for studying stem responses to the environment independent of signals coming from the roots. For instance, injecting the putative cryoprotectant glucose into detached cladodes using a syringe with a fine needle (0.6 mm external diameter for *O. ficus-indica* and 0.4 mm for the smaller cladodes of *O. humifusa*) mimics the low-temperature acclimation caused by reducing the day/night air temperatures by 20°C (Table 3; Nobel et al., 1995). Such an injection technique can also be used to study the effects of hormones and other compounds on the initiation of new organs on unrooted cladodes.

Injections of sucrose, KCl, and KNO_3 into unrooted cladodes of *O. ficus-indica* accelerate initiation of daughter cladodes (Table 3). Compared with the weekly injection of water equivalent to 1% of the cladode fresh weight for 6 weeks, injection of 1.5 M sucrose accelerates daughter cladode initiation by 1.4 weeks, injection of 750 mM KCl accelerates it by 3.0 weeks, and injection of 750 mM KNO_3 accelerates it by 4.8 weeks (Nobel, 1996b), although the mechanism for this growth acceleration is not apparent. The daughter cladodes have a higher water potential and a lower percentage dry weight than the unrooted detached cladodes on which they develop, again indicating that water enters primarily via the phloem.

Injection of hormones into unrooted cladodes of *O. ficus-indica* has various effects (Table 3). Injection of 20 FM gibberellic acid (GA$_3$ and GA$_4$) weekly for 6 weeks, leading to an average tissue concentration of 1 μM that promotes stem elongation and inhibits flower formation for various species, virtually eliminates the initiation of daughter cladodes (Nobel, 1996b). Such injection leads to extensive spine development on the few small daughter cladodes that are produced. Injection of massive single doses of gibberellic acid in the field in Sicily completely inhibits daughter cladode or fruit formation for *O. ficus-indica* (Barbera et al., 1993). Injection of 800 μM of the auxin indole-3-acetic acid, which can stimulate stem elongation and affects apical dominance, accelerates daughter cladode initiation on unrooted cladodes by 3.1 weeks (Nobel, 1996b). Injection of 800 μM of the cytokinin kinetin, which affects cell division and

production of shoot branches, accelerates daughter cladode initiation by 4.0 weeks. By accelerating initiation, injection of both indole-acetic-acid and kinetin lead to a greater biomass for the new organs over an 18-week observation period (Nobel, 1996b).

Table 3. Organ Initiation on Detached Unrooted Cladodes of O. ficus-indica

Condition	Result
Injection of glucose	Leads to increased tolerance of low temperatures
Injection of methylglucose	Similar to injection of glucose, indicating that tissue response is to solute/water ratio
Injections of sucrose, KCl, KNO₃	Accelerates daughter cladode initiation
Injection of gibberellic acid	Greatly decreases number of daughter cladodes
Injections of indole-3-acetic acid	Accelerates daughter cladode initiation or kinetin
Shading proportional	Greatly reduces new organ initiation (approximately to reduction in light)
Season for detachment	Daughter cladode initiation greatest in the spring (winter detachment), much less for other seasons
Day/night air temperatures	Low temperatures (15°C/5°C) favor fruits, high temperatures (35°C/25°C) favor daughter cladodes

Shading of detached unrooted cladodes of *O. ficus-indica* by 94% essentially eliminates the initiation of daughter cladodes over the 18-week observation period (Nobel, 1996b). Such shading is accompanied by less transpiration and lower photosynthetic activity in the detached cladodes (Nobel and Castañeda, 1997). For unrooted cladodes maintained unshaded for 14 weeks in a glasshouse with average day/night air temperatures of 28°C/15°C, initiation of new organs, most of which were daughter cladodes, varies seasonally. Initiation of new organs is greatest when the cladodes are detached in the winter, decreasing 64% for those detached in late spring and 97% for those detached in late summer (Nobel and Castañeda, 1997). Such seasonal and light responses (Table 3) are consistent with field observations on whole plants of *O. ficus-indica* (Acevedo et al., 1983; Nobel, 1982, 1988).

Unrooted cladodes detached in the winter have also been maintained for 14 weeks in environmental chambers with specific day/night air temperatures. At 15°C/5°C the new organs are 10 times more likely to be fruits than daughter cladodes, at 25°C/15°C either organ is equally likely, and at 35°C/25°C the new organs are 10 times more likely to be daughter cladodes than fruits (Table 3). How low day/night temperatures favor initiation of reproductive organs and high temperatures favor vegetative organs is not clear, but future investigation using unrooted cladodes maintained under various temperatures, thermoperiods, and photoperiods may help elucidate the mechanisms underlying such environmental responses.

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