

Three Decades of Ecophysiological Research (1976-2007) in the Northwestern Sonoran Desert Starring Two Savvy Succulents

This chronological history summarizes the principal findings of Park S. Nobel (Distinguished Professor of Biology Emeritus, University of California, Los Angeles) and his research group for Agave Hill. The site is a series of small hills with a mean elevation of 830 m in the Philip L. Boyd Deep Canyon Desert Research Center, just south of Palm Desert, California. The Research Center covers 24.8 square kilometers (9.6 sq miles) and is part of the University of California Natural Reserve System.

Research focused on a common desert agave, *Agave deserti* Engelm., and a barrel cactus, *Ferocactus acanthodes* (Lem.) Britton & Rose. Sympatric species were included for comparison. A quantitative understanding of plants in their native environment was emphasized together with accompanying laboratory measurements under controlled conditions and simulations using computer models.

Science works slowly, and many small steps are usually necessary to advance our knowledge substantially. In the present case, insights benefited from a confluence of disciplines ranging from engineering to plant anatomy plus an outstanding cadre of more than 50 collaborators on 113 publications. Numbers at the end of paragraphs refer to these publications, which are fully cited in the CV. This summary distills the main findings into a few sentences per paper, so the originals should be consulted for methodology and specific details.

1976

Agave deserti, the common agave in the northwestern Sonoran Desert, was transferred from the field to the laboratory along with some desert ferns (*Notholaena parryi*). By mistake, the ferns were watered for the first time after 12 weeks and shriveled up, whereas the water-conserving agaves were watered daily. Initially, the agaves had appreciable CO₂ uptake only during the nighttime, as is typical of Crassulacean acid metabolism (CAM) plants. But the excessive watering of the agaves eventually caused essentially all of their CO₂ uptake to occur during the daytime, as expected for C₃ plants (46).

Agave deserti has very shallow roots, with a mean depth of 8 cm, so it could respond to light rainfalls (e.g., 7 mm). Increasing nighttime temperatures from 5C to 20C decreased stomatal conductance 5-fold, showing the importance of cool temperatures for optimal CO₂ uptake (47).

1977

The barrel cactus *Ferocactus acanthodes* continued appreciable stomatal opening for 40 days in drying soil using water stored in its large, globular stem. During 7 months of drought,

just over half of the stem water was lost. But its shallow roots (mean depth of 8 cm) took up considerable water 24 hours after a rainfall. The optimal nighttime temperature for CO₂ uptake was a cool 13C. Flowering required about 6% of the stem's wet weight. A plant 34 cm tall increased in mass about 10% during a typical year, indicating that it was about 26 years old (49).

During the 159 days from inflorescence emergence to seed maturity for *Agave deserti*, about 17 kg of water was transferred from the leaves to support reproduction, with most going to the flowers (especially for their nectar). The inflorescence consumed the entire annual productivity of a plant, hastening plant death. Only about one seed in 1.2 million produced a plant, as reproduction occurred mainly vegetatively by offshoots (ramets) near the base of a plant (50).

Ferocactus acanthodes was modeled using over 100 internal and external regions (sub-volumes), leading to temperature predictions within about 1C of measured values. Eliminating transpiration in the model caused less than 1C rise in surface temperature, indicating that evaporative cooling was not important for this cactus. Stomatal conductance decreased as temperature increased. Spines moderated the surface temperature over 24-hour periods. Ribs increased convective heat exchange compared with a smooth surface (53).

As the photosynthetically active radiation (PAR; now often called the photosynthetic photon flux, PPF) increased during growth, the new leaves of the perennial subshrub *Encelia farinosa* became smaller and thicker. The thicker leaves had a greater chlorenchyma (photosynthetic tissue) surface area per unit leaf area and hence a higher CO₂ uptake rate (57).

1978

Rock outcroppings protected *Notholaena parryi* from direct sunlight (it occurred predominantly on their north sides) and also channeled water to its roots. The stipe had a small conducting area, leading to extremely high water potential gradients for this diminutive desert fern. It had a large number of chlorophyll molecules per photosynthetic unit, as is typical of plants from shaded habitats (55).

Two equivalents of acidity were produced for each mole of CO₂ taken up at night by *Agave deserti*. Nocturnal CO₂ uptake became maximal for 35 moles of photons incident per square meter the previous day, a relatively high level, suggesting that light was limiting for this CAM desert succulent. A large internal leaf area (about 82 times the leaf surface area) was required to support the moderate rate of CO₂ uptake (56).

The energy budget model developed for *Ferocactus acandodes* was extended to the much smaller cactus *Mammillaria dioica* [and the much larger *Carnegiea gigantea* ("saguaro") in Arizona]. In the absence of spines, *M. dioica* would be about 2C cooler at night and 5C warmer during the daytime. The effect was greatest at the apex, where a mat of pubescence further protected the apical meristem from daily extremes in temperature (59).

1979

Increases in temperature decreased stomatal conductance during both the daytime and the nighttime for *Agave deserti*. Stomatal responses to water vapor concentration and atmospheric CO₂ level were much less important than the effects of temperature (60).

Water stress during the seedling stage is the most crucial factor affecting establishment of *A. deserti*. In particular, its leaves must develop enough biomass during the first wet season to survive the ensuing drought. Only one year in the last 17 (1967) was suitable for establishment, consistent with the size of its six smallest specimens observed in 1,500 square meters at Agave Hill (62).

1980

The interception of light by cacti with ribs was simulated. Deeper ribs led to more surface area but less light interception per unit stem area, so total net CO₂ uptake was little affected by rib size (66).

The major factor influencing stomatal opening for the perennial bunchgrass *Hilaria rigida* was the availability of soil water. Thus CO₂ uptake was maximal for wet periods in the relatively cool winter/early spring and late summer/early autumn. Under optimal field conditions, its net CO₂ uptake rate (67 micromol m⁻² s⁻¹) was the highest reported for any species (68).

Nocturnal acidity increases of *Agave deserti* were 90% saturated for 25 moles of photons per square meter of leaf area. Simulated removal of half of the basal rosette of massive opaque leaves increased the photons on the remaining leaves but decreased the plant nocturnal acidity increase by 31%. Light absorption for plants on steep slopes facing in any direction was less than on the horizontal. Light was generally found to be limiting for its net CO₂ uptake, even under the high light regime of a desert (70).

Using a model that predicted the minimum stem surface temperature, the influences of stem mass, spines, and apical pubescence were evaluated for four species of *Ferocactus*. *Ferocactus acanthodes* had the highest minimum apical temperatures and also ranged to the coldest habitats. [Using the same model for cacti in Chile, the upper elevational limit of *Eriosyce ceratistes* and *Trichocereus chilensis* along a large latitudinal gradient indicated that the populations were responsive to temperature changes of only 0.1C] (72).

1981

The 30 smallest seedlings of *Ferocactus acanthodes* averaged 2.5 cm in height and apparently became established in late summer 1976. Eight of the last 18 years had sufficiently long growing seasons relative to the subsequent drought length to allow establishment (76).

Cladodes of platyopuntias such as *Opuntia chlorotica* oriented to get the highest light absorption at times of the year most favorable for their development. Stems of barrel cacti such as *F. acanthodes* tilted toward the equator; this raised the temperature of the apical meristem during the winter, as well as served as an informal compass (77).

Leaves on smaller clumps of *Hilaria rigida* had much higher transpiration rates but much less leaf area per unit ground area than for larger clumps. Consequently, the depth of water transpired did not depend markedly on clump size. The amount of CO₂ fixed per unit ground area also did not vary with clump size. Hence the pattern of large versus small clumps apparently is quite persistent in time (80).

When day/night air temperatures for various agaves and cacti were raised from 10C/10C to 30C/30C, the optimal temperature for nocturnal CO₂ uptake increased from 12C to 20C. The shifts occurred in a few days, indicating that the plants could respond to weather changes (82).

1982

For *Opuntia bigelovii* (“jumping cholla,” “teddy bear cholla”) maintained at day/night air temperatures of 30C/20C, nocturnal acid accumulation was half-inactivated by 1 hour at 46C and uptake of the vital stain neutral red decreased 50% at 52C; a heat treatment of 52C also caused the stems to become necrotic in 2 weeks. The plants had a 50% survival rate when exposed to 59C for 1 hour when acclimated to day/night temperatures of 50C/40C, indicating a great tolerance of high temperatures by this cactus (85).

The preferred orientation of terminal cladodes of *Opuntia chlorotica* was facing north-south (when one side faces north, the other side faces south). This is consistent with their development in the wintertime when most rainfall occurs at Agave Hill, as such an orientation maximizes the interception of light at that time of year (87).

Based on 50% inhibition of neutral red uptake, *Ferocactus acanthodes* tolerated -8.4C and *O. bigelovii* tolerated -7.3C, which were compared with similar cacti from other regions and support the notion that cacti are not particularly tolerant of freezing temperatures (89).

Peaks in the height distribution of *F. acanthodes* occurred at 5 cm and 19 cm. Based on the estimated annual growth, these peaks corresponded to establishment in 1976 and 1959, when the seedlings grew to a large enough size to sustain the plants through the first ensuing major drought (90).

1983

Removing spines from *Ferocactus acanthodes* reduced the PAR for 90% saturation of nocturnal acid accumulation by more than half. Similarly removing spines from *Opuntia bigelovii* caused a 60% greater stem volume over 2.5 years. Thus spines decrease plant growth. Spine removal increased stem temperature during the daytime and lowered it at night (93).

The number of ribs at mid height on *F. acanthodes* had major peaks at 5, 8, 13, and 21. These are all Fibonacci numbers (the next number is 34), obtained as the sum of the two previous numbers in the series (94).

A simulation model similar to the one developed for cacti predicted leaf temperatures for *Agave deserti* to within about 1C. Leaf temperature was highly sensitive to air temperature, whereas substantial nocturnal stomatal opening reduced leaf surface temperatures only about 1.4C for its massive leaves (95).

Calcium levels in *F. acanthodes*, *Opuntia basilaris*, and *O. bigelovii* were higher and sodium levels were lower compared with agronomic plants. Nocturnal acid accumulation increased with chlorenchyma nitrogen level, as expected (97).

The C₃ subshrub *Encelia farinosa*, the C₄ bunchgrass *Hilaria rigida*, and the CAM succulent *A. deserti* are sympatric codominant desert perennials at Agave Hill. The grass had thin leaves while the leaves of the succulent were extremely thick, leading to different strategies in their water relations (98).

Removal of plants surrounding *H. rigida* caused the remaining ones to become larger over a 1-year period. New culms were more prominent and root systems expanded when the competition from neighboring plants was removed (100).

The high and low temperature tolerances of *A. deserti* were compared with those of 13 other agave species. All exhibited acclimation to temperature extremes, but *A. deserti* acclimated particularly well at low temperatures, consistent with its more northerly distribution (101).

1984

Ferocactus acanthodes and *Opuntia basilaris* survived an 80% loss of stem water. Most of the net water loss came from the internal water-storage parenchyma. The greater water retention in the outer photosynthetic chlorenchyma resulted in less disruption of photosynthesis by these cacti during drought (104).

Opuntia bigelovii tolerated temperatures at least 4C hotter in the summer than in the late fall/winter. The shift in tolerance was quite rapid, about half occurring in 1 day and 90% occurring in 4 days (105).

Excised roots of *Agave deserti* and *F. acanthodes* lost most of their water uptake ability after 6 hours under drying conditions but regained their ability after 6 hours of rewetting. Thus the roots of these desert succulents would not lose much water to a drying soil but readily take up water after rainfall, acting like rectifies with respect to soil-plant water movement (106).

Soil surface temperatures can reach the extremely high value of 70C (158F) at Agave Hill. Shading reduced this by 11C (and raised minimum temperatures by 3C). Seedlings of *A. deserti* and *F. acanthodes* tolerated tissue temperatures over 60C when acclimated to high temperatures, and they tolerated -8C when acclimated to low temperatures (110).

An environmental productivity index (EPI) was developed based on the response of plants to temperature, water availability, and PAR. EPI closely predicted the growth and productivity of *A. deserti* determined by the monthly unfolding rate of new leaves. The component Water Index (maximum value of 1.00) was the most important contributor to EPI for *A. deserti* in this desert environment (111).

Roots of *A. deserti* and *F. acanthodes* lengthened 27% to 47% during two weeks after a substantial rainfall. Root tissue rapidly lost water during drought, thus shrinking and lessening contact with the soil; plants then lost little water to a drying soil. Roots of both species tended to be absent from the upper 2 cm of soil due to the high soil temperatures there (112).

Simulations indicated that increasing the number of ribs for *F. acanthodes* up to 34 (typical maximum number) at a typical rib depth increased the plant CO₂ uptake. Its rib depth and spacing varied with compass direction, which had little effect on CO₂ uptake (114).

1985

Growth of seedlings of *Agave deserti* was quite sensitive to salinity, e.g., 25 mM NaCl prevented growth in sand culture. Nocturnal acid accumulation was negatively correlated with chlorenchyma sodium. Seedlings tolerated calcium, a wide range of pH, and high boron (120).

Roots of *Ferocactus acanthodes* were sensitive to salinity (stress shown at 25 mM NaCl) but not to slightly elevated levels of copper or zinc (121).

The key to the ecophysiology of *A. deserti* is soil water. Only one year of the last 19 allowed seedlings to develop enough biomass to endure the drought in their first year (124).

Agave deserti had a high water-use efficiency (net CO₂ uptake per unit of water transpired). Its rosette growth habit led to a relatively uniform distribution of PAR over the leaves, which is optimal for CO₂ uptake and contributed to its high productivity for a desert plant (125).

The fatty acid composition of the chlorenchyma of *A. deserti* and *F. acanthodes* was similar to that of mesophytic leaves, except that these desert succulents had more saturation (e.g., more oleic acid). For *F. acanthodes*, shifting to higher temperatures increased fatty acid saturation (127).

1986

Leaf unfolding of *Agave deserti* at elevations from 300 m to 1200 m was highly correlated with EPI, formed as the product of indices for water, temperature, and PAR. Temperatures were optimal for CO₂ uptake at low elevations in the winter and at high elevations in the summer, whereas the Water Index steadily increased with elevation in response to a 3-fold increase in rainfall (132).

Raising the growth temperature raised the high temperature tolerated by *A. deserti* and *Ferocactus acanthodes*. The rise was half completed in 3 days and neared completion in 10 days. It was accompanied by the accumulation of "heat-shock" proteins (133).

For a group of *F. acanthodes*, the average monthly growth predicted using EPI was highly correlated with the production of new areoles at the apex. For individual plants, however, the areole production came in spurts consistent with Fibonacci numbers (134).

A computer model closely predicted the soil water potential as a function of depth in the soil and rainfall events. About two-thirds of the annual rainfall at Agave Hill evaporated from the soil surface. Succulent plants could take up water from 57 days to 229 days per year, depending on the amount and timing of the rainfalls (136).

Seedlings of *F. acanthodes* are subjected to the high temperatures near the soil surface, which can reach 70C. Except directly under the stems, high temperatures kept the roots out of the upper few cm of soil (137).

Parent-ramet connections for *A. deserti* greatly enhanced ramet growth and survivorship compared with its seedlings. Parents supplied water to ramets for up to about 14 years, when they achieved independence. This water source was crucial in environments where water is limiting and seedling establishment is rare (138).

Growth of seedlings and mature plants of *A. deserti* in hydroponics and sand culture was enhanced by increasing potassium, phosphate, and especially nitrogen. The rate of growth in the field was doubled by adding 100 kg N per hectare (140).

The ground area explored by the roots of small, medium, and large clumps of *Hilaria rigida* increased by 17% over 4 years in undisturbed sites but by 125% when the surrounding vegetation was removed. Culms then increased by 7% and 151%, respectively. Because of the relative lack of growth in undisturbed areas, spatial patterns appeared to be quite stable in time, indicating that some clumps were hundreds of years old (148).

1987

The percentage of rosettes of *Agave deserti* that flowered in a particular year was highly correlated with the amount of rainfall two years previously. Years with much flowering tended to be followed by years with little flowering. Small flowering rosettes were always attached to large flowering rosettes, suggesting that a chemical signal led to the precocious flowering of the attached small ones (150).

A model predicting soil temperature indicated that the maximum soil surface temperature was markedly influenced by shortwave irradiation, wind speed, air temperature, and rainfall events. Such temperatures decreased by about 2C for each 10% increase in shading, validating the major effect of nurse plants on the local microclimate (151).

A model predicted water uptake by *A. deserti* and *Ferocactus acanthodes* for soil layers at various depths. For a typical year, *A. deserti* took up 42% of the annual precipitation and *F. acanthodes* took up 25%. The mean root depth was only 10 cm, even though the roots were mostly excluded from the upper 5 cm because of locally high soil temperatures (153).

For the soil area explored by the roots of *A. deserti* and *F. acanthodes*, water uptake was predicted to be 85% of the maximum possible, indicating a high uptake efficiency. Average water uptake per unit root explored area was nearly constant per unit shoot surface area (154).

The reflectance of leaves of *A. deserti* correlated with their leaf relative water content. For *Encelia farinosa* and *Hilaria rigida*, the fraction of dead leaves needed to be taken into account to interpret the reflectance signal (158).

Acclimation leads to a tolerance of very high temperatures for electron transport and photosynthetic reactions for *A. deserti*, facilitating its survival in hot deserts (159).

Agave deserti has both established (long-lived) roots and rain roots (induced on established roots by water). The latter were shed an average of three times per year during recurring droughts in the field. Respiration required for growth and maintenance was much higher for the rain roots (160).

Predicted daily water uptake closely matched daily transpiration for *E. farinosa* and *H. rigida*, but not for *F. acanthodes*. For the latter with its large water storage capability, steady-state water flow is not expected in the field (163).

Taking into account the nocturnal change in tissue acidity and hence osmotic pressure, about half of the water transpired by *A. deserti* at night came directly from the leaves. The leaf water was recharged mainly during the daytime when the stomates closed and transpiration was greatly reduced, as is characteristic of CAM (165).

1988

Ramets and parents of *Agave deserti* are physiologically integrated and grow as a unit. Shading the ramets caused a substantial reduction in the reserves of non-structural carbohydrates in the parents. Shading the parents led to movement of carbohydrates from the ramets to the parents (170).

Shaded, isolated ramets of *A. deserti* could use their stored nonstructural saccharides to grow. Also, shaded, isolated mature plants could produce new leaves for 6 months (171).

Fertilization with 100 kg per hectare of P, K, Ca, and B for *A. deserti* had little effect, whereas 100 kg per hectare of N increased its rate of leaf unfolding by about 50%, underscoring the limitation of nitrogen for plant growth in desert soils (174).

Seedlings of *A. deserti* were observed only in sheltered microhabitats, mostly shaded by *Hilaria rigida*, leading to protection from high incident solar irradiation and hence high soil surface temperatures. The bunchgrass halved agave water uptake, reduced PAR up to 74%, but was associated with 60% higher soil nitrogen. Predicted net CO₂ uptake was approximately halved compared with an exposed seedling (176).

1989

For *Agave deserti* under wet conditions, 55% of nighttime transpiration was derived from water stored in the plants. The higher osmotic pressure in the green chlorenchyma versus the whitish water-storage parenchyma caused water flow into the chlorenchyma during drought. During drought root resistance also increased substantially. Recharge of plant water storage took about 1 week after rainfall (178).

The daily pattern of respiration for both established and rain roots of *A. deserti* closely followed the daily pattern of root temperature. Respiration increased 7-fold from 5C to 40C and decreased with root age. Extensive drought caused respiration to cease for rain roots and was not re-established upon rewetting (180). Similar responses occurred for *Ferocactus acanthodes* (182).

Respiration increased with soil O₂ up to about 16% for established roots of *A. deserti* and 5% for its rain roots. Soil CO₂ levels of 2% abolished respiration and killed root cortical cells in about 4 hours. The soil CO₂ level in the field averaged 0.1% in the root zone, much lower than for most agronomic plants. These responses may explain why desert succulents tend to occur in porous, well-aerated soils (183).

Water uptake by *Hilaria rigida* substantially reduced the water availability for seedlings of *A. deserti* and *F. acanthodes* associated with this nurse plant. The nurse plant lowered P and Na but raised N and K, especially for the shallow layers. The increased nitrogen substantially benefited the seedlings (187).

Most seedlings of *F. acanthodes* occurred with nurse plants, which reduced maximum temperatures by about 10C. Shading and competition for water by the nurse plants both reduced seedling growth (189).

Ferocactus acanthodes exhibited appreciable water storage and large daily fluctuations of osmotic pressure in the chlorenchyma. The internal redistribution of water was dominated by these changes in osmotic pressure, not by transpiration (190).

1990

Agave deserti flowers after 50 to 55 years. During the course of flowering, nonstructural carbohydrates in the leaves decreased from 38% to 6% of the leaf dry mass. The released sugars were transferred to the growing inflorescence, providing 70% of its requirements (the remaining 30% came from concurrent photosynthesis in the leaves and the inflorescence). Severing the rhizome connection arrested the development of inflorescences for small rosettes attached to the flowering large rosettes (193).

Root growth for *A. deserti* was completed 1 month after soil rewetting. It was greater in the summer with its warmer temperatures but varied 18-fold among years with their different rainfall amounts and timing. Root spatial overlap with the nurse plant *Hilaria rigida* reduced seedling growth (194).

The root hydraulic conductivity of *A. deserti* increased 4-fold as the temperature was increased from 0.5C to 40C. The hydraulic conductivity was highest for young (3-week-old) roots, becoming halved at 10 weeks and halved again at 6 months (196).

Roots of *A. deserti* and *Ferocactus acanthodes* tolerated soil anoxia (0% O₂) for days whereas elevated carbon dioxide levels (2% CO₂) led to death of root cells in hours. Hence restriction of these desert succulents to porous soils may reflect the inhibitory effects of CO₂ rather than the requirement for high O₂ levels. Also, desert soils have a low gas-phase CO₂ level of 0.1% compared with 1% or more that is typical in the root zone of non-desert species (201).

Parent plants of *A. deserti* could export 3.3% of their assimilated carbon to attached ramets in 7 days. Shading the ramets caused more carbon to be imported by them. The physical integration enabled ramets to draw upon the reserves of the parent for up to 14 years, facilitating ramet growth in a resource-limited environment (205).

1991

Predicted water uptake by individual roots of *Agave deserti* and measured root hydraulic conductivity closely matched the measured transpiration of the leaves. Also, the predicted root respiration closely matched the measured respiration. Thus the respiratory cost of water

acquisition by the root system can be accurately assessed based on the behavior integrated for individual roots (210).

Root hydraulic conductivity for *Ferocactus acanthodes* increased with root age up to 11 weeks and then decreased. The hydraulic conductivity gradually increased with soil temperature up to 50C, but it rapidly decreased as the soil water content decreased. The latter provides a rectifier-like behavior for water movement between soil and roots during soil drying (211).

As the soil dried, the water potential of roots of *A. deserti* became similar to that of the shoot and remained so as the soil became very dry. Also, as the plants were shaded, the root water potential became similar to that of the shoot, again indicating little flow of water through the plant then (215).

As the soil dried during 1 month, cortical lacunae (air spaces in the cortex), cell shrinkage, and cell collapse were more apparent for lateral rain roots than for established nodal roots of *A. deserti*. The younger was the root, the less that rewetting reversed this. Cortical lacunae, embolism, and increasing suberization caused the hydraulic conductivity to decline during drought, thereby helping limit water loss to a dry soil (216).

Tritiated water and stable isotopes showed that water moved from the water-storage parenchyma to the chlorenchyma at night for *A. deserti* and *F. acanthodes*. This reflects the increasingly higher osmotic pressure in the chlorenchyma due to nocturnal carbon fixation (217).

Echinocereus engelmanni has short stems in tightly packed clumps, whereas *Opuntia acanthocarpa* has much taller, freely branching stems. The denser spine coverage for the former resulted in half as much nocturnal acidity increase and CO₂ uptake. For *O. acanthocarpa*, three-fold greater root area per shoot area was consistent with its three-fold higher transpiration (224).

1992

New roots of *Agave deserti* and *Ferocactus acxanthodes* have low respiratory costs for growth compared with other species. The carbon costs represented mainly carbon incorporated structurally into the roots, not growth respiration. For *A. deserti*, the water acquired from the soil per unit carbon expended was twice as high for lateral (rain) roots compared with 2-year-old nodal (established) roots (228).

The average annual flowering percentage indicated that the mean life expectancy of *A. deserti* was 53 years. Over a 29-year period, successful seedling establishment occurred only twice. About 99% of reproduction was by ramets. Annual ramet production varied about 15-fold due to different environmental conditions, which could be accurately predicted using EPI (229).

Soil sheaths protected young roots of *A. deserti* during 30 days of drought. Embolism increased during drought, which decreased the axial conductance, especially for older roots. Rewetting the soil restored the conductance in about 7 days (230).

Large drops in water potential were predicted and measured along the xylem of roots of *A. deserti*. Thus the driving force from wet soil to the xylem of young roots may be relatively small compared with the force required along the roots (231).

Roots of *A. deserti* and *F. acanthodes* 2 mm in diameter radially shrank about 20% during 30 days of soil drying, leading to an air gap. The predominant limiting factor for water movement was the root hydraulic conductivity during the first 7 days of drying of wet soil, the root-soil air gap during the next 13 days of soil drying, and the soil hydraulic conductivity thereafter. The soil was hence the main long-term rectifier in the soil-root system (232).

Mucilage content in the stems increased from *F. acanthodes* to *Opuntia basilaris* to *Opuntia acanthocarpa* to *Echinocereus engelmannii*. The relative capacitance for stem water storage increased in the same order. Associated solutes also influence the water-release characteristics of mucilage and its role as a water capacitor (234).

During soil drying, the hydraulic conductance at the root-stem junctions of *A. deserti* and *F. acanthodes* decreased substantially due to embolism. Because the embolism is readily reversed upon rewetting, these junctions acted as rectifiers (236).

Embolism at the junctions between main roots and lateral roots of *A. deserti* and *F. acanthodes* decreased axial hydraulic conductivity as the soil dried. Such embolism decreases water flow from the plants to the soil during drought (237).

The drought-induced decreases in hydraulic conductivity of lateral roots of *A. deserti* and *F. acanthodes* reflected the dehydration of cortical cells as well suberization of various root layers. Some of the decrease was reversed upon rewetting the soil, which also induced the formation of secondary lateral roots (238).

For roots of *A. deserti* about 3 mm in diameter, the hydraulic conductance of the air gap surrounding a root decreased as the gap size increased. An eccentric location of roots in the air gap, as expected in the field, led to a higher conductance than a concentric location (239).

For *A. deserti*, *F. acanthodes*, and *O. acanthocarpa*, the number of lateral roots per unit length of main root averaged seven-fold higher alongside rocks compared with rock-free regions. The number and length of lateral roots was even higher under rocks. Boulders also increased the local root frequency for *E. engelmannii*. The primary influence of rocks on root proliferation and branching was the local increase in the availability of water, not their influences on soil temperature (240).

About half of the lateral roots of *A. deserti* abscised after 3 weeks of drought, which was defined as beginning when a plant could no longer take up water from the soil (241).

For *A. deserti* and *F. acanthodes* in the field, mycorrhizae were present along 2% to 11% of the roots. The mycorrhizal infection apparently enhances water and nutrient uptake, especially for P and Zn (244).

1993

During wet conditions, the hydraulic conductivity, radial conductivity, and axial conductance increased with distance from the tip for lateral roots of *Ferocactus acanthodes*. The increase in axial conductance and its decrease during drought were associated with changes in the number of conducting xylem vessels. Rewetting decreased emboli and led to the recovery of axial water flow (248).

During soil drying, the radial conductivity at main root-lateral root junctions for *Agave deserti* and *F. acanthodes* actually increased due to the formation of an apoplastic pathway. As opposed to the monocotyledon *A. deserti*, the dicotyledon *F. acanthodes* formed new conduits in its secondary xylem during 21 days of soil drying and only 10% of its lateral roots abscised during 1 month of drought (249).

For *A. deserti*, the radial conductivity decreased with distance from the root tip, favoring water uptake by the distal (younger) portion. For *F. acanthodes*, the axial conductance increased greatly away from the root tip, favoring water uptake from the proximal (older) portion. For roots with different simulated vertical orientations, water uptake was highest for the younger roots of *A. deserti* but for the older roots of *F. acanthodes* (255).

1995

For *Agave deserti*, suberization greatly decreased the radial conductivity at mid-root after 1 month of drought. Rewetting could not overcome all of the effects of suberization and collapse of cortical cells, thus new apical growth and the development of new lateral roots was necessary for complete restoration of its root system conductivity. The cortical apoplast was a significant pathway for its radial water flow (278).

The carboxylation capacity of *Encelia farinosa* grown in full sunlight was greater than for plants grown in the shade. Sun plants also had higher photosynthetic electron transport rates. Under water stress, stomatal conductance decreased more for the shade plants (280).

1996

Doubling the atmospheric CO₂ concentration increased daily net CO₂ uptake for *Agave deserti* by 49% over 17 months, decreased daily transpiration by 24%, and hence doubled the water-use efficiency. More leaves, each with a greater surface area, were produced per plant under the doubled CO₂ concentration. Thus, an 88% stimulation in dry mass accumulation occurred under the doubled CO₂ level (288).

The optimal temperature for root elongation in the winter was 25C for *Encelia farinosa*, 30C for *A. deserti*, and 35C for *Pleuraphis (Hilaria) rigida* in the winter and 2C to 3C higher in the summer. Summer temperatures favored photosynthesis and root elongation for *E. farinosa* and *P. rigida*. A doubled atmospheric CO₂ concentration increased root elongation rates only for *A. deserti* (291).

After maintaining *E. farinosa* under a doubled atmospheric CO₂ concentration for 3 months, its photosynthetic rate was 46% higher in the morning, decreasing to 15% higher in late afternoon, compared with rates under current CO₂ levels. The increases were accompanied by higher sugar and starch concentrations. The carbon movement out of the leaves was faster under the doubled CO₂ concentration (293).

For *E. farinosa* and *P. rigida*, the ratio of intercellular CO₂ concentration (or partial pressure) to atmospheric CO₂ concentration depended linearly on the vapor pressure deficit (the difference in partial pressure of water vapor between the ambient air and the leaf; 296).

1997

Droughting *Agave deserti* for 3 weeks led to about 30% radial shrinkage of its roots. The resulting air gaps decreased water loss by the roots, which was important in the early stages of drought (300).

Roots of *A. deserti*, *Encelia farinosa*, and *Pleuraphis rigida* averaged only 9 to 10 cm in depth. New roots initiated in the winter were shallower, while those in the summer were deeper, reflecting the accompanying soil temperatures. A lower leaf water potential allowed *P. rigida* to extract water from dryer soils than *A. deserti*; *E. farinosa* had more leaf area and a higher transpiration rate than *P. rigida*, leading to more water uptake by the former (302).

Thirty-three perennial species were identified at Agave Hill, with *A. deserti* (33% of total ground cover), *E. farinosa* (13%), and *P. rigida* (15%) being the highest. On all but south-facing slopes, *A. deserti* was dominant (303).

Based on an EPI analysis of the three co-dominants at Agave Hill, *A. deserti* was the most drought tolerant and *P. rigida* was the least. The highest photosynthetic rate occurred for *P. rigida*. For *A. deserti*, new leaves unfolded year-round in response to rainfall, leading to the highest annual net CO₂ uptake per unit ground area, especially due to its older leaves (307).

For *E. farinosa*, the key for relative frequency versus ground slope was its greater root growth on the warmer slopes during the winter. For *A. deserti*, the key was water availability during the seedling stage. The wetter conditions on north-facing slopes led to much larger clumps of *P. rigida* there. Hence root properties may exert the primary influence on the relative frequency of these three species, as the soil temperature and water availability are crucial (308).

1998

Agave deserti is apparently the first flowering plant showing that oligofructans (fructose polymers with a terminal glucose) are synthesized and transported in the phloem. The main sugar in the phloem sap was sucrose, followed by the oligofructan 1-ketose, fructose, glucose, and then other oligofructans (312).

The net CO₂ uptake rate and Rubisco activity increased in parallel for developing leaves of *Encelia farinosa*. Approximately half of its net carbon gain was incorporated into plant dry weight over a 17-month period. The ecological success of *E. farinosa* apparently reflects a high CO₂ uptake rate and the retention of a substantial fraction of the leaf carbon gain (315).

New roots could be initiated for *A. deserti* in dry soil using water stored in its succulent shoot. Production of new lateral roots and renewed apical elongation of roots was substantial 10 days after soil rewetting. Developmental plasticity along a root allows it to capitalize on intermittent or heterogeneous supplies of water (317).

1999

Net CO₂ uptake and transpiration for *Agave deserti* occurred mainly at night, whereas root water uptake was relatively constant over a 24-hour period. Its leaf thickness decreased

when transpiration commenced. Water uptake began immediately after soil rewetting. Much of its root system is redundant under wet conditions, but the entire root system is required for rapid water uptake and recovery from drought (323).

Cavitation occurred in the roots of *A. deserti* as drought progressed; 3 months of drought caused a 70% loss of root conduction due to cavitation. The susceptibility to cavitation slightly limits water uptake from a wet soil but helps reduce water loss to a dry soil (324).

2000

For *Agave deserti*, the possible closure of water channels (aquaporins) helped limit water loss to a drying soil. The delayed development of suberized cell layers allows its roots to maximize water uptake from a wet soil (such as under rocks). The immature (recently induced) roots near its base helps it capture water just after a rainfall (326).

2001

Vegetative reproduction via detached distal stem segments occurs for *Cylindropuntia acanthocarpa*, *C. bigelovii*, *C. echinocarpa*, and *C. ramosissima*. *Cylindropuntia bigelovii* had the weakest stem junctions, a high rooting ability, and utilized this reproductive strategy the most. It also had the most spines per unit stem area, which can enhance dispersal by attaching to passing animals (333).

Aquaporins influenced water uptake by *C. acanthocarpa*. Their closure reduced the hydraulic conductivity of the roots by 20% to 40% and were quite important in the stele (334).

Xylem cavitation caused the axial hydraulic conductance of leaves of *Agave deserti* to reversibly decrease during water stress. During drought, its leaf water potential decreased more slowly than for the commercial *Agave tequilana*. Water loss to a drying soil was hence slower for *A. deserti* (335).

2002

From elevations of 230 m to 1,050 m, the mean height of *Cylindropuntia acanthocarpa* doubled and its frequency increased 14-fold. Nurse plants were apparent for only 4% of the small plants at the lowest elevation but for 57% at the highest elevation, where putative freezing damage was most noticeable. The increases in *C. acanthocarpa* with elevation reflected both a greater ability for CO₂ uptake and greater root growth leading to more water uptake. Its greatest ecological success occurred at the highest elevation, where it became most vulnerable to freezing (339).

Soils at Agave Hill varied from sandy (<3% rocks by volume) to rocky (up to 35% rocks). More water was available and at higher water potentials for the sandy sites. As the rockiness increased, *Agave deserti* became less common and had fewer and shallower roots. Growth for *Pleuraphis rigida* was also greater in the sandier sites. The greater variability in root deployment for *A. deserti* may reflect its evergreen leaf habit and slower growth, allowing it to endure periods of lower water availability than *P. rigida*, whose leaves die during drought (350).

2004

For *Agave deserti* under wet conditions, aquaporins were a major contributor to raising the hydraulic conductivity in the distal and proximal parts of roots but not at mid-root. Drought (10 days) eliminated the enhancement by aquaporins. The role of such water channels was greatest in the metabolically most active tissues (359).

2005

Seedling establishment for *Fouquieria splendens* (“ocotillo”) required shading by nurse plants as well as local water accumulation. It was highly sensitive to low temperatures, which sets its upper elevational limit, but extremely tolerant of high temperatures. Its young roots have a mean depth of 19 cm. Leaves were produced multiple times per year in response to rainfall. The maximum age of local plants was estimated to be about 100 years (366).

2007

Dudleya saxosa (“rock live-forever”) occurred predominantly where the ground was covered more than 90% by rocks. It was common near highly reflective exposed quartz veins, whose surface on a spring day was 11C cooler than adjacent patches of bare soil. Its leaves and extremely shallow roots (mean depth of 5 cm) had only modest tolerance of low temperatures, as is typical of desert succulents. It was not as tolerant of high temperatures as sympatric succulents, causing *D. saxosa* to favor cooler north-facing microhabitats (370).

Often growing in rock crevices, roots of *D. saxosa* occupy extremely small soil volumes that can hold only about 10 g of water. The leaves had a thick cuticle, which conserves water, and 24 mesophyll cell layers, consistent with the large mesophyll surface area per unit stem area for other desert succulents. Under wet conditions, most CO₂ uptake occurred during the daytime. After 46 days of drought, it switched to CO₂ uptake primarily at night via CAM. The underground corm can supply water to the shoot during 2.5 months of drought (272).

Major Conclusions

The overall result of these three decades of collaborative study at Agave Hill can be distilled into a few main take-home lessons for the two savvy succulents that played leading roles and their supporting sympatric cast. For instance, many root cellular properties and the inherent difficulty for water movement through dry soil save such desert plants from dying by desiccation during drought. Using nocturnal CO₂ uptake with its limited water uptake, “CAMing it up,” is crucial for agaves and cacti. They do not like freezing temperatures but are exceedingly tolerant of high temperatures, including those above 60C (140F). Yet for photosynthesis they need all of the light that they can get. Light also affects stem orientation for cacti.

In any case, water is the key, especially for seedlings, just as it is for society as a whole. CAM succulents also respond well to increasing atmospheric CO₂ levels as far as photosynthesis

and growth are concerned. An Environmental Productivity Index based on CO₂ uptake responses to light, soil water, and ambient temperature accurately predicts the growth of agaves and cacti in different environments. And detailed computer models can accurately predict the effect of cactus spines, shoot absorptance, and plant morphology on plant temperature and ecological ranges (and led to highly technical careers for many of my collaborators). Plus beauty never hurts ... for cacti, agaves, and all of us!

As a final note, in the late spring of 1988 the former Palm Springs mayor and ex-UC Regent Philip L. Boyd visited Agave Hill during a three-day field research project by my Plant Physiological Ecology class from UCLA. He was visibly delighted to see 16 students eagerly using his eponymous reserve! In turn they and I were extremely grateful for his philanthropic vision.