Leafy flowers of the cactus *Pachycereus gaumeri* greatly increase photosynthetic surface area

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What function do the leaves on flowering branches of cacti have? The answers may surprise! All photos by the author.

By evolving to be 'leafless', cacti became adapted to surviving in xeric (dry) habitats. Because most have no large foliage leaves, their surface area is small and they lose less water to the dry air (Mauseth, 2000) (Fig. 1). Unfortunately, this also means they have less surface area to catch the sunlight that powers photosynthesis. All plants face this trade-off between conserving water and gathering solar energy, but in moist habitats, conserving water is not necessary and plants can be very leafy. In xeric habitats, water conservation is important and plants must reduce their surface area by having fewer or smaller leaves or by shedding their leaves during dry seasons.

Opuntias are a good example. When new pads or joints emerge in spring each has many leaves, some of which are actually quite large (Fig. 2). After a few weeks the habitat dries out, the leaves shrivel and fall off, reducing the plant's surface area; *Opuntia* leaves never persist from spring until autumn. Each *Opuntia* stem can make the one set of leaves only, so even if it were to rain several times in a year, the stem could not produce a new set after the first has been shed. The plant is not able to take full advantage of the later moisture. In contrast, an ocotillo (*Fouquieria splendens*) puts out new leaves from any part of its stem after a good rainfall (Figs. 3 & 4). Each axillary bud produces any number of flushes of ephemeral leaves. Consequently, ocotillos have leaves when leaves are beneficial and they shed them whenever necessary. Would it not be great if cacti could do the same thing? As it turns out, some cacti can.

Leaf biology in cacti is turning out to be much more interesting than most of us ever suspected (Mauseth, 2007, 2016a; Mauseth, Rebman & Machado, 2016). All cacti produce leaf primordia at their shoot tip; no cactus is truly leafless. The primordia develop into large, obvious foliage leaves in plants of *Pereskia*, and they grow into smaller, ephemeral leaves in *Opuntia* and its relatives. In some genera of subfamily Cactoideae, leaf primordia stop growing and developing while they are still little more than a lump consisting of a dozen or so cells. In other genera leaf

Fig. 1 This shoot of *Pachycereus (Pterocereus) gaumeri*, like most cacti, has a very low surface area because its foliage leaves are just microscopic bumps below each areole. The spines are modified bud scales, but they are dead: they neither lose water nor photosynthesise

Fig. 2 This very young pad of *Opuntia violacea* has a small, awl-shaped leaf at every areole and thus has extra photosynthetic capacity in springtime. Each leaf will fall off as days become hotter and drier. Notice that last year's pad in the background did not make a new set of leaves this year

Fig. 3 Ocotillos (*Fouquieria splendens*) are only this leafy after a good rain; they most often resemble dry sticks. Big Bend National Park, USA

primordia develop into tiny leaves that have an upper and lower side, vascular tissues, and even a minute leaf blade. Furthermore, when many cacti flower, they produce large, obvious leaves on their flowering branches (Fig. 5). What most people call flowers in cacti are actually flowering branches with the true flower located inside; a true flower does not have areoles on it. I wrote an article for the *Cactus and Succulent Journal* (US) describing and illustrating some of these leafy flowering branches (Mauseth, 2016b) where I hypothesised that these leaves might help nourish the flowers, but it seemed as if such leaves would be too few and small to be of much consequence. Since then, one of my specimens of *Pachycereus* (*Pterocereus*) *gaumeri* has bloomed. Its flowering branches have particularly abundant, large leaves, and this allowed me to measure the amount of extra photosynthetic surface area the flowering branches provide (Figs. 6 & 7).

The flowering branch that I examined was 60mm long from the point where it was attached to the stem to the open petals, and its opening was 53mm in diameter; it weighed 24.4 grams. The leaves were removed one by one and measured (Fig. 8). There were 92 leaves that were green, plus another nine leaves that intergraded into petals, being pale green. Petals were white. Of these 92 green leaves, the ones at the base of the flowering branch were smallest, eight being less than 7mm long and less than 3mm wide. The next higher

Fig. 4 Just days after a rain, this ocotillo is beginning to make leaves at every axillary bud. Prior to the rain, this shoot would have appeared almost lifeless

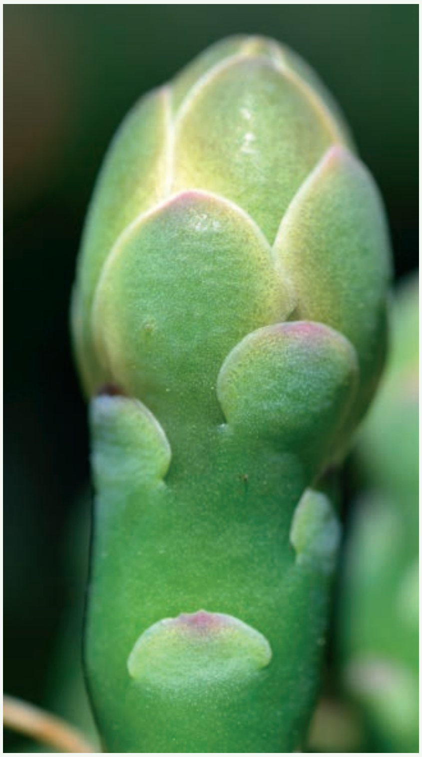

Fig. 5 The beautiful scales on *Gymnocalycium* flowers are actually leaves with stomata and photosynthetic tissue. *Gymnocalycium bueneker*i

Fig. 6 Just outside the stamens are white petals of a *Pachycereus gaumeri* flower, and these are surrounded by green structures that are actually leaves on the flowering branch

15 leaves were larger, being up to 13mm long by 4mm wide. Leaves continued to be progressively longer and wider up the flowering branch, with the middle 28 leaves being 15–30mm long and 6–9mm wide. The uppermost 41 leaves were as much as 44mm long and 12mm wide.

When measuring leaf area, some people measure only the area of one side. This is appropriate if the main photosynthetic cells are located only next to the upper surface, the side that receives sunlight. The area of the upper side is then correlated with the amount of sunlight captured. In most leaves, almost all the stomata (pores) that allow the absorption of carbon dioxide are located in the underside of the leaf; in these leaves the surface area of the lower side of the leaf gives an estimate of the ability to absorb carbon dioxide. On the other hand, in many succulent leaves, photosynthetic cells are located next to both the upper and

Fig. 7 Leaves on the exterior of a flowering branch of *Pachycereus gaumeri.* (The true flower parts such as petals, stamens and carpels are located completely within this branch.) Note the numerous large leaves here; the branch is 60mm long

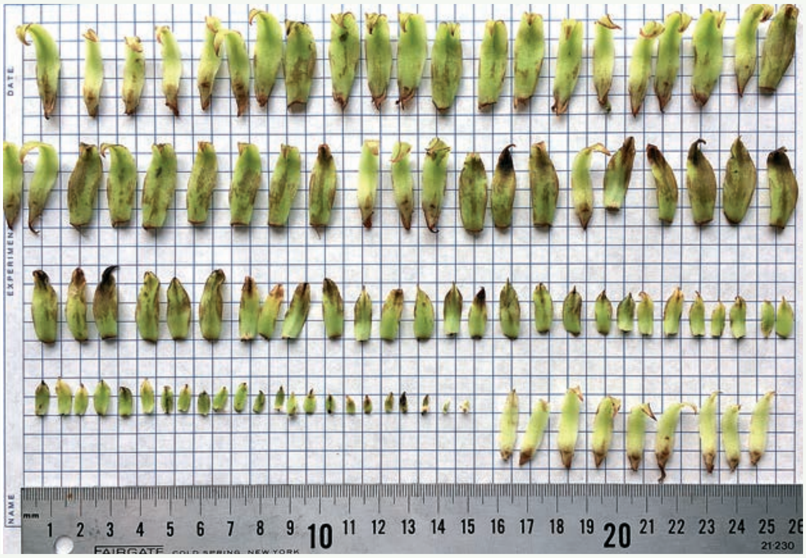

Fig. 8 Individual leaves removed from the flowering branch of Fig. 6. The flowers are nocturnal and began closing just after I photographed it. The leaves wilted and discoloured as I removed them. Leaf tips are curled up so their full length is not readily visible here. The nine leaves on the lower right are transition forms (pale green) and were not included in the measurement of photosynthetic surface area

the lower side of the leaf, and stomata also occur on both sides. Consequently, in succulent leaves it is more appropriate to measure the combined area of both the upper and lower surface: the leaf absorbs carbon dioxide through both surfaces and both sides carry out photosynthesis. Leaves on the *Pachycereus gaumeri* flowering branch were thick (3mm at the midrib, 0.5mm near the margins), had stomata on both sides, and were green throughout, so the leaf area given below includes both upper and lower surface area. The largest leaf had a surface area of 860mm², and 57 leaves had a surface area of 200mm² or more. Together, all the leaves of the flowering branch provided a total surface area of 34,046mm²; that is the equivalent of the two sides of a square sheet of paper 130mm along each side. Each page of *CactusWorld* is 180mm wide and 245mm tall, and thus has a surface area of 44,100mm² on each side, or 88,200mm² on both sides; each flowering branch of *P. gaumeri* provides as much surface area as four-tenths of a page of this journal. For a cactus, this is an enormous amount of surface area. Because each leaf is attached directly to the flowering branch, the sugars produced by the leaves are readily available to the flower itself.

The ribs of my specimen of *Pachycereus gaumeri* are 30mm tall and the areoles are 19mm apart along the crest of each rib. Therefore the rib adjacent to each areole has 19×30mm multiplied by two sides, equals 1,140mm² of surface area, counting both sides of the rib. Comparing the surface area of a rib with that of a flowering branch, we have 34,046mm²/1,140mm² = 29.9. The leaves of the flowering branch provide 30 times more photosynthetic surface area than does the section of rib immediately adjacent to it.

Just as with ocotillo, *Pachycereus gaumeri* produces these leaves only when the habitat is favourable: a plant flowers when it has adequate nutrients, water and temperature. When *P. gaumeri* and many other cacti are healthy enough to reproduce, they not only make flowers but also a large leaf surface area as well. My plant of *P. gaumeri* has not yet produced fruit, but in *The New Cactus Lexicon*, Hunt reports that fruits of *P. gaumeri* are “scaly and spiny.” It may be that the leaves of the flowering branches persist after pollination and nourish the fruit and seeds as they develop. That happens in dragon fruit (*Hylocereus undatus*). Furthermore, these leaves are ephemeral because when a cactus sheds a flower or fruit, it sheds these leaves also. As in ocotillo, cacti with leafy flowering branches have leaves when they are beneficial but ‘throw them away’ when no longer needed.

A number of other species of Cactoideae also have numerous large leaves on their flowering branches, so *P. gaumeri* is not unique. Perhaps it is not even the most extreme example. Cactus biology surprises us once again.

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