Trends in Distribution and Size of Stomata in Desert Plants

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Introduction
Stomata are microscopic pores on stems and leaves of most green land plants which help to regulate gas exchange, particularly carbon dioxide, \( \text{CO}_2 \), and water vapor, \( \text{H}_2\text{O} \). Carbon dioxide is essential for the process of photosynthesis. This process not only produces food for the plant and excess stored food which may be utilized by herbivorous animals—including mankind, but also produces oxygen gas, \( \text{O}_2 \), as a biproduct. Because the aerial portions of a plant are covered by a waxy layer nearly impervious to \( \text{CO}_2 \), the cuticle, this gas enters the plant primarily through the stomates.

Individual living plant cells are often composed of 95% or more water. Because they are enclosed within the same waxy cuticle, which is also nearly impermeable to water, the internal air spaces between cells within the plant are nearly saturated with water vapor. As stomates open to admit \( \text{CO}_2 \) into the plant, \( \text{H}_2\text{O} \) is simultaneously lost through these same pores. When the plant is growing under conditions of adequate water supply, this trade off of \( \text{H}_2\text{O} \) loss for \( \text{CO}_2 \) gain is not harmful to the plant—in fact it is essential! The loss of water through the stomates, transpiration, is the driving force which allows more water and dissolved solutes to be drawn up from the roots through the plant (Raven, Evert & Curtis, 1981). A problem quickly arises, however, when available water is in short supply. Water lost by transpiration cannot easily be replaced and water deficits within the plant soon arise. This problem is particularly severe in arid, xeric, environments; consequently desert plants, xerophytes, have evolved a number of physiological and morphological features to minimize its effect.

The cells of many desert plants are simply able to tolerate lowered water content without injury (Levitt, 1980). According to some workers these plants are the only “true” xerophytes. Many xerophytes possess long taproots which enable them to penetrate to deep reservoirs of ground water while others have extensively branched shallow root systems which are efficient at trapping what minimal precipitation occurs (Levitt, 1980). Some desert plants in coastal areas may even trap moisture from fog or dew through their aerial parts (Gindel, 1970). A large number of xerophytes avoid drought by quickly flowering and producing drought resistant seeds following a rain. These ephemeral plants die as subsequent drought becomes more severe but their seeds remain viable for one or more years until the next favorable growing season. In a similar fashion, many perennial xerophytes lose their leaves, or even whole shoots as conditions become more drier. Some such drought deciduous species may produce and shed several crops of leaves per year as conditions dictate.

The leaves of xerophytes are generally small (Maximov, 1929). This not only serves to minimize the surface area over which transpiration may occur, but it also minimizes heat build up within the tissues (Smith, 1970). The dense hairs and spines covering the aerial portions of many desert plants serve a similar function (Juniper and Jeffree, 1983).

For over one hundred years it has also been recognized that certain modifications of stomates are characteristic of xerophytic plants (Haberlandt, 1884). The stomates of most plants, including many xerophytes, occur at the surface of
the leaf or stem (Fig. 1B,D), but in other desert plants they may be sunken beneath the surface (Fig. 1A), or concentrated in crypts below the surface (Fig. 1C). Likewise the density and size of stomates have been implicated as xeromorphic adaptations—here, however, the literature is full of contradictions.

In 1884, Haberlandt claimed that stomatal densities are decreased in desert plants. With fewer stomates per unit surface area there would be less transpiration—a favorable adaptation in a xeric environment. In the same year Volkens (1884) stated that there is no correlation between the density of stomates and the xeric habitat. In fact in later studies he and others claimed that desert plants may actually have an increased stomatal density (Volkens, 1887; Maximov, 1929). The advantage in this is that increased transpiration would produce evaporative cooling—also a favorable adaptation in a xeric environment. Although the first school of thought predominated through the middle of this century and the latter predominates today, both are argued in current textbooks of plant physiology. Hall (1976), Bidwell (1979) and Ting (1982) state that stomatal density is decreased while Devlin and Witham (1983) and Noggle and Fritz (1983) state that densities are increased in xerophytic plants.

The apparent contradiction in the current literature was the stimulus for a preliminary study undertaken by a student and myself (Strobel and Sundberg, 1984). The results of this study suggested that succulent and non-succulent xerophytes evolved different stomatal strategies to deal with water stress. In the study described here a much larger number of desert plants, growing under natural conditions, were examined to test our preliminary results.

Materials and Methods
Field collections and laboratory examination was done at the Desert Botanical Garden, Phoenix, AZ, during the first two weeks of January, 1984. A total of 134 species, representing 19 desert lifeforms (Crosswhite and Crosswhite, 1984), were examined. Of these the stems and/or leaves of 56 were succulent or semi-succulent while those of 81 were nonsucculent (The leaves and stems of Asclepias subulata, Caralluma frerei and Pedilanthus sp. were treated separately).

A total of five tissue samples for each species were collected from fully sunlit plants. The number of stomates per calibrated field of view was determined from peels or fresh paradermal sections of each sample. The average stomatal length was calculated from a sample of ten randomly selected stomates measured with an ocular micrometer. Both surfaces of each leaf were examined. Photomicrographs were made of all fresh sections.

In those cases where counts and/or measurements could not be made directly (eg. Hesperaloe, Canotia, Casuarina and Grewia) specimens were fixed in FAA and later embedded in paraffin, sectioned, and examined morphometrically as described previously (Strobel and Sundberg, 1984). Statistics were computed on an Apple IIe microcomputer using biometry programs developed by Dr. Dwight Kincaid, Lehman College, City University of New York.

Materials for SEM were fixed in 10% acrolein, washed in two changes of H2O and dehydrated in DMP [Posteck and Tucker, 1976]. Following dehydration the tissue was brought through two changes of absolute acetone, one change of amyl acetate and critical point dried. The specimens were gold coated with a Denton sputter coater and examined with an ISI-Super I scanning electron microscope.

Results and Discussion
An examination of the photomicrographs in Figure 2, all taken at the same magnification, quickly suggests that stomata of xerophytes may be either widely separated or densely distributed over the surface of the plant. Furthermore, the size of the stomatal opening may vary widely. The impression is that densely distributed stomates are generally smaller while widely distributed stomates are generally larger.

Our original suggestion (Strobel and Sundberg, 1984) was that low stomatal frequencies are associated with succulent tissues while high stomatal frequencies are associated with non-succulents. To test this hypothesis the mean frequencies for all succulents were calculated and compared to similar values for all non-succulents. These data are presented graphically in Figure 3. The average value for non-succulents is 165.03mm-2 while the average for succulents is 32.64mm-2. Stomatal values in most plants range from about 100 to 300mm-2; therefore succulents are characterized by a reduced number of stomates per unit surface area. These desert plants reduce water loss by reducing the number of stomates through which water may transpire. This is in agreement with actual transpiration studies which have been done on succulent plants (Black et al., 1976; Stocker, 1976; Kluge & Ting, 1978). An interesting peculiarity in this regard is that the rate of transpiration in succulents is highest at night during periods of water stress (Kluge & Ting, 1978). Most, if not all, desert succulents are CAM plants (Crosswhite, 1984), therefore the relatively few stomates are open predominantly at night. Carbon dioxide is fixed into organic acids and stored within the cells. During the following day these acids provide a CO₂ source for photosynthesis while the stomates remain closed, thus reducing H₂O loss.

Associated with the low density of stomates in succulents is their relatively large size (Fig. 1B,D, 2A). The large open area of individual stomatal apertures would tend to counter the overall area decrease in stomatal area, per unit surface area, caused by deceased density. In this way maximum gas exchange occurs when the stomates are open. Furthermore, Ting and Szarek (1975) have argued that because of the generally round shape of the transpiring surface of succulents, another factor, boundary layer resistance, is greater than the resistance to gas diffusion provided by stomates. The result is that the large stomata of succulents are effective at regulating gas exchange over their entire range of apertures, a phenomenon noted by Kluge (1976).

In contrast to succulents, the stomatal densities of non-succulents fall mostly within the typical range of more mesophytic plants and actually include some of the highest stomatal densities recorded. In the present study such high values included 580mm-2 [Buddleja saligna], 523 mm-2 [Guaiacum coulteri], 457mm-2 [Pitheclobium flexi-
Figure 1. Locations of stomata in desert plants relative to the plant surface. A: Canotia holacantha (X1000). B: Opuntia Ficus-indica (X400). C: Nerium oleander (X700). D: Stapelia nobilis (X1000). Stomata are located at the surface (B) or even slightly elevated (D) in most succulents. In many non-succulents they are sunken in chambers below the surface. (A) or concentrated in subsurface crypts (C) [see arrows].

Figure 2. Relative size and density of stomates on leaves of desert plants. A: Cereus peruvianus. B: Lycium fremontii. C: Aloinopsis. D: Pithecellobium flexicaule. Magnification 1250x.

Figure 3. Average stomatal density and stomatal length of succulent and non-succulent desert plants. Circles represent non-succulents, squares represent succulents. The standard errors of the means are indicated by the vertical bars.

was noted by Maximov (1929) and has been subsequently reaffirmed by others [Ehler, 1975; Stocker, 1976].

The adaptive advantage of high rates of water loss in these xerophytes is to reduce tissue temperature by evaporative cooling. Unlike succulents, whose cells are able to tolerate very high daytime temperatures, a major problem of non-succulent xerophytes is to avoid heat buildup in the tissues (Levitt, 1980). Evaporative cooling, due to high rates of transpiration, can actually depress internal tissue temperatures below that of the surrounding air [Levitt, 1980].

Ting and Szarek (1975) have noted that in the relatively flat leaves of non-succulents, the resistance to diffusion, due to the boundary layer of air around the leaf, actually becomes more important than stomatal resistance by the time the stomates are half open. Maximum gas exchange, therefore, will occur not with few, relatively large stomata, but rather with many smaller stomates. Although an individual small stomate will be less efficient at allowing gas exchange per unit pore area than an individual large stomate, a considerably larger number of small stomates may be packed into a unit leaf area thus providing for greater total transpiration and consequently greater evaporative cooling potential.
Figure 4. Regression lines for stomate length on stomatal density in succulent and non-succulent desert plants. Succulents, $y = 17.70 - 0.02x$. The slopes of the regression lines are significantly different.

Conclusions

It is apparent from the data presented above that two distinct stomatal strategies have evolved in desert plants: relatively large, infrequent stomates on the surface of succulents and smaller, more numerous stomates on the surface of non-succulents. In each case the stomatal size and frequency provides an adaptive advantage to plants of a particular life form. The large stomates provide for maximum gas exchange at night in succulent CAM plants while their infrequent occurrence helps to minimize water loss during the day when the stomata are usually closed. The frequent, small stomates of non-succulents allow for high daytime transpiration rates, therefore cooler tissue temperatures.

The results of this study also clarify the contradictory descriptions of stomatal frequency found in the literature, and referred to at the beginning of this paper. Both increased and decreased stomatal frequencies are found in desert plants—depending on their life form. Authors must be careful to specify if by xerophytic plant they are referring to succulents, non-succulents, or all xerophytes.

References


