Modulation of stomatal conductance in response to changes in external factors for plants grown in the tropical climate

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Abstract

Plants are greatly modular organisms that can adapt efficiently to changes in external environmental conditions. The effects of light intensity, humidity, and temperature on the stomatal conductances of five plants (*Ficus elastica*, *Ficus microcarpa*, *Tilia Americana*, *Acalypha wilkesiana*, and *Jatropha gossypiifolia*) grown in the tropical or sub-tropical climate were investigated. The leaves obtained from these plants were different in morphology, and yet the adaptive trends were found to be similar across the species. Our data showed the light intensity, humidity and temperature significantly affected the stomatal conductances, with humidity having a greater effect on conductance than temperature. Our data also suggested that the peak in stomatal conductances for these plants occurred at a relative humidity range of ~60-80%. Even though the average stomatal conductances of the red colored leaves were higher than the green leaves from the same plant, the difference was not statistically significant.

Keywords

Adaptations in plants, Hydraulic factors, Stomatal conductance, Transpiration, Light intensity, Humidity, Temperature, Morphology, Photosynthesis, Tropical plants.

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Introduction

Plants are highly adaptive and modular organisms that can regulate their physiological processes to survive under varied environmental conditions (1, 2). Adaptations are unique characteristics of any living organism so that they can sustain and thrive in changing habitats and plants are no exception. These adaptations can be of different types – morphological, physiological, anatomical, and/or behavioral (3, 4). Morphological adaptations deal with the changes in morphological features (structure, form, or shape) of the plant species. These include the height of the plant, shape, size, and thickness of the leaves, presence of thorns, structure, length of the roots, etc. Physiological adaptations include changes occurring during physiological processes like photosynthesis, metabolism, transpiration, etc. Anatomical adaptations are the adaptations taking place at the levels of cells and tissues, and these are the root causes behind the observed morphological and physiological changes. And finally, even though it is more prevalent in animals, some plants also exhibit a fourth type of adaptation – behavioral. One common example of behavioral adaptation in plants is tropism, i.e. growth towards sunlight.

As can be seen, the list of different adaptations in plants is quite extensive. The focus of this research study was directed toward one of the major physiological processes observed in plants; transpiration (5, 6). Transpiration is the process of absorption of water through the root, its transport through the plant, and its loss from the aerial parts of the plant, such as leaves and stems. The loss of water primarily takes place from the leaf surfaces through evaporation. Stomata (also called stoma or stomate) are microscopic openings or pores present predominantly in the epidermis of leaf surfaces, even though can be present on stem surfaces as well to a lesser extent (7, 8). Two guard cells surrounding the stomata control their opening and closing, based on the change in osmotic pressure, and hence dictate the gaseous exchange at the stomatal level. The intake of carbon dioxide (CO_2) or the loss of water (H_2O) through the stomata is called stomatal conductance (9-11).

Light intensity, temperature, humidity, atmospheric CO_2 level, and leaf water potential are some factors that affect stomatal conductance (12-14). Except for the temperature, the other factors can be grouped into two categories, hydraulic factors (air humidity and water supply) and photosynthetic factors (light intensity and CO_2 level). Even though the hydraulic factors generally tend to dominate the photosynthetic factors, in reality, the process is complex and dynamic as these factors themselves also fluctuate (15). Hence, estimating the individual effect of one factor independently is challenging. The role played by the light intensity on stomatal opening, and hence the conductance, is well-established and generally consistent across different plant species (16-18). In general, with the increase of light intensity, the extent of stomatal opening increases, as does stomatal conductance, till an optimal point. On the other hand, the effect of temperature and humidity on stomatal conductance are more complex and variable in nature, depending on the plant species and other contributing factors (19-23).

A literature survey revealed that different factors affect the stomatal conductance in plants (15, 20, 24, 25). Due to the ease of experimentation and availability of resources, we studied the effect of light intensity, temperature, and humidity on the stomatal conductance. The effects of these factors on the stomatal conducatance for these five plants has not yet been reported in the literature. These five plants were selected because all of them grow in tropical or sub-tropical climates, and their leaves were diverse in terms of their shapes, sizes, and colors, and previously unexplored for stomatal conductance studies. These plants were also easily accessible for experimentation.

We measured the stomatal conductance values of these plants under different conditions to determine possible correlations with light intensity, temperature, and humidity. We also measured the stomatal conductance values for leaves containing different photopigments, green and red.

Materials and Methods

General
All the experiments were conducted at the Prayoga Institute of Education Research campus (Ravugodlu, Bengaluru, India). All basic lab safety protocols were followed.

Measurement of stomatal conductance
Stomatal conductance readings were measured using a portable AP-4 porometer (Delta-T Devices, Cambridge, UK). Before measurement, the instrument was calibrated following the instructions in the manual. At least three different leaves were selected for each plant and a minimum of six measurements were made for each leaf. The average stomatal conductance was calculated. Initially, readings were collected at three different times; 10 am, 1 pm, and 4 pm. For the final analysis, the data collected at 4 pm was not included because stomatal conductance was low due to the decreased intensity of light. The temperature and relative humidity of the air were measured using the 'Barometer and Altimeter' app (version 1.9, developed by EXA Tools), and light intensity was measured using the 'Lux Light Meter Pro' app (version 031.2022.01.11, developed by Doggo Apps) (26, 27). These two apps were open-source, available for the android environment and used for convenience. Before measuring the stomatal conductance at any particular time, the CO_2 level in the air was measured using a portable JD-3002 Air Quality Tester, (Guangdong, China) and was expressed in parts per million (ppm). To study the effects of various temperatures on stomatal conductance, the measurements were performed in a relative humidity range of 72-74%. For the variable humidity and temperature studies, their values were in the range of 18-87% and 23-27 °C, respectively.

Plant species
Details about the plants selected for this study can be found in Table 1.

Table 1. Attributes of the plant species selected for the study

Common name	Scientific name	Family	Leaf Color	Leaf morphology
Rubber plant	*Ficus elastica*	Moraceae	Mostly green, marked with yellow and/or maroon	Oval shaped; thick; 4-14 inches long, 2-6 inch broad
Chinese banyan (bonsai)	*Ficus microcarpa*	Moraceae	Mostly green, with hint of yellow	Small, oval; thick; 1.5-2 inches long, 1 inch broad
Amercan basswodd	*Tilia Americana*	Malvaceae	Mostly dark green	Relatively bigger, heart-shaped with serrated margin; thin; 5-8 inches long, 3-4 inches broad
Copperleaf	*Acalypha wilkesiana*	Euphorbiaceae	Mostly red or reddish brown	Relatively bigger, heart-shaped with serrated margin; thin; 4-7 inches long, 2-4 inch broad
Cotton-leaf physicnut	*Jatropha gossypiifolia*	Euphorbiaceae	Green or Red or both	Medium sized, three lobed leaves; 1.5-4 inches long, 2-5 inches broad

Statistical Analysis

Plotting the graphs and t-test calculations (unpaired, two-tailed) were performed using Prism 6 (GraphPad, San Diego, USA). A *p*-value less than 0.05 was considered to be statistically significant.

Results

Variation of stomatal conductance with light intensity

Stomatal conductance was measured at 10:00 am, 1:00 pm, and 4:00 pm, when light intensities were different. The light intensity between 10:00 am and 1:00 pm was in the range of 38,000 to 43,000 lux, and was minimum after 4 pm; in the range of 8,000 to 12,000 lux. Even though most literature reports suggested that the ideal time to measure stomatal conductance was in the morning (28), we did not find a significant difference between the stomatal conductance values measured in the morning or around noon (Figure 1). During the initial set of data collection, the changes in temperature and relative humidity were minimal. For all practical purposes, we assumed that the air CO_2 level remained unchanged throughout the measurement period. Our results indicated that stomatal conductance increased with an increase in light intensity and *vice versa*.

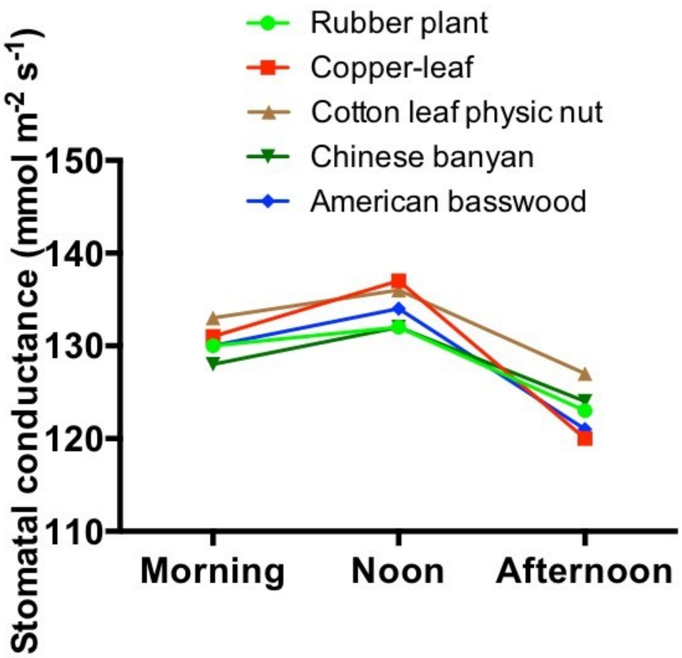

Figure 1. Changes in stomatal conductance values with light intensities (different times of the day). In general, stomatal conductance was found to be higher in the morning and at noon than in the afternoon.

Variation of stomatal conductance with variable humidity and temperature

Both humidity and temperature are known to be important factors in controlling the stomatal conductance of all plants. The exact effects of both these factors are still not well understood and depend on many factors including plant specificity. To investigate how these two factors influence the stomatal activities of the plant species used in this study, we measured the stomatal conductance under variable ambient humidity and temperature. Relative humidity (RH) is the amount of water vapor present in the air expressed as a percentage of the amount of water vapor that would be present in the same volume of saturated air at the same temperature. Our results indicated that the stomatal conductance reached a maximum when the relative humidity of air was 60 to 80%, with conductance values being lesser on either side of the peak (Figure 2-A). Even though stomatal conductance values were the highest in this RH range (60-80%), they did not follow any particular pattern, especially for the rubber plant and the bonsai Chinese banyan. For example, the stomatal conductance values for the rubber plant were 136.22 and 159.96 mmol m^{-2} s^{-1} at RH levels of 71% and 74%, respectively, but relatively lower (118.58 mmol m^{-2} s^{-1}) at 73%. Similarly, the stomatal conductance values for the Chinese banyan (bonsai) were 162.84 and 143.40 mmol m^{-2} s^{-1} at RH levels of 71% and 74%, respectively, but exhibited lower values of 119.00 and 111.89 mmol m^{-2} s^{-1} at 73% and 76%, respectively. For the >6 stomatal conductance measurements per leaf, the maximum relative standard deviation obtained was 29.25% (see supplemental data).

When we measured the stomatal conductance values at different temperatures, we did not find any correlation or pattern (Figure 2-B). Stomatal conductance values are known to increase with temperature (21). however, in our experiments, we observed a wide range of stomatal conductance at 25 °C for all the plants studied. For example, the rubber plant and the American basswood exhibited stomatal conductance ranges of 118.58-159.96 mmol m^{-2} s^{-1}, and 125.85-151.29 mmol m^{-2} s^{-1} respectively. For some plants, the conductance values at 27 °C were lower than those at 23-25 °C. This suggested that the temperature was not the only factor that influenced stomatal conductance.

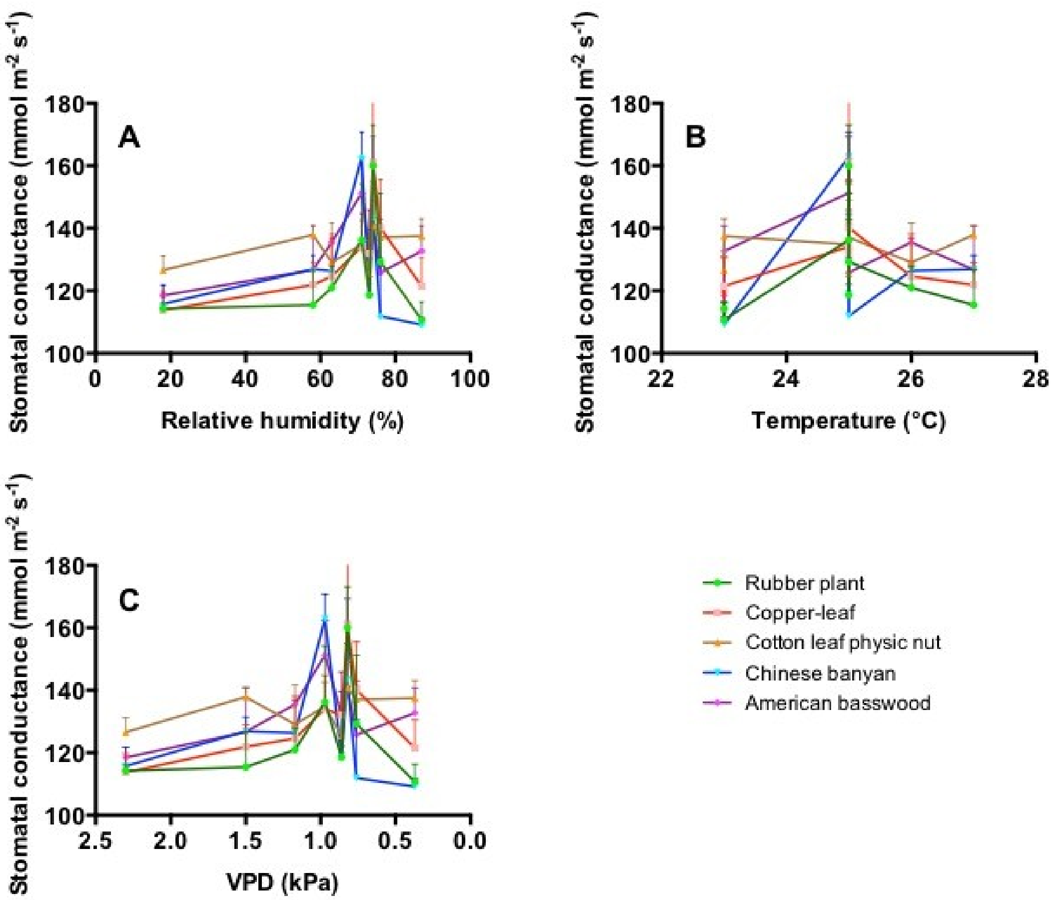

Figure 2. Changes in stomatal conductances with : A) relative humidity (RH), B) temperature, C) vapor pressure deficit (VPD). During these measurements, neither RH nor temperature was fixed.

Vapour pressure deficit (VPD) is the difference between the amount of water vapor present in the air and the amount of water vapor that the air can hold in the saturated condition. Even though relative humidity is the most commonly used parameter to describe the moisture content in the air, it is not always the most appropriate (29). Relative humidity is a temperature-dependent parameter, because the amount of water vapor that the air can hold, changes with temperature. On the other hand, VPD is a temperature-independent property, making it more suitable to measure water loss from plants when temperature and humidity cannot be independently controlled. When plotted against VPD, stomatal conductance exhibited a similar pattern as it did when plotted against the RH. Stomatal conductance in all five plants was maximal when the VPD value was in the range of 0.8-1.2 kPa (Figure 2-C).

Variation of stomatal conductance with temperature within a fixed relative humidity range

Since the stomatal conductance did not show any correlation with temperature with varying humidity, we next decided to measure the same effect under a more controlled condition. We assessed the changes in stomatal conductance at different temperatures when changes in humidity were negligible. We performed three sets of measurements for all the five plants on three different days at 10 am. The RH values during these measurements were in the range of 72-74%. We found that the stomatal conductance generally increased linearly with temperature (Figure 3). The exceptions were the American basswood and copperleaf at temperatures from 23 to 28 °C, when their conductance decreased. However, for these two species also, conductance increased when the temperature changed from 28 to 35 °C. Our data suggested that, under conditions of constant humidity and light intensity, stomatal conductance generally increased with temperature for the five species studied.

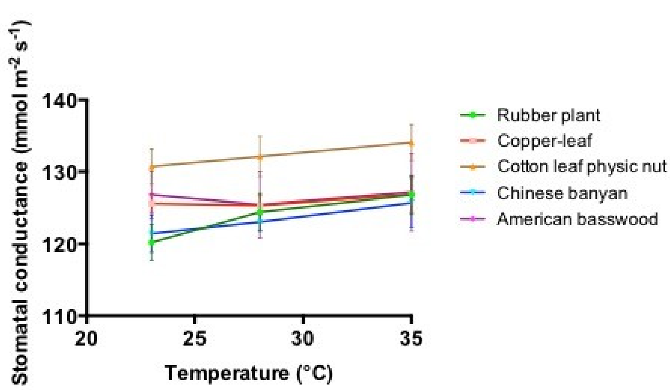

Figure 3. Increase in stomatal conductances with temperature, when relative humidity was fixed at 72-74%

Variation of stomatal conductance with different plant pigments

As mentioned earlier, the cotton leaf physic-nut had leaves of two primary colors – green and red. Interestingly, we found that the average stomatal conductance of the red leaves (136.55 mmol m^{-2} s^{-1}) was higher than that of the green ones (132.25 mmol m^{-2} s^{-1}) for this plant (Figure 4). The green and red color of these leaves are primarily due to the presence of plant pigments chlorophylls and anthocyanins, respectively. This difference in conductance was not statistically significant (p = 0.2538). A direct comparison of the red leaves of the copperleaf plant with the green leaves from the other plants could not be made as several other factors including the sizes, shapes, and thicknesses of the leaves differed significantly between the species.

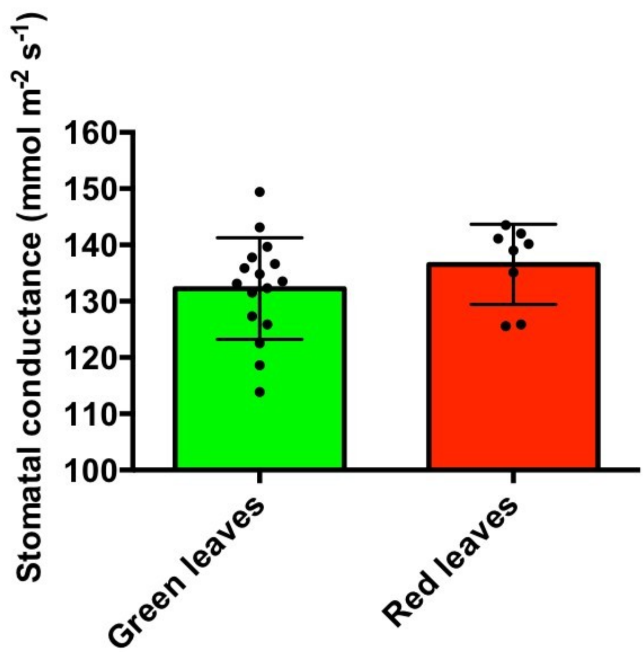

Figure 4. Stomatal conductances recorded for green and red leaves of the same plant (cotton-leaf physic nut). The black dots represent the individual stomatal conductance values. The height of the colored bars and the error bars denote the mean stomatal conductance and standard deviation, respectively.

Discussion

In this study, we studied the effect of environmental factors affecting the stomatal conductance of five different plant species growing in tropical or sub-tropical climates. The plant species were rubber plant, copperleaf, cotton-leaf physicnut, Chinese banyan bonsai, and American basswood – all of which grow in Bengaluru, India; where the study was conducted. We investigated the effect of three environmental parameters on the stomatal conductance of these plants, namely, light intensity, air humidity, and temperature. Since we were primarily interested in the changes in stomatal conductance of the same plant in response to environmental changes over a short period of time, different stomatal sizes and densities among the different plants did not influence our findings.

We first analyzed the effects of light intensity on the stomatal conductance of these plants. Light intensity is known to play a critical role in the stomatal conductance process, as the opening and closing of stomata are governed by the intensity of light. Stomatal opening in response to light follows two different pathways – red and blue light response (30). The red-light response involves the photosynthetic pathway that controls stomatal responses so as to maximize photosynthesis, whereas the blue-light pathway is the guard cell-specific pathway, that does not depend on the photosynthetic process. Regardless of the type of pathway, light intensity is a major factor in determining stomatal conductance. In general, stomatal conductance increases or decreases with the increase or decrease in light intensity, respectively. We observed the same trend in this study for all the five species. The light intensities were ~ five times higher at 10 am and 1 pm, compared to the intensity at 4 pm. The mean stomatal conductance values were also higher at 10 am and 1 pm, and lower in the late afternoon (Figure 1). Even though stomatal conductances are known to be maximum in the morning, and gradually decrease as the day progresses, our results indicated that the stomatal conductances did not significantly change when measured at 10:00 am and 1:00 pm. This can be due to a number of reasons, such as environmental factors, leaf water potential, or plant-specific properties. Nevertheless, as stomatal conductances were found to be consistently higher at 10 am and 1 pm, we decided to use both these time periods for the rest of the measurements to assess the effects of humidity and temperature.

We first performed the measurements on different days when these two parameters were dynamic i.e. both were changing at the same time. The range of RH and temperature were 18-87% and 23-27 °C, respectively over the study period. We observed a spike in the stomatal conductance values for all five plant species when the RH was in the range of 60-80%. Stomatal conductance was lower on either side of the peak. This indicated that the RH level of 60-80% is necessary to maximize stomatal conductance. Literature data on the dependence of stomatal conductance varied based on the species, climate, and status of the other factors (15, 19, 20, 22). Stomata tend to close when relative humidity is low or VPD is high (31). This may serve to minimize the water loss from the plants under high evaporative demand (29, 32). We observed a similar behavior in all the five species. Stomatal conductance decreased with a decrease in RH. When the RH was relatively higher, i.e., the air contained a significantly high amount of water vapor content, transpiration decreased. This manifested in a low stomatal conductance. In between these low and high RH extremes, there seemed to be an optimal state ~60-80 %, when stomatal functioning and moisture content in the air driving the transpiration process led to high stomatal conductances.

Interestingly, stomatal conductances at different temperatures during these varying humidity measurements were found to be random and no correlation was observed between the two, which seemed to be in agreement with most of the literature reports. Even though the other environmental factors remained essentially unperturbed during these measurements, the relative humidity did not. To determine if RH was indeed playing a major role in this, we opted for two different strategies. First, we plotted the stomatal conductances against vapor pressure deficit (VPD). Even though RH is the most commonly used parameter to describe the moisture content in the air, it is not the best-suited one in certain circumstances due to its dependence on temperature variation. Instead of RH, a more accurate way of representing the moisture content in the air while discussing stomatal conductance would be VPD as it is a temperature-independent parameter. We observed that the stomatal conductances changed with VPD following the same trend as the RH, which suggested that air humidity is a much more influential factor than temperature, in detrmining stomatal conductance.

Next, we measured stomatal conductances at different temperatures at constant humidity. As all these experiments were performed outside under normal environmental conditions, it was not possible to precisely control the humidity level. Instead, we measured the stomatal conductances at different temperatures when the humidity level was almost constant (72% to 74%). We found that; in general; the stomatal conductances increased with the rise in temperature. At high temperatures , the contrasting needs to achieve evaporative cooling and to simultaneously prevent water loss, lead to unpredictable stomatal conductance. Hence, different plant species behave in contrasting ways with respect to stomatal opening/closure in response to increasing temperature (21, 31, 33, 34). Due to this competing and contrasting nature of different physiological processes observed in plants, it becomes difficult to explain multiple observations under dynamic conditions. To understand the effects of environmental factors on stomatal conductance, several mathematical models have been proposed in the literature (9, 35), including those that invoke feedforward and feedback effects on the coupling between humidity deficits, stomatal conductance and transpiration (36, 37).

To investigate any possible role that photopigments might play in the stomatal conductance process, we compared the stomatal conductances of leaves with different colors. We found that the stomatal conductance values of green leaves (rubber plant, Chinese banyan bonsai, and American basswood) were comparable with that of red leaves (copperleaf). However, a such a between-plant comparison could be error-prone due to several confounding factors such as different number of stomata, stomatal densities, stomatal pore diameters, morphological sizes, shapes, and thicknesses of the leaves. Hence, we chose the cotton-leaf physic nut for this part of the study. Cotton-leaf physic nut had two different colored leaves – green and red. The leaves were identical with respect to all the morphological features except for the color, making them ideal to assess the role of photopigments in stomatal conductance. Our results indicated that the mean stomatal conductance of the red leaves was higher than that of the green ones, but not significantly so. Hence, while it is possible that the presence of different photopigments may affect stomatal conductance over a long time period (38), it did not affect the experimental results of our study.

An interesting trend that stood out from all the above-mentioned observations is the consistency of the experimental outcomes for all plant species despite the obvious differences in morphology. The trend of changes in stomatal conductance in response to temperature and humidity followed the same pattern for all five plants and was independent of the differences in leaf size and shape.

Limitations

In its present form, this research suffered from a few limitations. The atmospheric CO_2 level was found to be between 387 ppm and 395 ppm during this field study. Stomatal conductance changes with CO_2 when there is a considerable change in the air CO_2 content. Hence, its effect on stomatal conductance was assumed not to play a major role in this study. Different plant species may transpire maximally during different time periods throughout the day. This was not taken into consideration and the measurements were performed at two different predetermined times of the day. We were interested in assessing the effects of environmental factors on stomatal conductance at a particular point in time in general and not on maximal stomatal conductance. However it cannot be discounted that feedforward or feedback mechanisms could influence stomatal conductance differently at different conductance rates. It must also be noted that all the measurements were conducted above the respective dew points, the formation of dew was not visible. However, the extent of the differences between the experimental temperatures and the respective dew points varied from each other, and this was not taken into consideration for this study. The different plants studied were on a regular watering schedule, hence the soil moisture content was assumed to not affect stomatal conductance.

Conclusion

The effects of the environmental factors of light intensity, temperature, and humidity on the stomatal conductances of five plants growing in the tropical climate of Bengaluru, India were determined. As expected, light plays a critical role in the opening and closing of stomata and its intensity is an important factor in keeping stomata open. We also observed that both air humidity and temperature are important factors that affect stomatal conductance. Humidity appeared to be a more influential factor than the temperature, since the stomatal conductance was maximum for all the plants when the RH value was 60% to 80%, in parallel with the results obtained from the temperature independent factor of vapor pressure difference; where the maximum stomatal conductance occurred between 0.8 kPa and 1.2 kPa. We also found that the stomatal conductances increased with a rise in temperature only when the relative humidity value was near-constant. With fluctuating relative humidity, the stomatal conductance change with temperature was unpredictable and did not follow any trend, implying that stomatal conductance was influenced more by humidity than by temperature.

We also found that the nature of photopigments did not affect stomatal conductance. Even though the measured stomatal conductances of the red leaves were greater than the green leaves of the cotton-leaf physicnut, the difference was not statistically significant. The general pattern of changes in stomatal conductances in response to the factors studied was found to be independent of the morphological features of the leaves.

As the obvious next part of this study, we intend to determine the effects of CO_2 levels, leaf water potential, and effects of blue and red light separately. Also, the entire study was carried out with plants in their native positions and under ambient environmental conditions. This was inconvenient and susceptible to errors due to changes in meteorological conditions during the data collection processes. Hence, in the future, we intend to carry out these measurements using a confined chamber where we can control the temperature, humidity, light intensity, and CO_2 level, perhaps leading to more precise, accurate, and actionable assessments. These latter include the genetic manipulation of stomatal conductance rates to produce drought resistant, high yield crop cultivars (39), understanding the physiological mechanisms that determine the genetic variability in the heat sensitivity of photosynthesis (40), and for providing a basis for modeling and predicting feedforward and feedback effects between terrestrial vegetation and global climate (41).

Data

The data reported in this study is available in the supplemental file.

Acknowledgments

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