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DIURNAL *SERIANTHES NELSONII* MERR. LEAFLET PARAHELIOTROPISM REDUCES LEAFLET TEMPERATURE, RELIEVES PHOTOINHIBITION, AND ALTERS NYCTINASTIC BEHAVIOR

Thomas Edward Marler

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DIURNAL *SERIANTHES NELSONII* MERR. LEAFLET PARAHELIOTROPISM REDUCES LEAFLET TEMPERATURE, RELIEVES PHOTOINHIBITION, AND ALTERS NYCTINASTIC BEHAVIOR

Thomas Edward Marler

Western Pacific Tropical Research Center, University of Guam, Mangilao, Guam 96923, USA.
thomas.marler@gmail.com

Abstract: The diel cycle of *Serianthes nelsonii* leaflet movements was characterized under four levels of shade from full sun to 22% sunlight transmission to determine the photoprotective components of diurnal leaflet movements and the relationship to patterns of nocturnal leaflet movements. Treatments also included negating paraheliotropism by re-orienting plants every 15min throughout the photoperiod such that the plants never experienced a predictable solar vector. The timing of leaflet closure to avoid high light, the shape of the diurnal curve depicting leaflet angle, and the maximum extent of leaflet closure were influenced by the shade treatments. Protection of leaf function by paraheliotropism was also influenced by shade treatment, with the full sun plants exhibiting the greatest level of protection. Leaflet heat gain was reduced 50% by leaflet movement as determined by direct measurements of leaf-to-air temperature differences. Midday quantum efficiency of photosystem II was increased 120% by leaflet movement as determined by direct measurements of pulse modulated chlorophyll fluorescence. The extent of nyctinastic leaflet closure was greatest in the high light plants that moved the most midday and least in the shaded plants that moved the least midday, indicating the extent of diurnal paraheliotropism controlled the amplitude of nocturnal leaflet movement. *Serianthes nelsonii* is highly skilled at using movement to reduce leaflet exposure to the solar vector, providing instantaneous behavioral control over heat gain and photoinhibition. This case study of an endemic tree species in Micronesia has added to the nascent field of conservation physiology, and indicated that heliotropism of *S. nelsonii* leaves may provide the species with the ability to minimize high light damage during increased temperatures associated with climate change.

Keywords: Chlorophyll fluorescence, conservation physiology, Fire Tree, Guam, pulvinus.

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INTRODUCTION

Serianthes nelsonii is a legume tree endemic to the two southernmost islands of the Mariana Island archipelago. Many legume species are equipped with pulvini at the base of leaflets or leaves which enable rapid leaf movements. General observations of this plant reveal the leaves exhibit this characteristic legume leaf response of diurnal and nocturnal leaflet movements, indicating the location of a pulvinus at each petiolule. The tree is known locally as 'Hayun Lagu' in the United States Territory of Guam and 'Tronkon Guafi' in the United States Commonwealth of the Northern Mariana Islands (USFWS 1987). The species is listed as Critically Endangered by the International Union for Conservation of Nature (Wiles & Williams 2017) and listed as Endangered under the United States Endangered Species Act (USFWS 1987). The need for more research to understand the biology of the species was a prominent component of the 25-year-old species recovery plan (USFWS 1994).

Plant movements can be classified into tropic movements which are controlled by a stimulus vector, and nastic movements which are independent of a directional stimulus (van Zanten et al. 2010). The diurnal movement of *S. nelsonii* leaflets is a tropic behavior, where the movements are employed to adjust to the sun vector throughout the day. The movements that reduce the angle of incidence of the solar beam are referred to as paraheliotropic movements (Ehleringer & Forseth 1980). In contrast, the nocturnal movements of *S. nelsonii* leaflets are nastic movements, as there is no directional stimulus that mediates the movements. These nocturnal leaflet movements are referred to as nyctinastic movements.

Conservation physiology has been described as a sub-discipline of conservation science (Wikelski & Cooke 2006). The benefits of adding conservation physiology to the palette of conservation science agendas is that physiology relies on cause-and-effect mechanisms that are illuminated through empirical approaches (Cooke et al. 2013). The ability to move leaves in response to the solar beam may benefit photosynthesis and carbon gain (Mooney & Ehleringer 1978; Forseth & Ehleringer 1983; Nilsen & Forseth 2018). Therefore, the observations that *S. neslonii* plants are able to move leaflets enabled the potential to add this case study to the paraheliotropism literature within the conservation physiology discipline.

My objective was to determine the diurnal benefits that *S. nelsonii* leaves receive by exploiting paraheliotropic movements of leaflets. This was accomplished with remote measurements of leaf temperature and chlorophyll fluorescence. The quantum efficiency of Photosystem II (ϕPSIIR) is useful for understanding the relative amount of absorbed light that is actually used in Photosystem II photochemistry (Genty et al. 1992; Murchie & Lawson 2013). This photosynthesis trait was employed to determine the level of protection against photoinhibition provided by *S. nelsonii* leaflet movement. I also measured nyctinastic movements to more fully understand how incident light during the day influenced these nocturnal leaflet behaviors.

MATERIALS AND METHODS

Nursery operations

Guam-sourced *S. nelsonii* plants were grown in a container nursery under four levels of incident light to provide 100%, 73%, 38%, or 22% of sunlight. Leaves were allowed to emerge and mature on the plants under each of the incident light levels. The plants were 60–80 cm in height when the leaflet behaviors were monitored in January and February 2015. Guam's weather during these months of the dry season is fairly homogeneous, with a high of 30°C, a low of 22°C, and a mean of 26°C for the duration of the study. A mean of 6.4h of clear sunshine occurred per day, and total photoperiod was 11.3h. The plants were well-watered to avoid drought stress.

Stochastic cloud passage was common for most days of measurement. These clouds reduced incident light in a heterogeneous manner and the duration of each cloud's blockage of the solar beam was also heterogeneous. The results for each of these days were not repeatable due to the heterogeneity of abrupt changes in light due to stochastic cumulus cloud cover. Therefore, I continued to collect data until a clear day and subsequent night occurred on 10–11 Feb 2015.

The movement of the mature leaflets was quantified directly with a protractor approximately every 2h. The angle between a horizontal plane and each leaflet was measured, such that an angle of 90^o represented a vertical leaflet and an angle of 0^o represented a horizontal leaflet. There were eight plants per shade level, and the leaflet angle measurements were made on three leaflets per plant, for a total of 24 measurements per shade level.

Physiology measurements

The influence of leaflet movement on leaf physiology was studied by re-orienting half of the plants in each shade treatment every 15min throughout a diurnal period to reverse the benefits of leaflet movement. The plants were placed on their sides on the nursery benches, then returned to a vertical position in an alternating pattern. This approach did not allow the leaflet movement on the treated plant leaves to avoid the natural incidence of the solar beam. The surfaces of the containers were shaded from direct sunlight when the plants were placed sideways during re-orientation to ensure the roots did not experience high temperatures.

The leaflet temperature was measured throughout diurnal periods with an infrared temperature gun (Milwaukee Model 2267-20, Milwaukee Tool, Brookfield, WI, U.S.A.). Accuracy of the infrared thermometer was initially checked by comparing to direct measurements of leaflet temperatures with a thermistor (PP Systems, Amesbury, MA, U.S.A.). The infrared approach was highly accurate for leaflets in all shade levels. There were four plants per treatment within each shade level, and leaflet temperature was recorded for three leaflets per plant for a total of 12 measurements per treatment within each shade level.

Chlorophyll fluorescence was measured with a FMS2 pulse modulated fluorometer (Hansatech, Norfolk, United Kingdom). The ϕPSIIR (Genty et al. 1989; Murchie & Lawson 2013) was quantified without dark-acclimation and during full exposure of the test leaflets to the incident light. The number of measurements was as described for leaflet temperature.

All data were plotted separately for the diurnal and nocturnal period. The influence of shade treatments on diel leaflet behaviors was discussed.

RESULTS

The earliest morning leaflet movement and the most severe leaflet angles occurred on sunny days. Plants exposed to full sun conditions were highly skilled at maintaining a very narrow angle between the leaflet surface and the solar vector (Fig. 1). As the sun increased in height from the east each morning, the leaflets closed to track the angle of the sun. At noon, these leaflets were oriented very close to vertical. As the sun set towards west each afternoon, the leaflets re-opened to track the angle of the sun. Plants in shaded growing conditions also moved in response to incident light, but the amplitude of leaflet movement was muted in comparison to leaves on full sun plants. Plants under 73% light transmission stopped the vertical movements at about 60° above the horizontal before re-opening in the early afternoon. Plants under 38% light transmission were even less in need of protecting themselves with paraheliotropism, so they stopped the movement at about 40^0 above the horizontal before re-opening in the afternoon. Plants in deepest shade moved their leaflets very little throughout the photoperiod, with a maximum of about 23^0 leaflet displacement during midday. The leaflet angle diverged among the shade treatments before 09.00h, and remained divergent until 18.00h.

Plants in all four shade treatments exhibited leaflet movements during the nocturnal period (Fig. 2). The leaflets began to close shortly after sunset, reached a maximum from 02.00–04.00 h, then began to re-open several hours prior to sunrise such that they were almost fully open before 08.00h. The nocturnal pattern and maximum nocturnal leaflet angle differed among the shade treatments, with the full sun and 73% sunlight transmission plants beginning leaflet closure earlier in the night and reaching a maximum angle of 85^0. In contrast, the plants receiving the deepest shade level began leaflet closure later in the night and reached a maximum of only 50^0 before beginning to re-open the leaflets. Synchronized patterns of leaflet movement for all four shade treatments are depicted in the video file (Video 1).

Moving the orientation of plants throughout the photoperiod to negate the benefits of leaflet paraheliotropism exerted a strong influence on leaflet temperature. When plants were allowed to use leaflet paraheliotropism to avoid high light, the leaflet temperatures of full sun plants were maintained to within 4.5^0C above ambient (Fig. 3, left). Interestingly, the paraheliotropism was more effective in reducing leaflet heat gain during midday than in early morning and late afternoon hours. In contrast, the treated full sun plants for which paraheliotropism was negated exhibited a leaf-to-air temperature difference of 8^0C (Fig. 3, right). Moreover, the shape of the diurnal curve was approximately bell-shaped for the treated full sun plants, rather than exhibiting a midday dip as for the control plants. The influence of shade treatments on the shape of the diurnal curve was similar among the three shade levels, but the influence on diurnal leaf-to-air temperature maxima diverged for the shade treatments. Leaves of the plants receiving 73% or 38% sunlight transmission exhibited a maximum leaf-to-air temperature difference of about 4^0C for plants that were allowed natural leaflet paraheliotropic movements (Fig. 3, left). In contrast, the treated plants exhibited maximum leaf-to-air temperature differences of 8°C for 73% light transmission and 6^0C for 38% light transmission

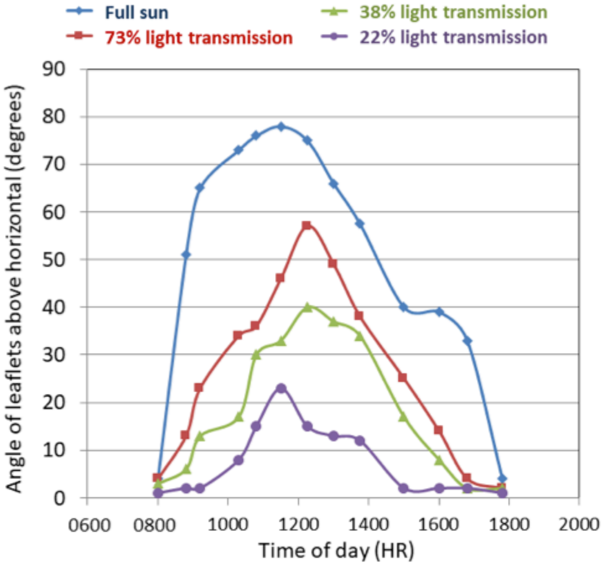


Figure 1. The diurnal cycle of *Serianthes nelsonii* leaflet movement on 10 February 2015 as influenced by percent sunlight transmission through shade treatments. N = 8.

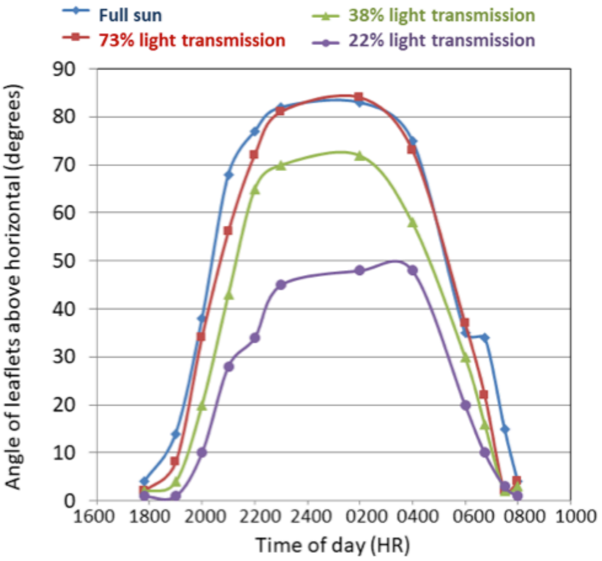


Figure 2. The nocturnal cycle of *Serianthes nelsonii* leaflet movement during the night following a clear day (10–11 February 2015) as influenced by percent sunlight transmission through shade treatments. N = 8.

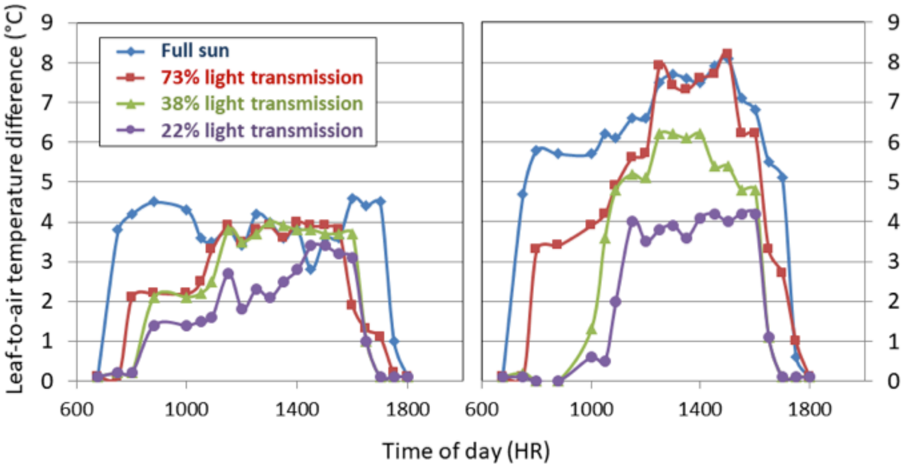


Figure 3. The diurnal cycle of *Serianthes nelsonii* leaf-to-air temperature difference as influenced by percent sunlight transmission through shade treatments on 10 February 2015. Leaflets were allowed to move to naturally avoid the solar beam (Left) Leaflets were not allowed to move to naturally avoid the solar beam (right). N = 4.

(Fig. 3, right). The plants receiving 22% light transmission exhibited the least differences between the treated and control plants, with a leaf-to-air temperature difference of about 3.4^{0}C for the control plants (Fig. 3, left) and about 4^{0}C for the treated plants (Fig. 3, right).

The direct temperature data provided a means of estimating the level of protection against high temperature stress afforded by *S. nelsonii* leaflet movement. Negating the benefits of leaflet movement generated leaf temperatures that were 8°C above ambient for the plants receiving the least protection by shade (Fig. 3, right). But allowing the natural paraheliotropic movements to avoid incident light provided 44–50 % improvement of leaf temperature for the full sun and 73% sunlight transmission treatments (Fig. 3, left). The leaf temperature improvement generated by leaflet movement of the plants receiving 22% sunlight transmission was much less, approximating 15% improvement of leaf temperature provided by leaflet movements.

Moving the orientation of plants throughout the photoperiod exerted a strong influence on ϕPSIIR.

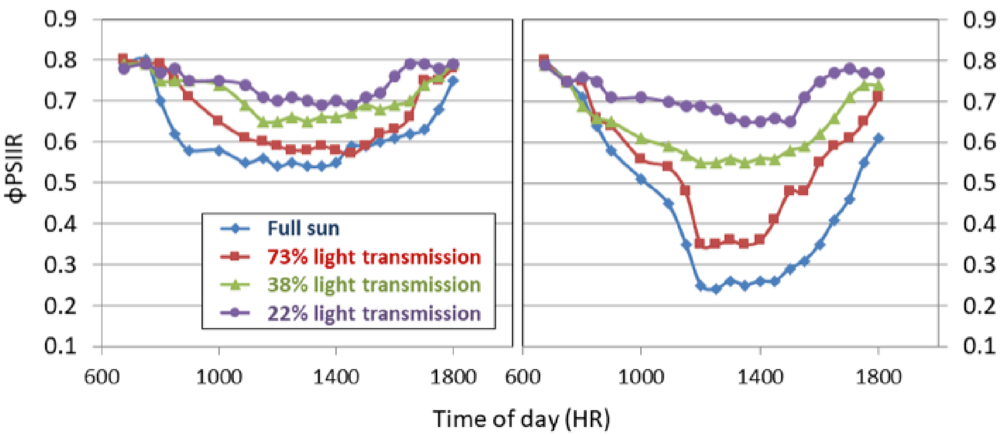


Figure 4. The diurnal cycle of quantum efficiency of Photosystem II for *Serianthes nelsonii* leaflets (ϕPSIIR) as influenced by percent sunlight transmission through shade treatments on 10 February 2015. Leaflets were allowed to move to naturally avoid the solar beam (left). Leaflets were not allowed to move to naturally avoid the solar beam (right). N = 4.

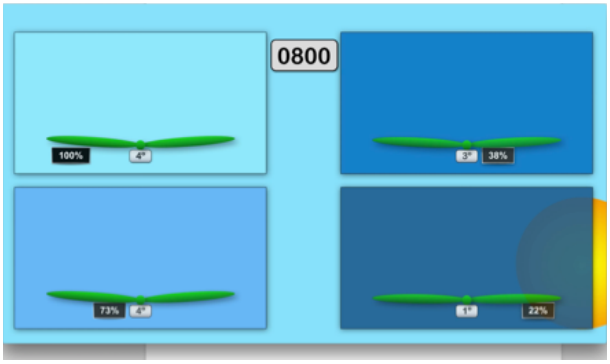
All four light treatments began the photoperiod with ϕPSIIR of 0.78 to 0.8. When plants were allowed to use leaflet paraheliotropism to avoid high light, the ϕPSIIR of leaflets of full sun plants declined to about 0.54 during midday (Fig. 4, left). In contrast, the full sun plants for which paraheliotropism was negated exhibited midday ϕPSIIR of about 0.24 (Fig. 4, right). The shape of the diurnal curves of ϕPSIIR were similar for all of the shade treatments. Midday ϕPSIIR for 73% light transmission plants was about 0.57 for control plants and 0.35 for treated plants. Midday ϕPSIIR for 38% light transmission plants was about 0.65 for control plants and 0.55 for treated plants. Middy ϕPSIIR for 22% light transmission plants was about 0.68 for control plants and 0.65 for treated plants. The ϕPSIIR of shaded plants that were allowed to exhibit paraheliotropism returned to the 0.78 or above by the end of the photoperiod (Fig. 4, left). In contrast, the ϕPSIIR of full sun plants recovered to 0.75 by the end of the photoperiod. For the treated plants which were denied the benefits of paraheliotropism, only the 22% light transmission plants were able to return ϕPSIIR to 0.78 or above by the end of the photoperiod (Fig. 4, right). This late afternoon recovery of ϕPSIIR was only 0.6 for the treated full sun plants.

DISCUSSION

My results indicated *S. nelsonii* plants are highly proficient at use of extreme control over leaflet movements as a strategy to regulate incident light load and protect the leaflets from high light damage when needed. The leaflet paraheliotropism enabled by pulvini afforded benefits for minimizing leaf-to-air temperature differences and improving quantum efficiency of Photosystem II. The daily ambient light load defined the extent of paraheliotropic movement of *S. nelsonii* leaflets and the level of protection that was provided by movement. Plants receiving high light load moved their leaflets early in the morning and reached leaflet angles near vertical for much of the photoperiod. In contrast, plants in deepest shade moved their leaflets very little throughout the photoperiod because they were not experiencing conditions in which they needed to avoid high light stress.

The ϕPSIIR data (Fig. 4) provided a means of estimating the level of protection against photoinhibition afforded by *S. nelsonii* leaflet movement. This fluorescence metric is useful for understanding the relative amount of absorbed light that is actually used in Photosystem II photochemistry (Genty et al. 1992; Murchie & Lawson 2013). The minimum ϕPSIIR for the full sun plants that were allowed paraheliotropic leaflet movements was 120% greater than the minimum ϕPSIIR for plants that were disallowed the protection of paraheliotropic movements. The level of protection afforded by paraheliotropism was moderated by the provision of shade. This was borne out by delaying the initial diurnal declines of ϕPSIIR in the morning and moderating the midday minimum of ϕPSIIR that was reached. For example, the level of midday protection for the plants receiving 22% sunlight transmission and allowed leaflet movement was only 8% greater than that of the plants that were disallowed the benefits of paraheliotropism. These benefits of leaflet movement were expected, as Photosystem II is particularly sensitive to thermal damage (Berry & Bjorkman 1980).

Diurnal control over leaflet angle also improves



Video 1. Animation of diel cycle of *Serienthes nelsonii* leaflet movements as influenced by four shade levels.

total canopy radiation interception and radiation-use efficiency on a daily basis because the leaflet angles of exterior leaves provide instantaneous control over sunlight penetration into the interior leaves of the canopy. Therefore, the use of tight instantaneous control over heliotropism confers a working photoprotective strategy and improves a tree's capacity to cope with daily environment variations. On cloudy days the outer leaflets may employ a diaheliotropic behavior whereby the lamina may be maintained perpendicular to the solar vector (Ehleringer & Forseth 1980). On those cloudy days the maximum use of the limited light by peripheral leaves may reduce photosynthesis of leaflets located inside the canopy by the process of mutual shading. On sunny days the outer leaflets may avoid the solar vector for most of the day by use of paraheliotropism, thereby increasing photosynthesis of leaflets located inside the canopy by allowing more sunlight to penetrate. The continuum between diaheliotropism and paraheliotropism has been reported for other species with pulvini-mediated leaf movements (Forseth 1990). This level of control over angle of the photosynthetic surface has been shown to profoundly benefit photosynthesis, carbon gain, and seed yield (Mooney & Ehleringer 1978; Forseth & Ehleringer 1983; dos Santos et el. 2006; Nilsen & Forseth 2018).

The reasons that leaflets of some species close at night are not fully understood, and the triggers that mediate nocturnal leaflet closure are not fully known. This nocturnal leaf movement is among the plant behaviors that follow circadian rhythms (Ueda & Nakamura 2007), and these circadian behaviors that can be anticipated by plants are advantageous to plant fitness (Dodd et al. 2005). *Serianthes nelsonii* plants in all four light treatments began to close after sunset, a process called nyctinasty. The ultimate magnitude of closure during the night was defined by the amplitude of closure that plants in each incident light treatment exhibited during the daytime. For example, leaflets of plants in the 22% sunlight transmission treatment never fully closed during the photoperiod because the shaded conditions mitigated high light stress and the need for protection from photoinhibition by leaflet movement was not severe. These same shaded plants exhibited an inability to fully close their leaflets at night and reached a maximum of only 50° above the horizontal. In contrast, the plants that received the high light treatments during the photoperiod exhibited an ability to fully close their leaflets at night, reaching a maximum of almost vertical. This nocturnal behavior may be under the control of learned behavior (Eisenstein et al. 2001), where the amplitude of tropic diurnal leaflet movement is perceived as a habitual behavior that controls the amplitude of nastic nocturnal leaflet movement. *Mimosa pudica* leaves have demonstrated similar learned behaviors of leaflet folding skills in response to doses of physical stimuli (Gagliano et al. 2014).

The timing of nocturnal leaflet closure and re-opening was generally synchronized among leaves of all four shade treatments even though the amplitude of closure was dissimilar. The re-opening of leaflets near the end of the nocturnal cycle began about 04.00h for all four treatments. By the time of sunrise, the leaflets were essentially fully open. The trigger for that synchronized *S. nelsonii* leaflet re-opening that begins several hours before sunrise is not known. Suggestions for what controls the timing of nocturnal leaflet movements include a circadian clock (Gorton & Satter 1983) or the lunisolar gravitational force (Barlow 2015). More research is needed to develop a greater understanding of the controlling mechanisms of the nyctinastic *S. nelsonii* leaf behaviors.

Conservation practitioners and planners need hard evidence to guide decisions. The recently described sub-discipline of conservation physiology (Wikelski & Cooke 2006) adds to the biodiversity conservation agenda by employing empirical approaches to determine cause-and-effect relationships of organisms and their environment (Cooke et al. 2013). For example, the detrimental effects of climate change on biodiversity conservation may be more fully understood by employing conservation physiology approaches (van Kleunen 2014). Ambient air temperature is highly influential in how legume leaflet movements benefit leaf function in high light conditions (Fu & Ehleringer 1989; Kao & Forseth 1992). My results indicate that threatened species such as *S. nelsonii* that are equipped with the ability to rapidly adjust the angle of the photosynthetic organ to the solar vector may be better able to adjust to warmer global temperatures in the future, as they may be able to maintain the leaf-to-air temperature differences to a minimum while responding to increased ambient temperatures.

In summary, the Recovery Plan for *Serianthes nelsonii* (USFWS 1994) stated the need to conduct more research is a critical component of recovering this important tree species. Toward that end, I have shown that the tight control of diurnal leaflet movements enabled by pulvini at the base of *S. nelsonii* leaflets provided benefits by reducing heat gain due to maintenance of a beneficial angle in relation to the solar vector. The reduction in high light stress also reduced photoinhibition as characterized by an increase in the quantum efficiency of Photosystem II for plants that were allowed to exhibit para-heliotropic leaflet movements. Finally, the nocturnal nastic leaflet movements were correlated with the diurnal light exposure and corresponding paraheliotropic movements, with plants exhibiting the greatest extent of diurnal movements also exhibiting the greatest extent of nocturnal movements.

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Article

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Notes

Partner
صندوق محمد بن زايد
للمحافظة على
الكائنات الحية
The Mohamed bin Zayed
SPECIES CONSERVATION FUND

Member
FJN

Publisher & Host
WILD
ZOOREACH
Threatened Taxa