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ARTICLE ADDENDUM

Increasing relevance of sunfleck research

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ABSTRACT
Contemporary reviews of leaf responses to sunflecks indicate gymnosperms exhibit slower photosynthetic inductions times than angiosperms, but the gymnosperms were represented exclusively by conifers. I recently reported that the gymnosperm *Cycas micronesica* exhibited photosynthetic induction times in conformity with some of the most rapid angiosperms and opined that representatives from non-conifer gymnosperms must be added to the published conifer database before gymnosperm-wide conclusions can be formulated. Guiding principles for this urgently needed research will maximize relevance and improve accuracy of conclusions.

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The accumulating literature on leaf physiology in response to sunflecks has included numerous spermatophytes. Recent reviews have indicated that angiosperms as a group exhibit more rapid photosynthetic induction following an abrupt increase in incident light. Unfortunately, the gymnosperm database was represented exclusively by conifers, so the other phylogenetic groups of gymnosperms were not included. I recently determined the leaf responses to sunflecks by the gymnosperm *Cycas micronesica* to find the inductions times for this cycad species were as rapid as many angiosperm taxa.[1] The results reveal that use of the term gymnosperm for the spermatophyte group comparisons in past reviews was misleading because the data failed to include non-conifer gymnosperms.

Based on simulations and direct measurements of conifer canopies versus broadleaf canopies,[2,3] extreme dissimilarities in sunfleck traits and penumbral effects on shadeflecks should be expected for the various extant non-conifer gymnosperm taxa. My analysis highlights the need to be more accurate in making phylogenetic group comparisons when one group is represented by a small fraction of the diversity within the group, and past reports on sunfleck physiology would have improved accuracy by comparing at finer phylogenetic scales, for example angiosperm species vs. conifer species.

The goal to understand the extent to which photosynthetic induction of gymnosperms differs from that of angiosperms would clearly be supported by the addition of cycad species to the global data set. Future research may be guided by several recommendations to minimize artifacts and increase relevance to the global research agenda. First, over-story canopy traits define sunfleck characteristics and penumbral effects on shadeflecks.[3] Experimental protocols for studying sunfleck use by each newly studied species, such as shadefleck light level and sunfleck duration, should first be defined from the natural habitats for each new model species. Otherwise the experimental results may not maintain biogeographical relevance. Indeed, incident light conditions vary greatly among natural settings for various cycad species (Fig. 1). Second, induction responses of cultivated plants may differ from those of *in situ* plants.[4] The addition of more cycad species to this research agenda should be conducted in natural settings of each species rather than botanic garden settings. Otherwise the results may have limited ecological relevance. Third, some species may exhibit non-responsive stomatal conductance throughout sun-cloud transitions in well-watered conditions, but switch to responsive stomatal conductance during sun-cloud transitions in drought conditions.[5] More research is needed for a range of cycad species to determine if this level of context dependency on stomatal control under heterogeneous incident light is exhibited by representatives of the Cycadidae. Fourth, the ability of plants to effectively exploit sunflecks throughout the diurnal period is not restricted to the speed of photosynthetic induction in sunflecks, although this is the most studied response variable. Effectively capitalizing on sunflecks is also dependent on building a toolbox to maintain mesophyll conductance of CO_2, minimize photoinhibition and thermal damage during longer sunflecks, reduce the rate of induction loss after sunflecks, sustain post-illumination carbon fixation, respond to ambient temperature changes, and maintain leaf hydraulic conductance.[3,6-10] These traits should be studied along with photosynthetic induction kinetics whenever possible to maximize integration of new knowledge with the established literature.

These results also address urgent conservation decisions by underscoring the adaptive repertoire of *C. micronesica* with regard to heterogeneous incident light conditions. Slower responses to sunflecks of full sun plants resulted from active acclimation of photosynthetic machinery to best utilize the excessive incident light in the open field habitats. Fast responses

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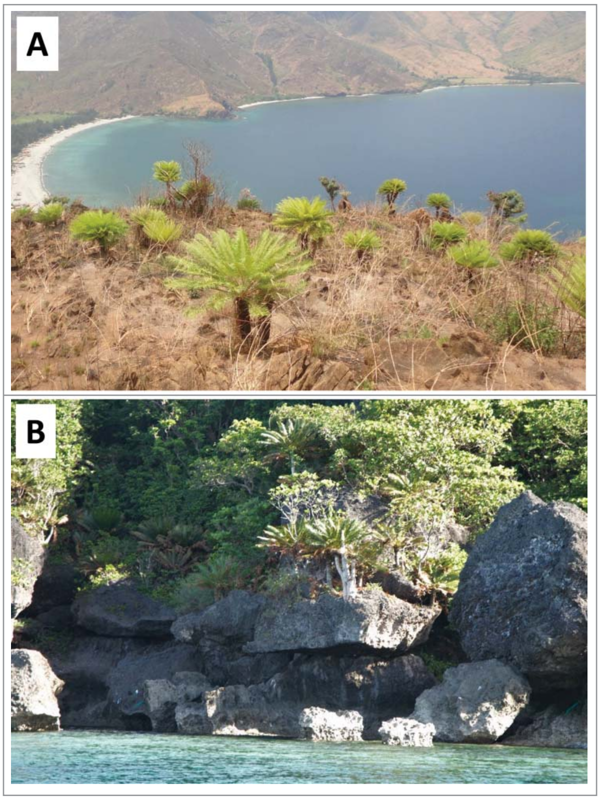

Figure 1. Some cycad species such as *Cycas zambalensis* (A) grow primarily in full sun conditions. Other cycad species such as *Cycas edentata* (B) exhibit facultative behaviors and grow in a range of sun/shade conditions. Differences such as these ecological niche preferences may guide continuing research on gymnosperm sunfleck physiology.

to sunflecks of understory plants resulted from active acclimation of photosynthetic machinery to best utilize the transient pulses of light. Reduced respiratory carbon losses of understory plants aided in maintaining a positive carbon balance in the light-limiting conditions. Shade-grown *C. micronesica* leaves also increased apparent quantum yield and reduced light compensation of photosynthesis in comparison to sun-grown leaves.[11]

An off-site conservation germplasm collection of this species is being managed on the island of Tinian, where plots have been positioned in an ecotone between native biodiverse limestone forest canopy tree cover and adjacent non-native monoculture *Leucaena leucocephala* tree cover. The understory *C. micronesica* plants have exhibited highly heterogeneous survival and growth rates.[12] The highly contrasting ability of sun vs. understory *C. micronesica* leaves to utilize sunflecks[1] indicates that heterogeneity in sunfleck quantity, duration, and quality throughout the emergent tree cover may be one factor that is influencing growth of the understory *C. micronesica* plants. Indeed, the ability to decrease the quality of sunfleck availability for competitor plants is one means by which non-native plants may facilitate their own invasions.[13,14] Measurements of dynamic incident light conditions in this and other *ex situ* germplasm collections may offer answers to questions concerning differences in germplasm performance among different managed planting sites. For *ex situ* conservation nursery production of *C. micronesica* seedlings, more research is needed to evaluate how post-transplant performance is influenced by supplying the nursery plants with fluctuating shade, such as with a slathouse, vs. supplying them with homogeneous shade, such as with a screen shadehouse.

Adding one cycad species to the published gymnosperm data has cast doubt on the accuracy of past conclusions where conifers have been used to represent gymnosperms in sunfleck research. More representatives from the Cycadidae, Ginkgoidae, and Gnetidae must be added to the published conifer database before gymnosperm-wide conclusions can be defended.

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