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DEMOGRAPHY AND ECOPHYSIOLOGY OF *CYCAS SIAMENSIS* IN A DECIDUOUS DIPTEROCARP FOREST OF NORTHEAST THAILAND

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ABSTRACT

Cycads are ecologically important in subtropical dry forests and savannas worldwide. The population structure, morphology and ecophysiology of *Cycas siamensis* Miq., a species found at high densities in deciduous dipterocarp forests of Southeast Asia, were studied in order to understand its ecological strategies of adaptation to its highly seasonal environment. Field studies were conducted in northeastern/central Thailand at the end of the dry season in 1995 and at the end of the wet season in 1996. *Cycas siamensis* is well adapted to fire and seasonal drought. Large numbers of juvenile plants were recorded in the population suggesting that post-establishment seedling survivorship in this fire prone environment is relatively high. The ecophysiology of the species readily allows rapid regrowth of leaves after fire from stored carbohydrate reserves in the same manner in which new cohorts of leaves are formed annually. New leaves develop rapidly within six weeks after a fire. Physiologically immature leaves have negative net photosynthetic rates indicating high rates of tissue respiration and low rates of water loss. Carbon isotope ratios indicated moderate levels of water use efficiency in mature leaves, levels expected of a drought deciduous species. Mean c_i:c_a ratios of seedlings indicated that they had lower water use efficiency than mature individuals at the end of the dry season, a strategy allowing them to maximize growth in order to build up sufficient carbohydrate reserves for the dry season. A maximum assimilation rate of 8.2 µmol $m^{-2} s^{-1}$ was recorded for mature leaves at the end of the wet season, at the high end of previously published rates for cycads. Photosynthetic rates were lower in the dry season.

INTRODUCTION

Cycads are primitive vascular woody plants that form important community components of subtropical dry forests and savannas in many parts of the world. One genus, *Cycas*, has notable ecological significance because of its wide geographic range and frequent abundance from East Africa through the Indian subcontinent to Southeast Asia, northern Australia and the western Pacific. Six to ten species of *Cycas* are known to occur in Thailand (depending on the taxonomic opinion), with most of these having relatively restricted ranges or distributions limited to specific limestone substrates (SMITINAND, 1972; HILL & YANG, 1999). A notable exception to this pattern of localized distribution is *C. siamensis* Miq. which is a widespread species.

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Cycas siamensis is a low cycad reaching a maximum stem height of 1.5–2 m. It can frequently be found in high densities in the understory of open deciduous dipterocarp forests of Thailand, Laos, Cambodia and Vietnam. These forests are generally dominated by *Shorea siamensis, S. obtusa, Dipterocarpus obtusifolius, D. tuberculatus* (all Dipterocarpaceae) and a variety of other low tree species (RUNDEL & BOONPRAGOB, 1995), and are characterized by very frequent ground fires (STOTT, 1984; 1988). Athough lightning is relatively common in these habitats, the majority of these fires are deliberately set. This has likely been the case for thousands of years. Virtually the entire forest community is deciduous, with leaf abscission beginning in December and early January for some species and continuing until most species are leafless by late March.

Despite the high densities of occurrence and widespread distribution of *Cycas siamensis*, remarkably little is known about its ecology beyond the fact that it is resilient to fire damage due to its rapid resprouting from an underground fleshy stem. In this paper we report on the morphological structure and population densities of *C. siamensis* in the deciduous dipterocarp forests of Sakaerat Environmental Research Station in northeast Thailand. We further report the first ecophysiological data on this species, describing the photosynthetic responses and stomatal conductances of *Cycas* leaves, and the nature of the changing leaf gas exchange parameters associated with the post-fire respouting of new leaves. These demographic and ecophysiological traits of *C. siamensis* suggest a distinctive adaptive strategy that is shared by other savanna cycads.

MATERIALS AND METHODS

Field studies were carried out at Sakaerat Environmental Research Station near Pak Thong Chai, Nakhon Ratchasima Province, 60 km south of Khorat in northeast Thailand (lat. 14º31'N, long. 101º55'E) during 1995 and 1996. This field station encompasses a research area of 81 km^2 on the northeastern slopes of the Central Highlands of Thailand near their transition to the Khorat Plateau. The topography of the station is largely gentle slopes and rolling terrain at 300–560 m elevation. The shallow soils are sandy clay loams derived from sandstone parent material and are poor in availability nutrients and soil waterholding capacity. The structure and dynamics of deciduous dipterocarp forest at Sakaerat have been previously described (SAHUNALU & DHANMANONDA, 1994). The groundcover beneath the canopies and intercanopy areas of the deciduous dipterocarp forestforest was covered by a low growth of *Arundinaria pusilla* (= *Racemobambos ciliata* (A. Camus) Chao & Renv.), an herbaceous rhizomatous bamboo commonly reaching up to 1 m height.

Mean annual precipitation at Sakaerat is about 1240 mm, with moderate to high monthly rainfall present from late May through October. Rains begins to decline in November with the transition to the dry season, and the early dry season from December through February is almost totally rainless. Scattered light rainfalls or showers typically occur in the late dry season well before the beginning of the wet season. Mean maximum air temperatures are 30–35ºC in the early dry season, but rise sharply to 38–40ºC in April and May. As the wet season begins in late May and June, mean maximum temperatures steadily decline from these high levels to a low of 25–26ºC in November and December when the dry season begins again (RUNDEL & BOONPRAGOB, 1995).

Field observations on the post-fire growth response of *C. siamensis* were made in April 1995 in an area of deciduous dipterocarp forest that had burned six weeks earlier. Three post-fire stages of resprouting recovery were apparent in *C. siamensis* at the time of sampling. These were immature leaves not fully expanded and lacking chlorophyll, fully expanded leaves pale gray-green in color and not yet photosynthetically active, and fully mature expanded green leaves with full photosynthetic capacity.

Measurements of population density and structure were carried out in November 1996 by sampling 13 5 x 5 m square quadrats scattered in a regular grid across an area of several hectares within a zone of 50–70% canopy coverage of deciduous dipterocarp forest trees. While this sample size was too small to accurately represent mean population density over the whole area, it allowed a large sample size for assessing size class distribution. Within these quadrats, each individual *C. siamensis* was counted and measured for trunk height (cm), mean leaf length (cm), and number of leaves. The overall number of live individuals measured was 101, with an additional 10 dead individuals also present. Qualitative observations were recorded classifying overstory canopy conditions and understory soil conditions for each plot and individual. Overstory canopies in plots were classified as open (< 25% canopy cover), lightly shaded (26–50% canopy cover), moderately shaded (51–75% canopy cover), or heavily shaded (> 75% canopy cover). Understory soil conditions were classified as rock crevices, exposed rock–*Arundinaria* mix, semi-open cover of *Arundinaria*, or dense *Arundinaria* cover.

Replicated gas exchange measurements (N = 3–5) were made on post-fire developmental leaf stages using a LI-6200 photosynthesis system (LICOR Inc., Lincoln, Nebraska) and compared to control plants away from the area of the fire in April 1995. Additional gas exchange measurements were made in November 1996 at the end of the wet season. For constructing photosynthetic light response curves, irradiance was provided using a projector bulb to focus light onto the leaf sample after reflection off a cold mirror to prevent heat load. Analyses of leaf nitrogen content and stable carbon isotope ratios and were carried out using pooled samples of five leaves from the study population. Analyses were made using standard techniques with a Finnigan isotope ratio mass spectrometer at the Stable Isotope Laboratory of the Department of Biology, Boston University (EHLERINGER & RUNDEL, 1988).

RESULTS AND DISCUSSION

High water use efficiency might be strongly selected for in *Cycas siamensis* if this species remained active throughout the dry season. Many individuals, however, respond to the height of the winter drought by losing their leaves. While dry season deciduousness is uncommon in cycads, it has been reported in other *Cycas* species experiencing long dry seasons under monsoonal climate conditions (ORNDUFF, 1992). It is also suspected in *Encephalartos poggei* and several related species growing on white sand in Zaire and known in *Bowenia serrulata*, but in no other genera (Pete Vorster, personal communication) New leaves of *C. siamensis* are typically formed late in the dry season in March, and these leaves are mature well before the onset of monsoonal rains in May. How then does the demography and ecophysiology of *C. siamensis* adapt this species to its fire-prone environment?

Demography and Morphology

The mean density of *Cycas siamensis* in the sample area was 0.3 individuals m^{-2} (range of 0.1–0.6 cycads m^{-2}). Individuals with a trunk height of 50 cm or more made up only 9% of the population, with the tallest trunk reaching 66 cm in height. Juvenile plants with a trunk height of 4 cm or less comprised 57% of the total population sampled (Fig. 1), with most of these (50% of all plants sampled) being seedlings with no trunk developed. Large proportions of seedlings without trunks have also been reported for populations of *C. armstrongii* in northern Australia (WATKINSON & POWELL 1997).

Within the stands that we sampled we found 10 cycads that were dead in place. Two of these were large plants 45 cm in trunk height, while the remainders were seedlings. We do not know the rate of decomposition for dead plants but these data suggest that survivorship of seedling cycads once they are established is relatively high. Frequent ground fires that destroy young seedlings, however, may complicate this interpretation.

Overhead canopy closure above individual cycads was strongly centered on lightly shaded (51% of individuals) and moderately shaded tree canopies (48% of individuals), the most common habitat types present. One individual occurred in a small forest gap, while no individual cycads were found in dense areas of *Arundinaria* grassland without canopy cover. We hypothesize that fires in this habitat might be too intense for seedling survival. Groundcover characteristics were largely either a moderately dense cover of *Arundinaria* (56% of individuals) or exposed rock–*Arundinaria* mix (37% of individuals). No cycads were found growing out of cracks in rock outcrops and only 6% occurred in areas with dense cover of *Arundinaria.*

The number of leaves on an individual *C. siamensis* showed a significant pattern of change with a steady increase in leaf number with trunk height until an asymptote was reached at a trunk height of about 10 cm (Fig. 2). There was no significant pattern of increase in leaf number with greater trunk height, although the maximum leaf number of 30 was found on the largest cycad. We observed no pattern of sexual dimorphism in leaf number as has been reported for *Macrozamia* in Australia (ORNDUFF, 1991). Moreover, leaf number is not an indicator of sexual maturity in *C. siamensis* as has been reported for *Macrozamia* (ORNDUFF, 1990). The smallest sexually mature individuals that we have observed for both males and females of *C. siamensis* were well above 20 cm in trunk height. Seedlings without a woody trunk had only 1–3 leaves.

Mean leaf length was about 80 cm (with a range of about 60–100 cm), and did not vary significantly with plant size once a trunk height of 2 cm was present (Fig. 3). *Cycas panzhiluaensis* in China have been described as reaching mature leaf sizes once they attain a trunk height of 10 cm (HE *ET AL.*, 1995). Seedlings without a woody trunk were found to have a wide variation in mean leaf lengths from 18–83 cm.

Photosynthetic Capacity and Water Use Efficiency

The mean maximum rate of photosynthetic assimilation in fully mature leaves of *Cycas siamensis* shortly after the end of the wet season in November 1996 was 8.2 µmol $m^{-2}s^{-1}$. Mean dry season rates of photosynthesis measured in April 1995 averaged 4.9 µmol $m^{-2}s^{-1}$. Seedlings exhibited a lower photosynthetic rate of only 3.3 µmol $m^{-2}s^{-1}$ at this time. Our seasonal range of photosynthetic values for mature leaves closely brackets

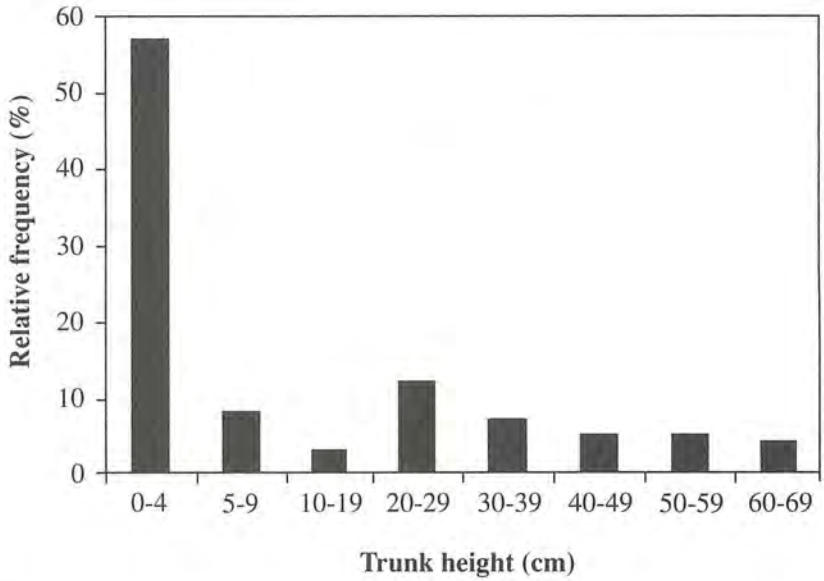

Figure 1. Relative size distribution of individuals of *Cycas siamensis* (N = 101) by trunk height class at Sakaerat Environmental Research Station.

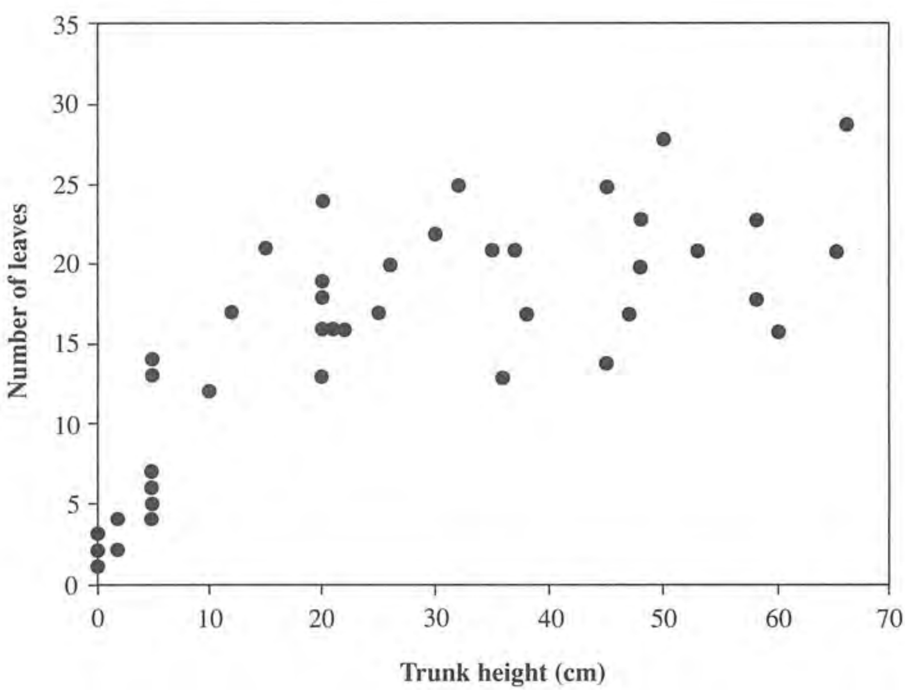

Figure 2. Relationship of leaf number to trunk height in *Cycas siamensis* at Sakaerat Environmental Research Station.

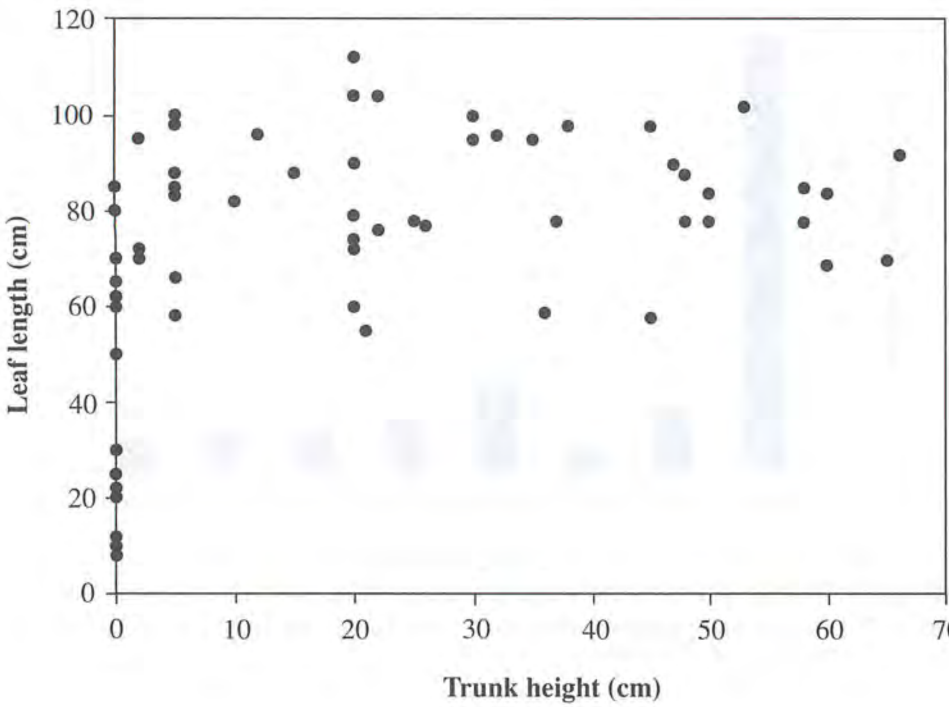

Figure 3. Relationship of mean leaf length to trunk height in *Cycas siamensis* at Sakaerat Environmental Research Station.

Table 1. Photosynthetic characteristics of leaves of mature and seedling *Cycas siamensis* in a control area and for regrowth of mature individuals in an area six weeks after above-ground tissues were killed by fire. Data collected in April 1995 in the late dry season. See text for discussion. ND = values cannot be calculated from negative rates of photosynthesis.

	Assimilation (μmol $m^{-2} \cdot s^{-1}$)	Stomatal conductance (mmol $m^{-2} \cdot s^{-1}$)	ci/ca ratio	Carbon isotope discrimination (o/oo)	Foliar nitrogen ($mg \cdot g^{-1}$)
Non-fire area					
Mature	4.9	86	0.55	–27.0	18.7
Seedling	3.3	46	0.68	–26.4	32.9
Post-fire					
Immature	–15.2	29	ND	–25.8	27.7
Expanded	–6.1	21	ND	–26.0	25.0
Mature	4.9	56	0.51	–26.1	16.8

the high and low ranges of photosynthesis reported in one published account of leaf gas exchange in 16 cycad species grown in an outdoor garden in Florida (MARLER & WILLIS, 1997). Mean stomatal conductance of newly mature leaves of *C. siamensis* at the end of the dry season in 1995 was 86 mmol $m^{-2}s^{-1}$ (Table 1), a rate at the low end of values reported for garden grown cycads.

Cycas siamensis showed a photosynthetic response to photon flux density (PFD) suggesting that this species is well adapted to open sun conditions. In measurements made in November 1995, photosynthetic assimilation saturated at a PFD of about 950 μmol $m^{-2}s^{-1}$, a level similar to that of tree species in the same community and corresponding to levels higher than typical levels of solar irradiance during the wet season (Fig. 4; Rundel *et al.*, unpublished data). These data are consistent with the observation that *C. siamensis* does not occur under conditions of dense canopy shade.

A moderately high level of water use efficiency in *C. siamensis* was indicated both by the ratios of internal to ambient CO_2 concentration (c_i:c_a ratio) and carbon isotope ratio ($\delta^{13}C$). The mean c_i:c_a ratio present during gas exchange measurements at the end of the dry season was 0.55, indicative of strong stomatal control of CO_2 exchange. An absence of stomatal control and free diffusion of CO_2 would give a c_i:c_a ratio of 1.00, while increasing levels of stomatal control allow internal levels of CO_2 to draw down as photosynthesis occurs and thus produce lower ratios. Seedlings of many woody species in seasonal climates are selected for less efficient water use efficiency to allow them to maximize growth so that they can build up sufficient root tissue to survive water stress occurring in the dry season (DONOVAN & EHLERINGER 1991). Seedlings of *C. siamensis* followed this expected pattern and were less efficient in their use of water at the end of the dry season than mature plants as indicated by a c_i:c_a ratio of 0.65 (Table 1). Seedlings also possessed much higher concentrations of foliar nitrogen (32.9 mg g^{-1}) than mature plants (18.7 mg g^{-1}).

Measures of carbon isotope ratio ($\delta^{13}C$) provide a means of assessing integrated water use efficiency during the period in which leaf structural carbon was assimilated. More negative values of $\delta^{13}C$ indicate lower levels of water use efficiency. The $\delta^{13}C$ value of *C. siamensis* was –27.0 o/oo on this sample date, indicative of moderate levels of water use efficiency comparable to that of many tree species in the same habitat (Rundel et al. unpublished data). The $\delta^{13}C$ of seedlings was only slightly higher than adult plants with a value of –26.4 o/oo.

Ecophysiology of Post-fire Regrowth

The savanna and forest habitats in which many cycads grow expose these plants to frequent ground fires during the dry season. Although most of these fires burn quickly through grasses and other light fuels and do little or no harm to mature trees and larger saplings, the above ground tissues of many cycads are killed though little or no mortality occurs. We have observed two post-fire characteristics of *Cycas siamensis* that parallel results reported for fire response of *Zamia pumila* in pine savannas of Florida (TANG, 1990; NEGRON-ORTIZ & GORCHOV, 2000). New leaves resprout very rapidly from the fleshy stem following fires and sporophyll production is stimulated in many female plants.

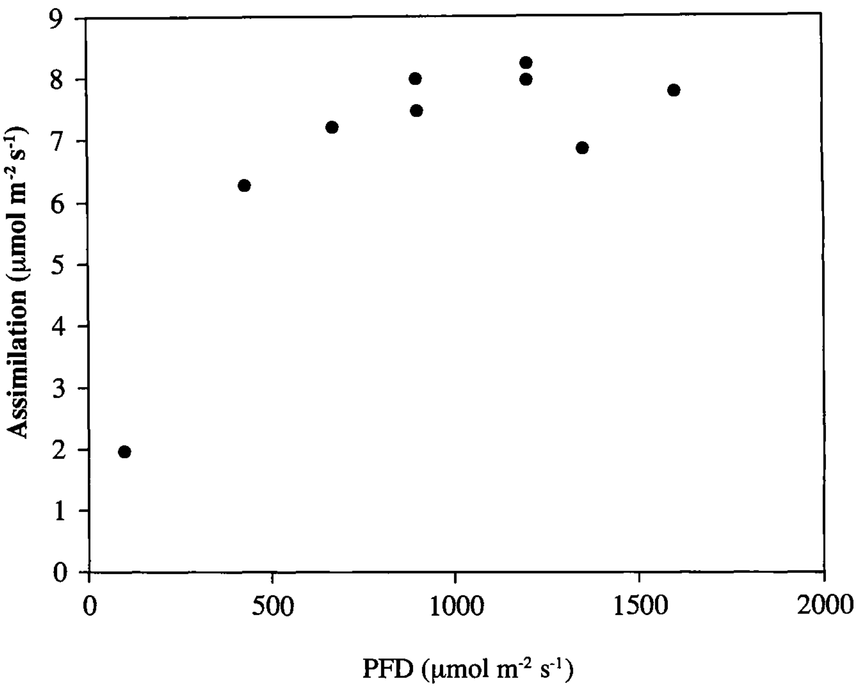

Figure 4. Light response curve for *Cycas siamensis* relating the rate of photosynthetic assimilation to photon flux density (PFD).

In April 1995, less than 6 weeks after a fire in the deciduous dipterocarp forest at Sakaerat Environmental Research Station and under conditions of extreme soil drought, leaf flushing in *C. siamensis* was occurring rapidly. The only other woody plants showing new resprout tissues at this time were small saplings of *Shorea siamensis*, a species that possesses an enlarged woody root crown. We carried out ecophysiological measurements on three stages of new leaf development in *C. siamensis*: (a) plants with pale immature leaves: (b) plants with fully expanded but physiologically immature leaves gray-green in color; and, (c) plants with fully mature green leaves. All of these stages were present at the same time on different individuals.

Despite high foliar nitrogen contents of 27.7 and 25.0 mg g^{-1}, respectively, in the two stages of developing leaves, no net photosynthesis was occurring at either stage. The small pale leaves of the first stage had a remarkable negative rate of –15.2 μmol $m^{-2}s^{-1}$, indicating strong respiratory activities associated with carbohydrate translocation and tissue development (Table 1). The fully expanded but physiologically immature leaves also had a negative rate of net photosynthesis of –6.1 μmol $m^{-2}s^{-1}$. Fully mature green leaves on adjacent plants had a positive rate of net photosynthesis of 4.9 μmol $m^{-2}s^{-1}$. There was a low rate of water loss from both stages of developing leaves as indicated by stomatal conductances of 29 and 21 mol $m^{-2}s^{-1}$, respectively. Fully mature green leaves on adjacent plants had a stomatal conductance rate of 56 mol $m^{-2}s^{-1}$ (Table 1).

Carbohydrate reserves from the fleshy trunk enable *C. siamensis* to expand new leaves rapidly after fire. This carbohydrate pool is the same as that used to flush and mature new leaves under the natural annual turnover of leaf biomass, as indicated by the consistent pattern of $\delta^{13}C$ in control leaves and post-fire stages of leaf regrowth (Table 1). Developing post-fire leaves have larger concentrations of nitrogen than mature leaves, even at immature stages when photosynthesis is not yet occurring. This nitrogen must also have its origin in storage pools in the base of the trunk and possibly in other belowground tissues.

CONCLUSIONS

The demographic and ecophysiological traits of *C. siamensis* suggest that it is well adapted to fire disturbance and seasonal drought, selective pressures characteristic of dry forest and savanna ecosystems. Leaves of this species are able to regrow rapidly after fire utilizing stored carbohydrate reserves in the same manner in which new cohorts of leaves are formed annually. Carbon isotope ratios indicate moderate levels of water use efficiency in mature leaves, levels expected of a drought deciduous species. This species occurs in semi-open canopy environments, but not in deep shade nor in open grassland. We suggest that it is restricted from the former habitat due to its light requirements for photosynthesis and from the latter habitat due to more intense fires that would potentially exclude seedlings. While its assimilation rates are at the high end of those reported for cycads, its restriction to nutrient poor soils is possibly because it is able to compete more successfully with angiosperms in this environment.

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