

Xylem hydraulic and photosynthetic function of *Gnetum* (Gnetales) species from Papua New Guinea

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Summary

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- *Gnetum* (Gnetales) species are suggested to be unique extant gymnosperms that have acquired high photosynthetic and transpiration capacities as well as greater xylem hydraulic capacity and efficiency compared with all other extant gymnosperms. This is because *Gnetum* is the only extant gymnosperm lineage that combines vessels, broad pinnate-veined leaves and an ecological distribution in wet, productive lowland tropical rainforest habitats. Yet, field-based observations on the group's ecophysiological performance are lacking.
- To test a hypothesis that *Gnetum* species are ecophysiologicaly analogous to light-demanding woody tropical angiosperms, stem xylem hydraulic performance, photosynthesis and stomatal conductance were investigated in *Gnetum* as compared with a diverse group of co-occurring woody plants in a lowland tropical rainforest.
- It was found that *Gnetum* species combined low photosynthetic capacity and low stomatal conductances with a low stem water transport ability. The physiological observations are consistent with the general occurrence of *Gnetum* species in shady, primary forest habitats.
- These results on *Gnetum* ecophysiology indicate that the coupling of vessels, broad pinnate-veined leaves and the liana habit do not signal the evolution of a highly opportunistic, light-demanding life history in gymnosperms.

Key words: angiosperm diversification, evolutionary convergence, Gnetales, xylem hydraulics.

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Introduction

The Gnetales (*Ephedra*, *Welwitschia*, *Gnetum*, approx. 66 species) are unique among living gymnosperms because they bear so many angiosperm-like characters (Doyle & Donoghue, 1986; Friedman, 1998). These characters have traditionally been viewed as evidence for a close evolutionary relationship between Gnetales and angiosperms. The major characters thought to be responsible for the close link between Gnetales and angiosperms include strobili with flower-like morphologies (a variant of double fertilization, reduced megagametophytes and microgametophytes, and the presence of an outer envelope on the ovule), vessels in the wood, lignin chemistry (Maule

reaction) and a tunica layer in the apical meristem (Doyle & Donoghue, 1986; Friedman, 1998). A whole-plant angiosperm gestalt is strikingly developed in *Gnetum*. *Gnetum*, comprising approx. 35 species of lianas and trees, are angiosperm lookalikes. For example, they bear broad-bladed, pinnate-veined leaves (up to 10 cm wide) with multiple vein orders on shoot systems with a distinctive jointed, decussate phyllotaxis (Tomlinson & Fisher, 2005). Ecologically, *Gnetum* species are common residents of wet, lowland tropical rainforests (Markgraf, 1951; Stevenson & Zanoni, 1991). However, the vegetative systems and ecologies of the other major gnetalean lineages contrast sharply with those of *Gnetum*. *Ephedra* (approx. 30 species) occur as arid-adapted shrubs to scandent shrubs with nearly

leafless, broom-like photosynthetic stems (Ickert-Bond & Wojciechowski, 2004). *Welwitschia* (one species) is a desert plant with a unique habit. It consists of a short, stout trunk bearing only two leaves that continuously grow from the base over the plant's lifetime (Henschel & Seely, 2004).

Recent molecular phylogenetic studies, while supporting monophyly of the group, have assigned the Gnetales to numerous evolutionary positions that are distant from angiosperms. The Gnetales have been placed as a sister group to all other extant gymnosperms (cycads, conifers and *Ginkgo*) as sister to the conifers, or derived from within Pinaceae (Burleigh & Mathews, 2004). Although the exact placement of the Gnetales in seed plant phylogeny requires more work (Burleigh & Mathews, 2004), all multiple gene-based phylogenies so far indicate that the similarities in form between Gnetales and angiosperms are probably the result of evolutionary convergence.

Consistent with the hypothesis of evolutionary convergence, characters suggested to link *Gnetum* and other Gnetales with angiosperms differ in their details. As examples, gnetalean vessels are derived from tracheids with circular pits, whereas angiosperm vessels are derived from tracheids with scalariform pits; the tunica consists of a single layer in Gnetales, but as two cell layers in angiosperms; double fertilization produces endosperm in angiosperms, but not in Gnetales; the finest venation in *Gnetum* leaves consists of a subepidermal system of hydrophilic and intrusively developed fibers, instead of very fine and dense primary vascular strands as in most angiosperms (Carlquist, 1996; Friedman, 1998; Tomlinson & Fisher, 2005). Furthermore, conifer-like characters occur in *Gnetum* and in other Gnetales, including pollen droplet-mediated pollination (Kato *et al.*, 1995), occasional tracheary elements with margo-torus pits in some species (Carlquist, 1996), phi-thickenings in roots (Gerrath *et al.*, 2002) and circular-bordered pitting in the primary xylem (Carlquist, 1996) – but these features could be convergences with conifers.

The striking general morphological convergence between angiosperms and the Gnetales, in particular *Gnetum*, raises the question of where *Gnetum* fits along the broad continuum of ecophysiological performances exhibited by angiosperms. Previous discussions have proposed that *Gnetum* taxa function most similarly to opportunistic light-demanding pioneer tropical trees and lianas, an ecology that would set the lineage apart from most other extant gymnosperms. The specific weedy functional features that are believed to characterize *Gnetum* include high rates of leaf photosynthesis and transpiration, rapid growth and seedling recruitment in highly disturbed habitats (Doyle & Donoghue, 1986; McElwain *et al.*, 2005). While needle-leaved, tropical pines can exhibit high transpiration and photosynthetic capacity, as well as recruitment in large disturbance zones that are unlimited in light availability (Bond, 1989; Grotkopp *et al.*, 2002; Lusk *et al.*, 2003; Brodribb & Feild, in press), the evolution of xylem vessels and broad pinnate veined leaves in *Gnetum* suggests that the carbon-use efficiency involved in the possible development of high

photosynthesis and transpiration capacities may be much greater than in pines. This is because *Gnetum* vessels may lower the investment costs of sapwood area allocation needed to support a given shoot water supply and their broad leaves may lower self-shading costs (Brodribb & Feild, 2000, in press; Feild, 2005). Further supporting this point, single-veined tropical lowland podocarp conifers that have evolved broad leaves nonetheless exhibit greater sapwood area costs compared with vessel-bearing angiosperms (Brodribb *et al.*, 2005; Brodribb & Feild, in press). The liana habits exhibited by nearly all *Gnetum* taxa (Markgraf, 1951; Stevenson & Zanoni, 1991) further suggest the potential for an efficient weedy disturbance-tolerant ecophysiology in *Gnetum* because no other extant gymnosperm lineage has evolved a liana habit. Stems of *Gnetum* lianas (approx. 1 cm diameter) can possess large-diameter vessels (up to 300 μm) with simple perforation plates (Fisher & Ewers, 1995; Carlquist, 1996). This implies the evolution of a highly streamlined xylem hydraulic system in *Gnetum* and an ability of the wood to support high shoot transpiration. Despite extensive speculation on the functional capabilities of *Gnetum*, a conspicuous gap in our ability to evaluate these hypotheses is that there are currently no basic field observations on *Gnetum* ecophysiology.

In this article, we investigated comparative patterns of stem xylem hydraulic functioning, leaf stomatal conductances and photosynthetic performances of a community of four *Gnetum* species from a tropical lowland rainforest in Papua New Guinea. We chose to work in Papua New Guinea because the rainforests around Madang offer the unique opportunity to study a diverse community of *Gnetum* species that consists of two tree and two liana species in *Gnetum*. We compared *Gnetum* species with several co-occurring and abundant angiosperm trees and lianas as well as with a locally rare conifer. Overall, our goal was to determine whether *Gnetum* species are characterized by a high capacity for photosynthetic and xylem hydraulic function. We discussed the bearing of our results on the origin of angiosperm-like convergence in *Gnetum*.

Materials and Methods

Study site and species sampled

We studied a community of four *Gnetum* species from primary and secondary hill forests of the Kau Wildlife Preserve, Baitabag Village (145°41 E; 5°08 S; *c.* 0–50 m elevation above sea level). Our study site was approx. 20 km north of Madang, Papua New Guinea. Lowland rainforests in the Madang region are productive and dominated by evergreen angiosperms. The average annual rainfall in the Madang area is 3558 mm, with a moderately dry season from July to September. The mean air temperature is 26.5°C and varies little throughout the year. Additional details about the vegetation structure and composition of the site can be found in Saulei & Swaine (1988). We conducted observational work

Table 1 Classification, growth form and ecology for the 13 species investigated

Species	Family	Growth form	Position of adults in the forest
<i>Gnetum costatum</i>	Gnetaceae	Tree	Subcanopy, primary forest
<i>Gnetum gnemon</i>	Gnetaceae	Tree	Subcanopy, primary forest
<i>Gnetum latifolium</i>	Gnetaceae	Liana	Subcanopy to canopy, primary forest
<i>Gnetum</i> sp.	Gnetaceae	Liana	Subcanopy to canopy, primary forest
Angiosperms			
<i>Eupomatia laurina</i>	Eupomatiaceae	Shrub	Understory, primary forest
<i>Hibiscus</i> sp.	Malvaceae	Tree	Canopy, secondary forest
<i>Homolanthus novoguineensis</i>	Euphorbiaceae	Tree	Canopy, secondary forest
<i>Horsfieldia</i> sp.	Myristicaceae	Tree	Canopy, primary forest
<i>Gonocaryum</i> sp.	Icacinaceae	Liana	Subcanopy to canopy, primary forest
<i>Kleinhovia hospita</i>	Malvaceae	Tree	Canopy, secondary forest
<i>Piper aduncum</i>	Piperaceae	Shrub	Canopy, secondary forest
<i>Piper</i> beetle	Piperaceae	Liana	Understory, primary forest
<i>Tinospora</i> sp.	Menispermaceae	Liana	Subcanopy to canopy, primary forest
<i>Trema orientalis</i>	Ulmaceae	Tree	Canopy, secondary forest
<i>Trichospermum pleiostigma</i>	Tiliaceae	Tree	Canopy, secondary forest
Conifer			
<i>Podocarpus neriifolius</i>	Podocarpaceae	Tree	Subcanopy to canopy, primary forest

Ecological categorizations of each species are based on several years of forest plot census data in the field study site (L. Balun, unpublished, 1988–2007).

from September to October 2004 and from January to February 2007. No statistical differences, for almost all ecophysiological measurements, were observed between data collected during the wet periods of the dry season of 2004 versus the wet season conditions during 2007. Thus, the ecophysiological data collected during both of the sampling periods were combined. An exception to this pattern was found in our hydraulic measurements. In our second field season, we detected an experimental error (i.e. the induction of cryptic, cut vessels lacking endwalls by cutting stem segments too short) in data collected during 2004 that resulted in inflated values of stem hydraulic parameters. Thus, for stem hydraulic performance measurements, we only reported data from 2007.

We established a study site (100 m × 100 m) along a ridge in dense, 20–25 m tall primary forest. We studied four *Gnetum* species. These species included the only two known arborescent species in *Gnetum* (*G. gnemon* L., and *G. costatum* K. Sch.) and two liana taxa (*G. latifolium* Blume and a currently undescribed *Gnetum* species). For comparison, we conducted physiological measurements on eight common co-occurring angiosperm tree species, three angiosperm liana species and one locally rare conifer species. The species selected belong to the most abundant species in the community and they differed in adult canopy position and shade tolerance (Table 1).

For all species, we compared the photosynthetic and hydraulic performances of individuals from full-sunlight environments to sample the maximum capacity of each species for leaf and stem ecophysiological performance. This approach was chosen because unpublished observations on stem hydraulic and leaf

photosynthetic function indicated that for all species occurring in sun habitats, ecophysiological capacities are always much lower under shaded conditions (T. S. Feild, L. Balun, field obs., 2004, 2007). Ten individuals were sampled from exposed habitats that experience full light intensity (i.e. full sun, approx. 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR)) and high vapour pressure deficit (VPD) (midday VPD on clear days, 1.2–1.7 kPa) for much of the day (i.e. at least 10 h). Specific habitats that we sampled included plants in the edges of clearings or from high in the forest canopy (up to 15 m, as in the case of the two *Gnetum* lianas). We also sampled 10 individuals of two species that occurred only in the shaded forest understory. Average understory diffuse light intensities were typical of other lowland tropical rainforests, with a background diffuse light intensity of approx. 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR that is punctuated by frequent light flecks (Chazdon & Fetcher, 1984). Midday VPD measurements made on clear days in the understory ranged from 0.45 to 0.65 kPa. We performed VPD measurements using a newly calibrated portable porometer (Li-Cor 1600; Li-Cor Biosciences, Lincoln, NE, USA).

Stem xylem hydraulic conductivity

Stem xylem hydraulic conductivities (K_H) were measured using an electronic balance method (Sperry *et al.*, 1988). We first checked for emboli by flushing three stems of each species at 0.2 MPa for 30 min with filtered (to 0.2 μm) and manually degassed rainwater. If rain had occurred during the preceding day, we observed no change in stem K_H values for any of the

species following flushing, and observed no bubbles emanating from the stems. Consequently, we measured stem K_H values from plants following abundant rainfall to avoid the time-consuming low-pressure flushing treatment.

In the field, branches to be sampled were first bagged in moistened plastic during the early morning hours (06:00–08:00 h) for 30 min to slow transpiration. Then, we severed a large lateral branch from each plant. Branches were then transported to a nearby field laboratory, and stem segments without intervening branches or leaves along the segment were cut from branches while underwater. Because vessels with their endwalls removed at both ends can greatly increase stem hydraulic capacity measurements, we determined the length of the longest vessel using low-pressure air injection (using a hand pump) on a shoot segment and cut the segment back distally until the first bubbles were seen perfusing through the wood. Once this length was known, we made sure that the stem segments of each species used for stem hydraulic capacity measurements were 20–30% longer than the length of the longest xylem vessel. The close proximity of our laboratory to the field site meant that we could measure stems within 1 h of collection and thereby avoid any effects of stem necrosis on xylem hydraulic conductance. Next, both ends of the excised segments were carefully shaved with a double-edged razor blade. The diameter of an excised segment for all species sampled was standardized such that diameters were 3–4 mm with the bark removed. Hydraulic measurements were made on one stem segment from 10 individual plants for each species.

We attached stem segments to a plastic tubing manifold and measured the mass flow (g s^{-1}) through the segment under a pressure head of 0.008 MPa. Mass flow rate was calculated by collecting the water efflux in a graduated cylinder (protected from wind and evaporation by a Plexiglas shield and olive oil layer over the meniscus) and weighed on top of a portable electronic balance (Sartorius BL610; Denver, CO, USA; 0.001 g resolution). Stem temperatures ($27 \pm 2^\circ\text{C}$) were measured using a portable thermocouple reader, and all measured fluxes were corrected for temperature-dependent variation in viscosity by normalizing all values to 25°C (Sperry *et al.*, 1988). The K_H ($\text{kg m s}^{-1} \text{MPa}^{-1}$) was expressed as the volume flow rate divided by the pressure gradient and multiplied by stem length. We recorded flux measurements every 2 min until a steady-state value was reached (approx. 10 min).

Recent experimental results indicate that perfusing distilled water into stems during xylem hydraulic measurements can underestimate the K_H (Zwieniecki *et al.*, 2001; Van Iperen, 2007). This effect occurs because endwall pit pore radii between interconnected vessels can swell and shrink variably with xylem sap ionic concentration (Zwieniecki *et al.*, 2001; Van Iperen, 2007). Thus, for a perfusing solution, we used sterile mineral water with a cationic strength equivalent to 5 mM of monovalent potassium (K) and divalent calcium (Ca) cations to simulate *in planta* xylem sap artificially (Van Iperen, 2007). The perfusing solution was degassed manually using a

large-volume syringe. Because of high humidity and temperature, we changed the solution in the tubing system every day to reduce microbial growth.

While the debate continues on the specific ionic strength and concentrations of ions that should be used in the K_H measurements of wood, recent opinion indicates that solutions of mixed divalent and monovalent cations close to the ionic concentration of xylem sap (2–10 mM) are a more realistic approximation of xylem sap conditions versus distilled water (Van Iperen, 2007). However, it is important to note that the use of a constant ionic solution to simulate xylem sap ionic concentrations will not correct for all possible interspecific biases in xylem hydraulic responses to ions (Maherali *et al.*, 2006). This is because the increase in stem xylem K_H by ions is variable across angiosperms (0–200%; Boyce *et al.*, 2004). This variation results from differences in xylem sap ionic concentrations, composition and vessel length distributions that influence the number of endwall pits encountered during axial water flow through a stem across species (Zwieniecki *et al.*, 2001; Boyce *et al.*, 2004; Gasco *et al.*, 2006). Therefore, the use of a constant ionic solution in our measurements will not remove the potential for measurement error when different species are being compared (Maherali *et al.*, 2006). We note, however, that ionic responses of stem hydraulic conductance do appear to be small in at least *G. gnemon*. Measurements of xylem hydraulic responses of this species, under laboratory conditions, to step changes in KCl concentration indicated only a 20% increase in K_H . This result is consistent with the long vessel lengths (approx. 15 cm) in this species. This result also suggests that for the *Gnetum* taxa sampled, ionic effects on stem K_H are likely to be small.

From the K_H data, we calculated sapwood-area specific conductivity (K_S ; $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) by dividing stem K_H by the sapwood cross-section area (m^2). Sapwood cross-sectional area was measured under a dissecting microscope on hand-sectioned cross-sections of stems stained in safranin. The area contributed by the pith was subtracted (Sperry *et al.*, 1988). Outlines of fresh leaves were traced onto paper and the total leaf area was measured in the laboratory using a digital camera (Nikon CoolPix 990; Nikon) and image-analysis software (IMAGEJ; National Institute of Health, Bethesda, MD, USA). The Huber value was calculated as ($\text{HV} = \text{sapwood area (m}^2\text{) / distal leaf area (m}^2\text{)}$). We also calculated leaf specific conductivity (K_L ; $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$) by dividing K_H by the total leaf area supported (i.e. distally) by that branch.

Photosynthesis and stomatal conductance

We used chlorophyll (Chl) fluorescence emission to measure the photosynthetic capacity of leaves. The quantum yield of photosystem II electron transport (Φ_{PSII}) was determined in the light using a PAM-2100 fluorometer (Waltz, Effeltrich, Germany). We chose to use Chl fluorescence over more traditional gas-exchange methods to estimate leaf photosynthetic

performance because of the remoteness and the harsh, humid working conditions at our field site. Measurements of all species were carried out during cloudless days in Baitabag between 09:30 and 14:00 h.

We selected one fully expanded, undamaged leaf from 10 individuals of each species for observation measurements. Our measurement protocol first involved placing a leaf into the clip (top surface up) and shading it by hand for less than 2 s. Then, the actinic light of the fluorometer was triggered to produce $2000 \mu\text{mol m}^{-2} \text{s}^{-2}$ PAR at the leaf surface. Leaves were illuminated for 15–45 s with external halogen light until steady-state fluorescence (F_s) emission values were observed. When leaves were adequately photosynthetically induced (i.e. after at least 30 min of exposure to full morning sunlight), the F_s yields stabilized after approx. 15 s of actinic illumination. For leaves of the obligate shade species, we had to use a different procedure to ensure that leaves were photosynthetically induced. Small portions of shoots (with two or three leaves) were carefully detached from plants while underwater and without wetting the leaf surfaces, using a split funnel and sticky putty. Then, these shoots were moved to an open light gap and illuminated under full natural sunlight until F_s values were stable (typically taking 5–10 min of illumination). This procedure was used because under hot, humid tropical conditions, the actinic lamp of the fluorometer tended to overheat the instrument after 5 min of constant illumination. Moreover, naturally occurring sunflecks were too stochastic to ensure adequate light induction of photosynthesis.

Once a stable F_s value had been observed for every sample, the leaf was exposed to a brief saturation pulse (1 s, $4500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) to determine maximal fluorescence yield under an actinic light (F'_m). The ϕ_{PSII} was calculated at $(F'_m - F_s)/F'_m$ (Genty *et al.*, 1989). Preliminary measurements made throughout the day indicated that ϕ_{PSII} determined at a PAR of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ peaked between 10:00 and 12:00 h, and there was no evidence of strong midday depression of ϕ_{PSII} (T. S. Feild & L. Balun, unpublished data, 2004, 2007). Consequently, we measured ϕ_{PSII} for each species after at least 3 h of morning light exposure to ensure full photosynthetic induction and stomatal opening (Brodrribb & Feild, 2000; Brodrribb *et al.*, 2002).

Photosynthetic rates were expressed as electron transport rates (ETR), a component of leaf photosynthetic capacity (Brodrribb & Feild, 2000). The ETR was calculated as $\text{ETR} = (\phi_{PSII}) \times (I) \times (\alpha) \times (0.5)$, where I is the incident PAR; α is the leaf absorbance, taken here as 0.84 (Bjorkman & Demmig, 1987), and the coefficient of 0.5 accounts for the assumption that half of the absorbed light energy is distributed evenly between photosystem II and photosystem I (Genty *et al.*, 1989). The units of ETR are $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$, although it should be noted that values of ETR may not be precise as a result of the small variations in α among the species we sampled. We believe that differences in α are small because

the leaves of all species appeared to be very similar in colour, and none of the species sampled had undersurface anthocyanins or trichomes, which can result in significant differences in whole-leaf light absorbance (i.e. approx. 10% in light absorbency, Lee *et al.*, 1990; T. S. Feild & L. Balun, unpublished observations, 2004).

Following Chl fluorescence measurements, stomatal conductance (g_s $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) was measured in all species using a null balance porometer (Li-1600; Li-Cor) between 09:30 and 11:00 h when humidity was high (70–85% relative humidity) and irradiance was saturating (approx. $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR). The porometer was nulled slightly below ambient humidity, and one healthy and fully-expanded leaf from 10 individuals of each species was sampled for g_s . The mean g_s from these measurements was defined as $g_{s\text{Max}}$ for each species. The $g_{s\text{Max}}$ data were measured only from sun-exposed leaves because only sun leaves could be adequately exposed to intensities of light that were long enough for maximal stomatal opening in the field.

Statistical analyses

Regression analyses on the interspecific averages of leaf and stem performance variables were performed using linear functions from a plotting program (SIGMAPLOT; SSPS Inc., Chicago, IL, USA). Average values of ecophysiological traits between tree and liana *Gnetum* species were analysed using a Student's *t*-test.

Results

The average leaf-specific xylem hydraulic conductivities of excised stems (K_L) from sun-acclimated branches varied nearly five-fold across the study species, ranging from 1.12 ± 0.3 standard deviation (SD) $\times 10^4 \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ in the conifer *Podocarpus neriifolius* to $4.97 \pm 0.25 \text{ SD} \times 10^4 \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ in the light-demanding, angiosperm tree *Hibiscus* sp. (Fig. 1a). Across the angiosperms and one conifer sampled from high-light sites, the light-saturated leaf photosynthetic ETR varied three-fold and ranged from $109 \pm 11 \text{ SD} \mu\text{mol electrons m}^{-2} \text{s}^{-1}$ in *P. neriifolius* to $271 \pm 18 \text{ SD} \mu\text{mol electrons m}^{-2} \text{s}^{-1}$ in *Hibiscus* sp. (Fig. 1a).

The mean K_L of sun-acclimated branches of *Gnetum* species fell in the lower portion of the range found for co-occurring woody plants, varying from $0.87 \pm 0.25 \text{ SD} \times 10^4 \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ in the liana *Gnetum* sp. to $1.23 \pm 0.45 \text{ SD} \times 10^4 \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-1}$ in the tree *G. gnemon* (Fig. 1a). Consistent with this observation, the ETR values of sun-acclimated leaves of *Gnetum* species were lower than those of all angiosperms sampled from similarly sun-exposed habitats. The ETR values of *Gnetum* were instead nested among the capacities measured for shade-developed angiosperm leaves (Fig. 1). Across the sampled taxa, K_L was observed to be linearly related to ETR in shoots that were photosynthetically induced (Fig. 1a).

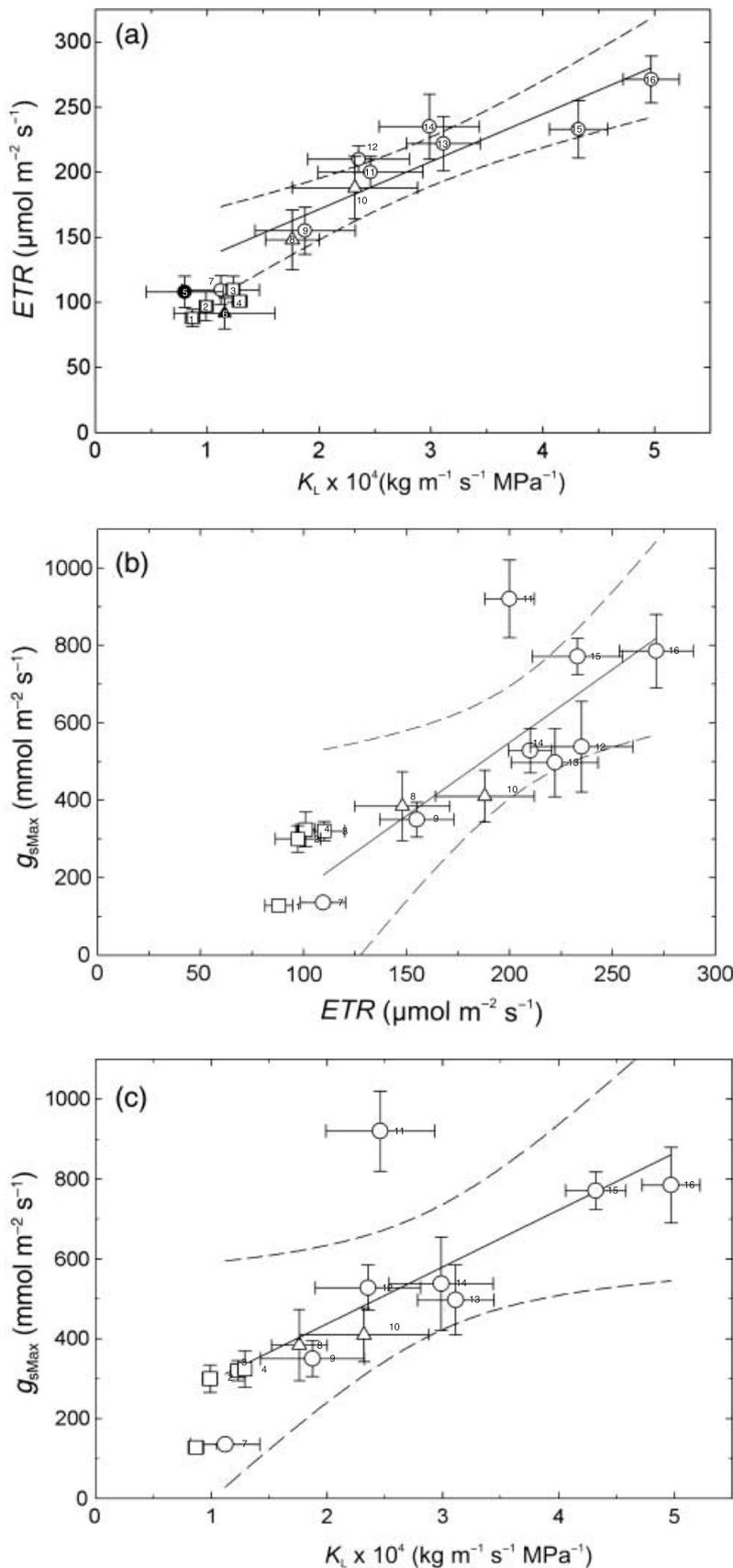


Fig. 1 (a) The relationship between mean leaf photosynthetic capacity (expressed as electron transport rate, ETR) and mean leaf-specific xylem hydraulic conductivities of stems (K_L) of shoots of angiosperms, a conifer and *Gnetum* species. A linear correlation ($r^2 = 0.81$; $y = 36.50x + 98.61$) between ETR and K_L was observed among the species sampled. (b) The relationship ($r^2 = 0.57$; $y = 3.78x - 208.08$) between maximum leaf conductance to water vapour ($g_{s\text{Max}}$) and ETR for sun-tolerant angiosperm trees and shrubs and a conifer as well as sun-tolerant angiosperm lianas as compared with shoots of the taxa *Gnetum*. (c) The relationship ($r^2 = 0.49$; $y = 151.21x + 142.87$) between maximum $g_{s\text{Max}}$ and mean K_L for sun-tolerant angiosperm trees and shrubs and a conifer, as well as sun-tolerant angiosperm lianas in comparison with shoots of the taxa *Gnetum*. Dashed lines around the relationship denote 95% confidence intervals. Numbers near each species mean denote the following species: (*Gnetum*) 1, *G. sp.* (liana); 2, *G. latifolium* (liana); 3, *Gnetum gnemon* (tree); 4, *Gnetum coastatum* (tree); (obligate shade angiosperms) 5, *Eupomatia laurina* (shrub); 6, *Piper beetle* (vine); (conifer) 7, *Podocarpus neriifolius* (tree); (sun angiosperms) 8, *Gonocaryum sp.*, (liana); 9, *Horsfieldia sp.* (tree); 10, *Tinospora sp.* (liana); 11, *Piper aduncum* (shrub); 12, *Trema orientalis* (tree); 13, *Homolanthus novoguineensis* (tree); 14, *Trichospermum pleiostigma* (tree); 15, *Kleinhovia hospita* (tree); 16, *Hibiscus sp.* (tree). Each point represents the average of 10 measurements from 10 individual plants; error bars denote the standard deviation (SD) around the mean. Symbols: (○) sun-tolerant angiosperm trees and shrubs as well as the conifer *Podocarpus*; (●) obligate shade angiosperm shrub; (▲) obligate shade angiosperm vine; (△) sun-tolerant angiosperm lianas; (□) *Gnetum* lianas and trees.

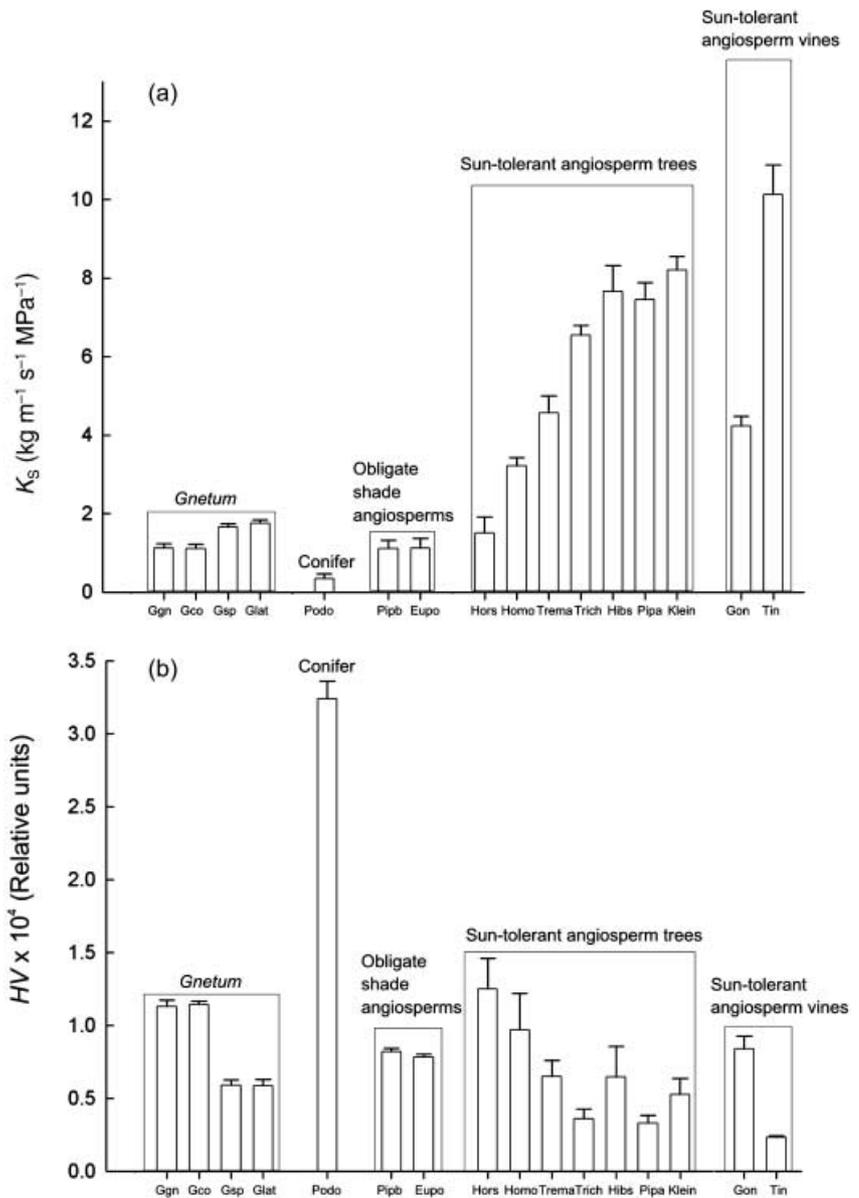


Fig. 2 The range of stem hydraulic capacities (a, K_S , maximum hydraulic conductivity per unit of xylem area) and sapwood area to leaf area allocation (b, Huber value (HV) multiplied by 10^4) of branches among the species sampled. Each bar represents 10 measurements from 10 individual plants; error bars denote the standard deviation (SD) around the mean. Abbreviations for each species: Ggn, *Gnetum gnemon*; Gco, *Gnetum costatum*; Gsp, *Gnetum* sp.; Glat, *Gnetum latifolium*; Podo, *Podocarpus neriifolius*; Pipb, *Piper beetle*; Eupo, *Eupomatia laurina*; Hors, *Horsfieldia* sp.; Homo, *Homolanthus novoguineensis*; Gon, *Gonocaryum* sp.; Trema, *Trema orientalis*; Trich, *Trichospermum pleiostigma*; Hibs, *Hibiscus* sp.; Pipa, *Piper aduncum*; Klein, *Kleinhovia hospita*; Tin, *Tinospora* sp.

Maximum stomatal conductances to water vapour (g_{sMax} , $\text{mmol m}^{-2} \text{s}^{-1}$) were linearly related to the ETR and to the K_L values among sun-developed shoots of the sampled angiosperm and conifer species (Fig. 1b,c). The mean g_{sMax} varied nine-fold across the sampled species, from 135 ± 12 SD $\text{mmol m}^{-2} \text{s}^{-1}$ in *P. neriifolius* to 920 ± 100 SD $\text{mmol m}^{-2} \text{s}^{-1}$ in *Piper aduncum*. Among *Gnetum* species, the average g_{sMax} ranged from 88 ± 6.7 SD $\text{mmol m}^{-2} \text{s}^{-1}$ in *Gnetum* sp. to 324 ± 45 SD $\text{mmol m}^{-2} \text{s}^{-1}$ in *G. costatum*.

The intrinsic hydraulic conductivity (K_S , or maximum hydraulic conductivity per unit of xylem sapwood area) for all four *Gnetum* stems from sun-exposed habitats ranged from 1.11 ± 0.11 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in *G. costatum* to 1.75 ± 0.13 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in the liana *G. latifolium*

(Fig. 2a). The K_S of *Gnetum* taxa overlapped with the lower portion of the range measured for the angiosperm trees sampled, which ranged from 1.11 ± 0.21 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in the obligate shade shrub *Eupomatia* to 8.21 ± 0.34 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in *Kleinhovia*, a light-demanding pioneer species (Fig. 2a). The K_S of angiosperm lianas ranged from 1.11 ± 0.21 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in the obligate shade plant *P. beetle* to 10.1 ± 0.76 SD $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$ in *Tinospora*. *Gnetum* lianas fell out in the lower part of this range. Compared with the vessel-less conifer *P. neriifolius*, the K_S values of *Gnetum* stems were approximately four times greater (Fig. 2a). Also, in sapwood to leaf area allocation (HV), *Gnetum* species had values of HV that were three to five times lower than found in *Podocarpus* (Fig. 2b).

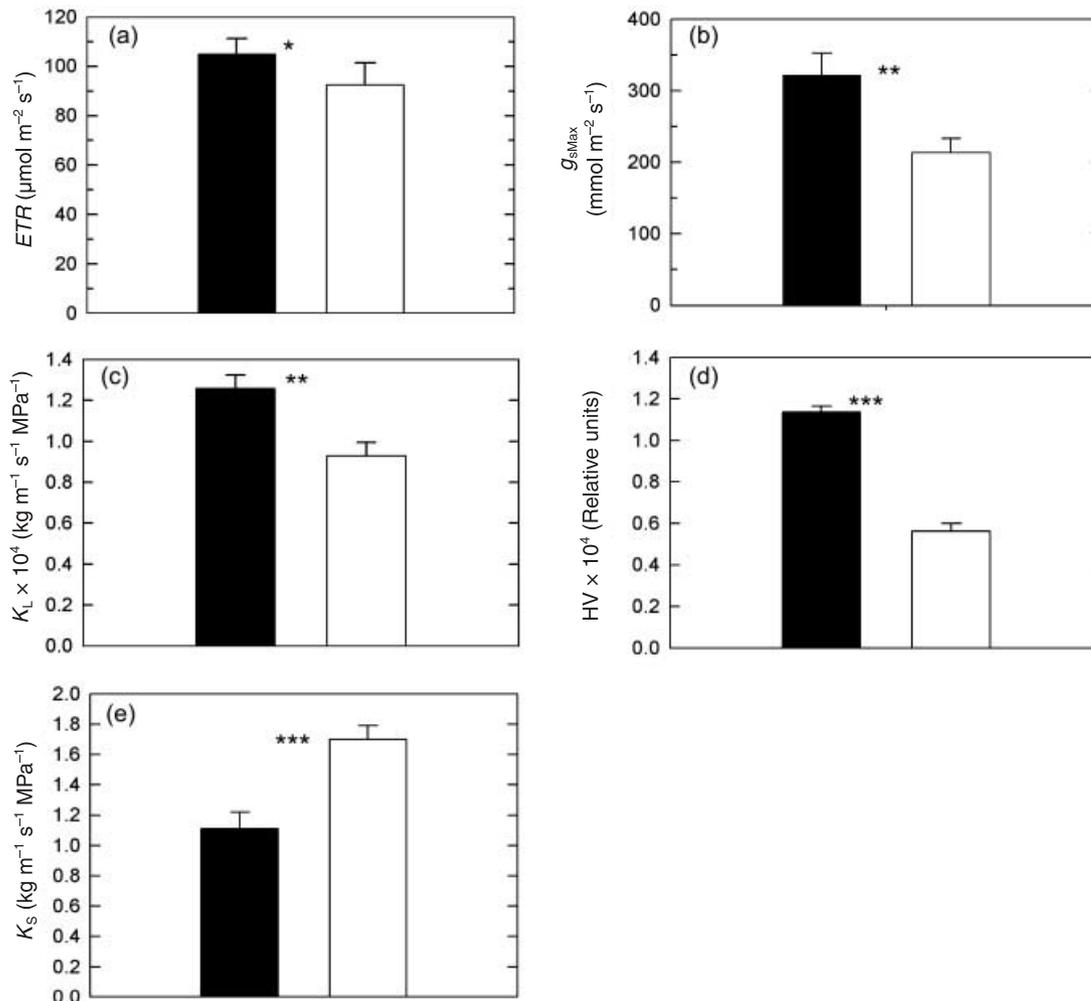


Fig. 3 Comparative leaf photosynthetic capacity (a), maximum stomatal conductance (b), leaf-specific xylem hydraulic conductivities of stems (c), leaf area to sapwood area allocation (d), and intrinsic hydraulic stem hydraulic efficiency on a sapwood area basis (e) of tree (closed bars) versus liana (open bars) *Gnetum* species. Units for ecophysiological variables are noted on the y-axes. Bars represent the averages of two species with 10 observations per species ($n = 20$). Asterisks between bars denote the significance of differences between growth form means: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Student's *t*-test).

Among *Gnetum* taxa, the ETR and K_L values were 12% and 30% lower in lianas compared with trees, respectively (Fig. 3a,c). Values of $g_{s\text{Max}}$ were 36% greater in *Gnetum* tree species than in lianas (Fig. 3b). The HV of *Gnetum* overlapped greatly with the range of values found for all angiosperm species sampled (Fig. 3b). Among *Gnetum* taxa, lianas exhibited a 32% greater K_S and a 48% lower HV compared with trees (Fig. 3d,e).

Discussion

Our results indicate that *Gnetum* species from Papua New Guinea are not ecophysiologicaly analogous to the most opportunistic woody plants that co-occur with them – light-demanding tropical angiosperm pioneers. Instead, *Gnetum* taxa exhibited ecophysiological performances that were most

similar to co-occurring obligate shade-adapted angiosperms. All of the *Gnetum* species that we sampled combined low-light-saturated photosynthetic rates (expressed as ETR), low maximum stomatal conductances ($g_{s\text{Max}}$), low hydraulic abilities of the stems to supply attached leaves with water (K_L), as well as relatively low intrinsic hydraulic efficiency of stems on a sapwood area basis (K_S) relative to co-occurring angiosperms regenerating in brightly lit disturbed habitats. The small interspecific differences in ecophysiological traits that we observed also paralleled differences in whole-plant form. For example, liana species exhibited greater xylem hydraulic efficiencies on a sapwood area basis and lower HV compared with trees. Tree species of *Gnetum*, however, expressed greater leaf photosynthetic rates, $g_{s\text{Max}}$ and shoot K_L .

In many aspects, ecophysiological functioning in *Gnetum* was similar to that of the co-occurring broad-leaved, shade-tolerant,

conifer, *P. neriifolius*, but with two important functional differences. First, values of g_{sMax} of three of the four *Gnetum* species were almost four times greater than the g_{sMax} values of *Podocarpus*. The only exception was the liana *Gnetum* sp., which displayed a g_{sMax} value similar to that of *Podocarpus*. Second, the K_S values provided by vessel-bearing *Gnetum* stems were approximately three times higher than those of vessel-less *Podocarpus* stems. A more efficient vascular stem pipeline of *Gnetum* stems resulted in a substantially reduced investment in xylem sapwood area to support a given value of K_L (Fig. 2). Both of these ecophysiological trends appeared to hold when other tropical conifers (i.e. podocarps and araucarians) were compared with *Gnetum* (Brodribb & Feild, 2000; Lusk *et al.*, 2003; Brodribb *et al.*, 2005). Nonetheless, values for K_S nested in the lower portion of the range observed for co-occurring, nonobligate understory vessel-bearing angiosperms (Fig. 2).

Observations on the ecomorphic structure of *Gnetum* in other studies are consistent with our measurements of low photosynthetic and xylem hydraulic capacities. First, all of the sampled *Gnetum* species, as well as several others, have been shown to develop thin leaves (approx. 250 μm) with a single minimally defined layer of palisade tissue. Also, air spaces are abundant in the mesophyll (Tomlinson & Fisher, 2005; Jauregui & Benitez de Rojas, 2005; T. S. Feild, unpublished data, 2007). This cross-sectional anatomy suggests that *Gnetum* leaves generally have a low ability to process collimated light that characterizes sun habitats and is consistent with our measurements of photosynthetic capacity (Smith *et al.*, 1997). Second, in accordance with other studies, we found that stomatal densities in *Gnetum* leaves are relatively low, which implies low shoot transpiration capacity (Jauregui & Benitez de Rojas, 2005). For example, *G. latifolium* and *G. costatum* leaves possess lower stomatal densities (mean = 104 and 125 stomata mm^{-2} in both species, respectively) in comparison with co-occurring light-demanding angiosperms (350–550 stomata mm^{-2} in *Kleinbovia*, *Piper* and *Trema*; T. S. Feild, unpublished data, 2007) and light-demanding tropical angiosperms from lowland rainforests (Roth, 1984; Popma *et al.*, 1991; Sack & Frole, 2006).

Finally, preliminary observations on vein structure in *Gnetum* reveals that vein densities of *Gnetum* leaves (average: 4.2 mm mm^{-2} in *G. latifolium* and 4.8 mm mm^{-2} in *G. costatum*; T. S. Feild, unpublished obs., 2007) are low and most similar to obligate shade-adapted angiosperms in lowland tropical rainforests (Sack & Frole, 2006; Brodribb *et al.*, 2007). Low vein density indicates that leaves function with low xylem hydraulic conductance and photosynthetic capacity (Sack & Frole, 2006; Brodribb *et al.*, 2007). However, a curious aspect of perhaps all species of *Gnetum* is that the venation system is crisscrossed by a fine mesh of intrusively developed, hydrophilic fibers, and stellate, lignified and pitted sclereids are closely associated with primary xylem veins (Jauregui & Benitez de Rojas, 2005; Tomlinson & Fisher, 2005). It has been suggested

that fibers and sclereids may function in water transport in *Gnetum* as well as in several conifers that are putatively closely related to *Gnetum* (Tomlinson & Fisher, 2005; Brodribb *et al.*, 2007). Because each of these features has the potential to bolster the hydraulic conductance of *Gnetum* laminae, future direct measurements of hydraulic conductance and fine-scale observation of microfluidic dynamics in *Gnetum* leaves are needed to assess the hydraulic role of extravention system structures.

Ecologically, the available data for *Gnetum* species are generally consistent with our measurements of low photosynthetic and hydraulic capacities. For example, seedlings and adults of *Gnetum* liana species are frequently noted as common residents of densely shaded understories of wet (> 2000 mm rainfall yr^{-1}), primary lowland tropical forests as well as in the understories of swamp gallery forests near slow-moving rivers (Markgraf, 1951; Stevenson & Zanoni, 1991). Adults of these species often form large canopy-dwelling lianas with very thick stems (Markgraf, 1951; Stevenson & Zanoni, 1991; Jauregui & Benitez de Rojas, 2005). However, there are some reports of *Gnetum* species occurring in more brightly lit and disturbed habitats in wet, lowland tropical habitats. For example, *Gnetum africanum*, *Gnetum buchholzianum*, *Gnetum loufense* and *Gnetum parvifolium* are reported from farm fallow, burned pastures, in addition to understory patches of degraded primary forests in lowland wet tropical regions (Fondoun & Tiki Manga, 2000; Clark *et al.*, 2004; T. S. Feild, observations in Vietnam and Thailand, 2007). However, we note anecdotally that the photosynthetic capacities of some of these *Gnetum* taxa, found in open, disturbed habitats, are low. Preliminary observations on the ETR capacity of *G. loufense* (mean = 98 ± 5 $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$; $n = 5$ leaves from five plants) in Hong Kong and of *G. latifolium* (mean = 95 ± 8 $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$; $n = 5$ plants) in Vietnam are nearly identical to the capacities reported here (T. S. Feild, pers. obs., 2004 & 2007).

It is also currently unclear how many of the reports of adult plants in high-light, open disturbed zones are the result of seedling recruitment. For example, *G. africanum* plants in pastures are reportedly resprouts from deep-rooted, underground tubers that initially established in the forest understory and survived clearing of a closed primary lowland rainforest in Cameroon (Clark *et al.*, 2004). Similarly, people often selectively leave *Gnetum* adult plants following forest clearing because *Gnetum* plants are a significant source of food and fiber (Clark *et al.*, 2004). However, we have anecdotally observed seedlings of *G. latifolium* establishing under the 'nurse' shade of pioneer trees and shrubs in fire-burned and deforested (logged) pastures near our study site in Papua New Guinea (T. S. Feild & L. Balun pers. obs., 2004 & 2007). Much more future work, focused on the ecological regeneration requirements of *Gnetum*, is needed to discern the specific ecological processes resulting in the occurrence of some *Gnetum* taxa in disturbed, high-light habitats.

Evolutionary implications

While exhibiting a functional leap over conifers in ecophysiological performance for some functional measures, such as K_S , HV and g_{sMax} (particularly compared with broad-leaved tropical podocarps and araucarians; Brodribb & Feild, 2000; Lusk *et al.*, 2003; Brodribb *et al.*, 2005, 2007), our observations indicate that *Gnetum* has not evolved ecophysiological capabilities that converge with those of co-occurring weedy, light-demanding woody tropical angiosperms that are characterized by high ETR, K_S and K_L values. Thus, the evolution of xylem vessels, broad net-veined leaves and liana habits in *Gnetum* are not necessarily automatic signs for the evolution of highly opportunistic, light-demanding ecophysiology in gymnosperms. Rather, our results are more consistent with a hypothesis that the co-occurrences of these vegetative traits in *Gnetum* coalesced in association with adaptation to wet, productive, closed tropical lowland rainforest habitats (Boyce, 2005; Feild, 2005). If these traits arose under shade, then we suggest that vessels and pinnate-veined leaves increased functional opportunism, but instead for greater growth efficiency under light-limiting conditions by reducing sapwood allocation relative to leaf area and permitting increased capture of spatially variable light (i.e. sunflecks) in the understory, respectively. Intriguingly, the coupled origin of vessels and pinnate leaves in early angiosperms and perhaps extinct gigantopterids also appears to have involved an initial diversification in low-light, wet tropical environments (Boyce, 2005; Feild, 2005). However, it is important to point out that the timings and community contexts surrounding the origins of leaf widening and vein reticulation, as well as vessels, across these three seed plant lines differ. Gigantopterids radiated during the Permian in lycopod/fern-dominated communities. Angiosperms radiated during the Early Cretaceous, in gymnosperm/fern-dominated communities. Finally, *Gnetum* appears to be recent newcomer, with the crown-group timed to the Eocene, and therefore diversification probably occurred in lowland angiosperm-dominated tropical rainforests that are similar to the habitats occupied today (Won & Renner, 2006). Additional integrative studies, taking into account phylogenies, fossil records and (paleo-)ecophysiologicals of all three clades, are needed to determine whether the ecological circumstances associated with the origins of pinnate-veined leaves and vessels are convergent across seed plants (Feild, 2005).

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