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PHOTOSYNTHESIS AND WATER USE EFFICIENCY OF 19 TROPICAL TREE SPECIES

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It is generally known that immediately after transplanting, seedlings are susceptible to water stress because of limited ability of their root systems to function normally. One of the symptoms in dipterocarp transplants exposed to direct sunlight is the drooping of the leaves which suggests that transpirational water loss may be a serious problem. Therefore, keeping transpiration low and avoiding excessive water loss are important for the establishment and survival of transplants. For example, leaf removal of *Shorea talura* seedlings was reported to be effective in minimising transplantation shock (Sasaki 1980). However, such a reduction of leaf area will also result in limiting photosynthesis, essential for growth. Thus, information on stomatal gas exchange, specifically the balance between the release of water vapour and the uptake of CO_2, is important to assess the potential success of species for transplantation in afforestation and reforestation efforts. In this study, photosynthesis and transpiration were examined for seedlings of 19 tropical tree species grown under nursery conditions to evaluate early growth and water use efficiency.

Potted 1- to 2-y-old tree seedlings grown in a shaded nursery located in the Chikus Forest Reserve in the state of Perak, Malaysia were used. The species studied were 11 dipterocarps, *Shorea leprosula* (meranti tembaga), *S. parvifolia* (meranti sarang punai), *S. acuminata* (meranti rambai daun), *S. paucifolia* (nemesu), *S. assamica* (meranti pipit), *S. curtisii* (seraya), *S. ovalis* (meranti kepong), *S. macroptera* (meranti melantai), *Dipterocarpus cornutus* (keruing gombang), *Hopea odorata* (chengal pasir) and *Neobalanocarpus heimii* (chengal); and 8 non-dipterocarps, *Tectona grandis* (teak), *Intsia palembanica* (merbau), *Cinnamomum iners* (kayu manis hutan), *Alstonia angustiloba* (pulai), *Azadirachta excelsa* (sentang), *Endospermum*

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malaccensis (sesendok), *Khaya ivorensis* and *Acacia mangium.* The diameter and the height of the pots were 15 cm and 23 cm respectively. The heights of the seedlings ranged from 30 to 60cm. Relative light intensity under the shade of the nursery was about 30 to 40%. All the seedlings were well watered prior to the measurements.

Five seedlings were selected from each species, and from each seedling one fully expanded mature leaf was chosen for gas exchange measurements. Net photosynthetic rate (Pn) and transpiration rate (Tr) were measured with a portable photosynthesis system (H4, ADC, U.K.). Measurements were taken in the morning from 0900 h to 1200 h (Malaysian Standard Time) when stomatal conductance and photosynthetic rate were relatively high, based on preliminary data. Vapour pressure deficit (VPD) of the air in the leaf chamber changed concurrently with changes in transpiration rate and varied from 0.003 to 0.015 Pa Pa^{-1}. The range of temperature, VPD of the ambient air, and photosynthetically active radiation (PAR) at the leaf surface were 30 to 33 °C, 0.012 to 0.015 Pa Pa^{-1}, and 350 to 700 µmol m^{-2} s^{-1} respectively. The measured leaves were detached, leaf area recorded and the leaves then dried (70 °C) to calculate leaf dry weight per unit leaf area.

Table 1. Rate of net photosynthesis (Pn), water use efficiency (WUE), and leaf dry weight per unit leaf area (DW/LA)

Species	Pn (µ mol m^{-2} s^{-1})	WUE (µ mol mmol^{-1})	DW/LA (mg cm^{-2})
Acacia mangium	24.18 ± 4.79	3.28 ± 0.50	9.09**
*Hopea odorata**	15.89 ± 2.03	3.73 ± 0.52	9.69 ± 0.29
Tectona grandis	14.46 ± 4.57	3.84 ± 0.52	6.59***
Cinnamomum iners	14.35 ± 0.74	2.77 ± 0.30	8.18 ± 0.53
Alstonia angustiloba	10.73 ± 0.51	3.06 ± 0.11	8.07 ± 0.06
Azadirachta excelsa	10.26 ± 1.05	2.55 ± 0.09	4.96 ± 0.04
Khaya ivorensis	10.18 ± 2.20	2.66 ± 0.24	9.17 ± 0.87
Endospermum malaccensis	9.09 ± 0.83	2.43 ± 0.17	5.61 ± 0.97
*Shorea leprosula**	7.85 ± 1.15	2.23 ± 0.17	6.96 ± 0.35
*S. parvifolia**	7.54 ± 1.53	2.88 ± 0.36	6.17 ± 0.26
*S. acuminata**	7.46 ± 0.84	3.71 ± 0.79	6.76 ± 0.39
*S. pauciflora**	7.31 ± 1.80	3.67 ± 0.71	8.59 ± 1.55
*S. assamica**	6.25 ± 0.79	1.86 ± 0.45	5.53 ± 0.27
*S. curtisii**	5.49 ± 1.13	3.41 ± 0.71	8.01 ± 0.39
Intsia palembanica	5.48 ± 1.27	3.90 ± 0.97	8.52 ± 2.95
*S. ovalis**	4.97 ± 1.29	2.15 ± 0.14	5.61 ± 0.15
*Dipterocarpus cornutus**	4.89 ± 0.34	3.20 ± 0.34	6.97 ± 0.47
*Neobalanocarpus heimii**	3.93 ± 0.72	2.77 ± 0.68	6.98 ± 0.27
*S. macroptera**	3.58 ± 0.79	2.92 ± 0.57	9.25 ± 0.63

* = dipterocarp species, ** = mean value of two large leaves, *** = value of one large leaf.

The results are summarised in Figure 1 and Table 1. Both Pn and Tr were lower in the dipterocarp species, except for *Hopea odorata,* than in the fast-growing species. Pn and Tr were highest in *Acacia mangium,* well known as a fast-growing and light demanding species. Other fast-growing species like *Tectona grandis, Alstonia angustiloba, Azadirachta excelsa, Khaya ivorensis,* and *Endospermum malaccensis* also showed relatively high Pn. Among the dipterocarp species studied here, *Hopea odorata* showed the highest Pn, more than twice that of other dipterocarps, comparable to that of *Acacia auriculiformis* (Ang & Maruyama 1994).

High Pn was also observed in the relatively fast-growing species of dipterocarps: *Shorea leprosula, S. parvifolia,* and *S. acuminata.* Slow-growing and shade tolerant species of both dipterocarps (*Dipterocarpus cornutus, Neobalanocarpus heimii*) and non-dipterocarp (*Intsia palembanica*) showed comparatively low Pn. *Shorea ovalis* and *S. macroptera* were exceptions to the trend with low Pn but are among the fastest-growing species in the red meranti group (Symington 1943). The Pn values of the fast-growing species were higher than those of deciduous temperate trees (Koike 1988), suggesting that the rapid growth of these species is attributable to their high photosynthetic capacity as well as environmental factors of the humid tropics such as relatively constant temperature and moisture that permit year-round photosynthesis.

The Pn values of dipterocarps in this study correspond closely to those of 1-y-old seedlings grown under the same light regime (400 μmol m^{-2} s^{-1}, Mori *et al.* 1990). Toma and Furukawa (1995) reported higher Pn for exposed canopy leaves of mature trees while Morikawa *et al.* (1980) reported lower Pn for 1-y-old seedlings raised under low light intensities. The Pn value of *A. mangium* in this study was twice as large as that of *A. mangium* seedlings planted on exposed sand tailing (Ang & Maruyama 1994). These differences may be due to the different growth stages as reported by Koike (1988) and/or to the different conditions under which the plants were grown.

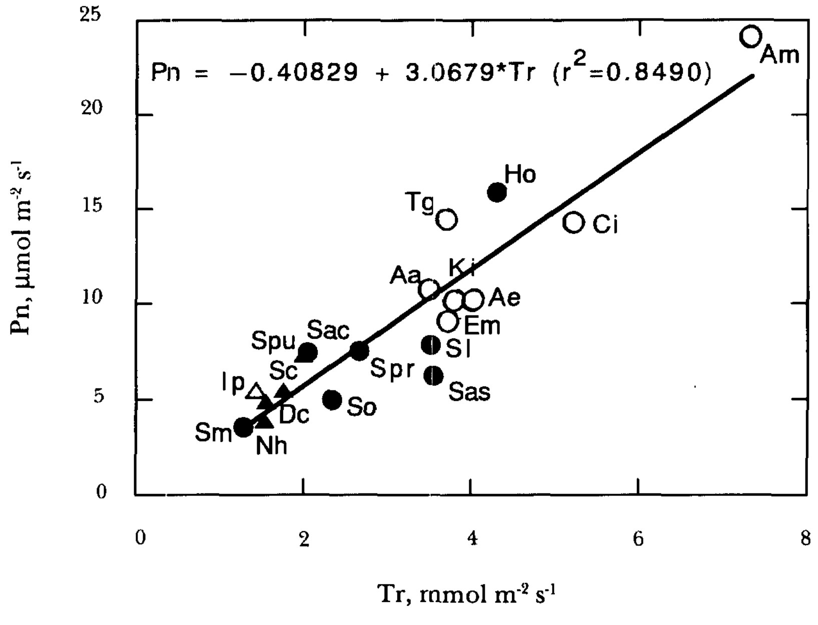

Figure 1. Relationships between transpiration rate(Tr) and net photosynthetic rate(Pn) of dipterocarps(closed symbols) and non-dipterocarps (open symbols) (Sm: *S. macroptera,* Nh: *N. heimii,* Dc: *D. cornutus,* So: *S. ovalis,* Ip: *I. palembanica,* Sc: *S. curtisii,* Sas: *S. assamica,* Spu: *S. paucifolia,* Sac: *S. acuminata,* Spr: *S. parvifolia,* Sl: *S. leprosula,* Em: *E. malaccensis,* Ki: *K. ivorensis,* Ae: *A. excelsa,* Aa: *A. angustiloba,* Ci: *C. iners,* Tg: *T. grandis,* Ho: *H. odorata,* Am: *A. mangium*)

Circles : relatively fast-growing species, triangles : relatively slow-growing species

Water use efficiency (WUE, the ratio of net photosynthetic rate and transpiration rate: Pn/Tr) was highest in *I. palembanica*, *T. grandis* and *H. odorata*, which occur naturally in the northern part of Peninsular Malaysia where dry spells are more pronounced. These species, therefore, are expected to have comparatively high WUE. WUE was lowest in *S. assamica*, a plant that occurs in low-lying areas in the vicinity of streams (Symington 1943).

Among the fast-growing species, *A. excelsa*, *K. ivorensis*, and *E. malaccensis* had relatively low WUE, suggesting that these species may require large amounts of water uptake to maintain their rapid growth. However, leaf dry weight per unit leaf area (DW/LA) was largest in *K. ivorensis*, suggesting that this species has thick leaves which may minimise transpirational water loss from the leaves.

For reforestation using a dipterocarp species, we concur with Ang *et al.* (1992) in recommending *H. odorata* because of its superior gas exchange characteristics. Among dipterocarps, Pn, WUE, and DW/LA values were all highest in *H. odorata*. We also would recommend using *I. palembanica* for its low transpirational water loss and high WUE even though it has a relatively slow growth. Another candidate for reforestation is *S. curtisii*, normally found on ridges and hill tops in the Hill Dipterocarp forests and coastal hills, which also had a relatively high WUE. In contrast, fast-growing species in the red meranti group such as *S. leprosula* and *S. ovalis* showed low WUE, suggesting that these species are prone to wilting and not suitable for open planting.

In this study, Pn and Tr were measured under a shaded and humid condition where stomatal closure is not a factor. However, even in the humid tropics, exposed leaves may show stomatal closure when differences in leaf-to-air vapour pressure are high (Ishida *et al.* 1996), leading to a constraint on photosynthesis. While our recommendation of suitable species is based on relatively unstressed seedlings, it is necessary to further investigate gas exchange of seedlings after transplanting when environmental conditions are more severe. Ultimately, the most suitable species may be those that can maximise water conservation through stomatal regulation during the initial period after transplantation.

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BOOK REVIEW

BRUENIG, E.F. 1996. **Conservation and Management of Tropical Rainforests. An Integrated Approach to Sustainability.** CAB International, Oxford, U.K. 352 pages. ISBN 0 85198 994 2. Price: £55.00 (US$99.00, Americas only)

For more than 40 years Professor Bruenig has been studying tropical rainforest ecology and management, principally in Sarawak but also in Amazonian Venezuela. This volume represents a highly personalised synthesis of his experience, put into a historical perspective, and highlighted by resounding recommendations. Anyone who has had the pleasure of an encounter with Professor Bruenig will hear his strong voice in the printed words. Those interested in Sarawak's forests will find the book filled with insight and bold truth. However, some of his claims stand unsubstantiated (but are probably true), his extensive and intriguing review of the literature is heavily biased towards his own work, and he ignores many recent and important contributions to the body of knowledge about tropical forest management and conservation. I nevertheless found something of interest in nearly every section, and especially appreciated his citations to early literature and the good use to which he puts forest profile diagrams.

The book begins with a general description of the tropical rainforest ecosystem (e.g. soil, canopy structure, dynamics, etc.). Upon this foundation he builds a series of chapters on sustainable and non-sustainable forest uses. In explaining why rainforests are so often abused, the author does not hesitate to condemn corrupt politicians and greedy concessionaires. He also plunges boldly into the treacherous waters of the rights of the Penan and other nomadic forest dwellers. The next chapters outline the history of rainforest silviculture and the principles of sustainable forest management. His treatment of the history of forestry in Sarawak is probably too detailed for readers unfamiliar with the region but it provides background for the author's approach to "naturalistic natural rainforest management". Silviculturalists will not be surprised by many of Bruenig's recommendations, most of which are commonsensical, but his treatment of silviculture is coherent and therefore useful. The book ends with chapters on short-rotation plantations (of which he does not approve in many settings) and timber certification (focussed mostly on the Initiative Tropenwald and ITTO). The concluding chapter is a well-warranted diatribe about foot dragging, autocratic mismanagement, lack of competence, acquisitive and aggressive urges, and the future of tropical forests. His vision is more starkly realistic than pessimistic, and his passion is always evident.

While most of the text was fairly easy to read, the author's "Biocybernetic Principles of System Design" eluded me (perhaps because I am too stubbornly wedded to saying things simply). Perusal of the 43-page "References and Further Reading" will be useful for many researchers; the literature on rainforest conservation and management is not treated particularly fairly, but the historical perspective is refreshing, especially for readers of German with ready access to the grey literature. I even found the glossary interesting.

The recent spate of publications on tropical forest ecology and management (e.g. Lamprecht 1986, Repetto & Gillis 1988, Panayotou & Ashton 1992, Sharma 1992) has served to consolidate the foundation for conservation and to point the way forward. Bruenig's book is of the consolidation sort. Beacons in the darkness of abused forest are more likely to be lighted by forest ecologists and silviculturalists working together with other environmentalists, economists, sociologists, and political scientists.

Professor Bruenig has much to teach the world about rainforests. His long-term dedication to rainforest conservation and management, together with his scholarship, makes this volume a useful reference for reserchers who follow in his wake, especially if they do not want to repeat the mistakes of history.

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