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PHOTOSYNTHETIC CAPACITY IN THAI CONIFERS

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ABSTRACT

Ecophysiological studies were carried out to determine photosynthetic capacity and associated gas exchange characteristics of seven species of conifers growing under common garden conditions in the Queen Sirikit Botanic Garden in the Mae Sa Valley near Chiang Mai, northern Thailand. Rates of net photosynthesis under conditions of non-limiting light and water availability ranged from a high of 7.9–8.0 μmol m^{-2}•s^{-1} in *Pinus kesiya* and *P. merkusii* to a low of 2.0 in *Podocarpus wallichianus*. Carbon isotope ratios (δ) of –24.1‰ in this latter species indicated a high degree of water use efficiency (WUE), while the two pines, *Cephalotaxus griffithii* and *Dacrydium elatum*, showed low WUE with δ values of –29.3 to –30.4‰. Thai conifers appear to have ecophysiological traits of photosynthetic capacity, stomatal conductance, and water use efficiency comparable to those of in North American temperate conifers. Our data suggest that inherent limitations in the structural characteristics of the photosynthetic and water transport systems in conifers are equally applicable to tropical as well as temperate conifers in mainland Southeast Asia.

INTRODUCTION

While there has been a rapidly increasing interest in recent years in the physiological ecology of conifers (SMITH & HINCKLEY, 1995), this work has focused almost exclusively on temperate zone conifers, particularly those in the genera *Pinus, Abies* and *Picea*. Relatively little is known about tropical conifers. Even within a well studied group like the pines in which there are many studies of photosynthetic capacity, there have been almost no ecophysiological studies of tropical species growing in areas where frost is not an environmental limiting factor (RUNDEL & YODER, 1998).

The conifer flora of Thailand is a small one, with only 11 species. Six of these are in the genus *Podocarpus* sensu latu, with other genera being *Pinus* (2 species), and *Calocedrus, Dacrydium*, and *Cephalotaxus* with a single species each. While all of these species are Southeast Asian endemics in the broad sense, and occur naturally in lower montane forests of northern and northeastern Thailand, they represent distinctly different patterns of biogeographic distribution. The genus *Cephalotaxus*, for example, is largely centered in Japan and China, and reaches its southern limit of occurrence with *C. griffithii* in northern

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Thailand. In contrast to this pattern, the genus *Dacrydium* is largely a southern hemisphere group, with its primary occurrence in southern Chile, New Zealand, Tasmania, and New Caledonia. It reaches its northern limit of distribution with *D. elatum* in northern Thailand. Two tropical pine species in Thailand, *P. kesiya* and *P. merkusii*, are widespread species in Southeast Asia and form the most southern occurrence of *Pinus* in the world, with *P. merkusii* reaching south of the equator in Sumatra.

We are not aware of any previous studies of photosynthetic capacity in conifer species from mainland Southeast Asia. Northern Thailand presents an appropriate area to study the ecophysiology of such conifers because all five genera and nine of the 11 Thai conifers occur naturally in this region.

Two questions interested us in carrying out this research. The first was: Do tropical conifers growing in a mild, seasonal monsoon climate have higher photosynthetic rates than temperate conifers? If warm growing season conditions with abundant water, low vapor pressure gradients with humid air, and the absence of a cold season present ideal conditions for conifer growth, one might expect photosynthetic rates higher than those of temperate conifers. However, if the structural characteristics of conifer foliage and their associated hydraulic systems with fiber tracheids constrain the potential for high rates of carbon fixation, then comparable rates would be expected. Direct comparisons within a single genus can be achieved here with *Pinus*. The second question is a special case of the first. The genus *Podocarpus* sensu latu includes a number of species whose foliage is flattened and broad, with "needles" reaching 50–70 mm in width in *P. wallichiana*. There have been very few reports of photosynthetic rates measured under field conditions for members of the Podocarpaceae. Recent studies with *Podocarpus oleifolius* in the high Andes of Venezuela (CAVIERES *ET AL.*, 2000) and *P. coriaceus* in the West Indies DUCREY, 1994) have reported relatively low rates of maximum net photosynthesis. Do broad-leaved conifers such as these have higher rates of photosynthesis than those species of *Podocarpus* and other conifers with narrow needles? If such higher rates of photosynthesis exist in broad-leaved *Podocarpus*, are they comparable to those of temperate hardwood trees?

MATERIALS AND METHODS

Study Species

Trees of seven conifer species were investigated in common garden plantings at the Queen Sirikit Botanic Garden in the Mae Sa Valley (ca. 700 m elevation; lat. 18°53' N, long. 78° 56' E) near Chiang Mai, close to the natural habitat of these species. With the exception of *Pinus kesiya*, which averaged approximately 10 m tall, experimental trees were young individuals 3–7 m in height. Two individuals of each tree and multiple leaves on each individual were studied, with the exception of *Podocarpus wallichianus* which was represented by only a single individual. All study trees were healthy individuals with good growth characteristics. The general characteristics of the conifer species included for study are described below. For more information see PHENGKLAI (1972), KRUSSMAN (1985), HIEP & VIDAL (1996).

Cephalotaxus griffithii Hook. is a small-to-medium size tree. It has stiff needles 2–5 cm in length, glossy green above but white below. It is distributed from Assam in East

India across North Burma to North and Northeast Thailand where it occurs at 1000–1800 m elevation in the lower montane zone of Chiang Mai, Chiang Rai, and Loei Provinces, as a subcanopy tree in moist evergreen forest.

Dacrydium elatum (Roxb.) Wall. ex Hook. Typically reaches 35 m in height and 70–120 cm in diameter. The leaves are small (8–16 mm) and scale-like, in densely overlapping arrangement on the fertile branches. It is reported to occur from East India across North Burma to Thailand, and south to Cambodia and Malaysia, and eastward to the Philippines and Fiji. It occurs at 1000–3000 m elevation in North, Northeast, East, and Central Thailand and is typically found along streams on soils derived from sandstone. In Indochina, this species has an elevational range of 700–2000 m. In the Cardamom and Elephant Mountains of South Cambodia it occurs in dwarf conifer stands on boggy sites, frequently with *Podocarpus imbricatus.*

Pinus kesiya Royale ex Gard. has a spreading or rounded crown, and needles occur in bundles of 3 and 100–250 mm in length. This species is distributed from Burma across mainland Southeast Asia to the Philippines. In Thailand is common in the North and Northeast at 1000–1600 m elevation. *P. kesiya* may occur mixed with montane hardwood trees or in relatively pure stands. It is relatively tolerant of frequent burning, and thus has expanded its dominance in many montane habitats under human intervention. The biogeographical and ecological patterns of distribution of this species in Thailand have been described in detail (WERNER, 1993; SANTISUK, 1997).

Pinus merkusii Jungh. & De Vriese likewise has a spreading to rounded crown; needles occur with 2 in a fascicle, and reach 150–250 mm in length. This pine occurs from East India across Southeast Asia to the Philippines to the east, and south to Sumatra where it becomes the only pine species that naturally occurs south of the equator. In Thailand it is a common species in the North, Northeast and East where it occurs in dry deciduous dipterocarp forests or lower montane forests at 600–1300 m elevation (SANTISUK, 1997). Rarely, this species may occur together with the higher elevation *P. kesiya.*

Podocarpus imbricatus Bl. [=*Dacrycarpus imbricatus* (Bl.) De Laubenf.] is a large forest tree reaching 30 m in height and 120 cm in diameter. Two forms of leaves are commonly present in this species, with both occasionally found on the same individual. Leaves on young or rapidly extending branches are linear, 6–12 mm in length, and arranged in two flattened ranks that collectively resemble a compound leaf. Older trees typically have small, awl-like leaves, resembling a small *Cryptomeria*, but only 2–5 mm long. This species is widely distributed across Southeast Asia from East India across Burma to Laos and Cambodia, and on to the west and south to the Philippines, Malaysia, Indonesia and New Guinea. It occurs in North, Northeast and Southeast Thailand scattered in evergreen forests at 700–1200 m elevation. It is a common associate of *Dacrydiun elatum* in dwarf conifer forests growing in boggy sites in the Cardamom and Elephant Mountains of South Cambodia.

Podocarpus neriifolius D. Don. is a large tree reaching 30 m or more in height and 200 cm diameter. Its coriaceous leaves are linear–lanceolate in shape but highly variable in size, with a typical length ranging from 50 to 200 mm and a width of 5–25 mm. This species is widely distributed from eastern India and southern China through Thailand, Laos, Cambodia, and Vietnam to Indonesia and Fiji. It occurs throughout Thailand where it is frequent in moist evergreen forests at 600–1300 m elevation.

Podocarpus wallichianus Presl. [=*Nageia wallichiana* (Presl.) De Laubenf.] can reach 48 m in height, although only 10–20 m in Thailand. Its coriaceous leaves are typically 100–180 mm in length, but remarkably 30–70 mm in width. It is distributed from East India across mainland Southeast Asia to Indonesia and New Guinea. It is found throughout Thailand in wet evergreen forests from sea level up to 2000 m elevation.

Field Measurements

All field measurements were carried out on December 5 and 6, 1996, in the Queen Sirikit Botanic Garden. This season corresponded to the first month of the dry season when clear skies, good soil moisture availability and moderate temperature extremes provide ideal conditions for tree growth. Study trees were growing under common garden conditions with comparable soils and water availability. Midday water potential measurements were made between 11:20 and 13:00 hours with a Schollander-type pressure chamber following standard procedures. The water potential of 3–4 samples of each species were summed and averaged to calculate mean midday water potentials in mega Pascals.

Gas exchange measurements were made with a LICOR-6200 gas exchange system using a closed flow architecture. An artificial light source was used to bring ambient light levels above 1200 μmol $m^{-2}.s^{-1}$, a level from our experience that is saturating for conifers. A cold mirror prevented heating of the conifer foliage. For most species studied, 6–10 cm^2 of the youngest fully mature foliage was placed into the cuvette. For the fine leaves of *Podocarpus imbricatus*, 13–18 cm^2 of foliage was used, while the dense whorls of small awl-shaped needles of *Dacrydium elatum* put 29–36 cm^2 of foliage into the cuvette. The actual projected leaf area of foliage used in each measurement was determined after measurements using a LICOR leaf area meter. Two foliar measurements of net photosynthesis, stomatal conductance, and internal CO_2 concentration were made for each individual studied. Leaf temperatures averaged 28°C (range 26–30°C) during gas exchange measurements, closely tracking ambient air temperatures. The mean relative humidity was 75% (range 63–80%), giving a mean vapor pressure gradient of 0.9 kPa. Natural ^{13}C ratios were measured at the Duke University Phytotron (Durham, North Carolina) on a SIRA Series II isotope ratio mass spectrometer (VG Isotech, Middlewich, UK) operated in automatic trapping mode after combustion of samples in an elemental analyzer (NA1500, Carlo Erba Instrumentazion, Milan, Italy). The reference CO_2, calibrated against standard Pee Dee belemnite (PDB), was obtained from Oztech (Dallas, Texas). Carbon isotope ratio was expressed as $\delta^{13}C$ in units of negative parts per thousand (‰). Values of $\delta^{13}C$ correlate directly with integrated water use efficiency over the period in which carbon tissues were formed in developing leaves (FARQUHAR *ET AL.*, 1982). Total leaf nitrogen values were obtained during these analyses by the Carla Erba elemental analyzer.

RESULTS

Midday water potentials were similar in all seven conifer species studied and their relatively high values suggested that these were all well-watered individuals (Table 1). The highest mean midday water potential (–0.70 MPa) was found in *Podocarpus neriifolius*, while the lowest was in *Cephalotaxus griffithii* (–1.24 MPa). There was little variation among replicate samples of water potential within any single species.

Table 1. Ecophysiological characteristics of water relations, gas exchange, foliar nitrogen level and carbon isotope ratio in seven species of Thai conifers growing in a common garden plantation at the Queen Sirikit Botanic Garden in the Mae Sa Valley near Chiang Mai, Thailand.

Species	Midday water potential (MPa)	Net photosynthesis (μmol $m^{-2}.s^{-1}$)	Stomatal conductance (μmol $m^{-2}.s^{-1}$)	Leaf nitrogen ($mg.g^{-1}$)	$\delta^{13}C$ (‰)
Ceplalotaxus griffithii	–1.24	5.52	59	21.0	–30.4
Dacrydium elatum	ND	4.05	50	14.4	–29.3
Pinus kesiya	–0.99	7.92	156	14.5	–29.4
Pinus merkusii	–0.90	7.98	143	14.0	–29.6
Podocarpus imbricatus	–1.10	6.53	85	13.0	–28.0
Podocarpus neriifolius	–0.70	3.06	80	13.0	–27.6
Podocarpus wallichianus	–0.95	1.99	46	13.9	–24.1

Net photosynthetic capacity under conditions with saturating light intensity was low, with values comparable to those seen in many temperate region conifers. Expressed on a projected leaf area basis, as is recommended for conifers (RUNDEL & YODER, 1998), the highest rates were found in *Pinus merkusii* and *P. kesiya* with 7.98 and 7.92 μmol $m^{-2}.s^{-1}$, respectively (Table 1). Rates of maximum photosynthesis in *Podocarpus* species varied from a high of 6.53 μmol $m^{-2}.s^{-1}$ in *P. imbricatus* to a low of 1.99 μmol $m^{-2}.s^{-1}$ in *P. wallichianus*. Intermediate values were found for *Cephalotaxus griffithii* (5.52 μmol $m^{-2}.s^{-1}$ and *Dacrydium elatum* (4.05 μmol $m^{-2}.s^{-1}$).

Maximum rates of stomatal conductance measured in these seven conifers closely followed the pattern seen in the photosynthetic data (Table 1). There is a significant positive linear relationship between net photosynthetic rate and stomatal conductance in our data (Fig. 1). The highest rates of stomatal conductance were found in *Pinus merkusii* and *P. kesiya* with 143 and 156 mmol $m^{-2}.s^{-1}$, respectively. The lowest rate of stomatal conductance was 46 mmol $m^{-2}.s^{-1}$ measured in *Podocarpus wallichianus*.

Leaf nitrogen contents were very similar in six of the seven species studies, with concentrations of 13.0–14.4 $mg.g^{-1}$. A significantly higher nitrogen concentration was found in *Cephalotaxus griffithii* with 21.0 $mg.g^{-1}$, despite its modest photosynthetic rate. Previous studies with conifers have not shown a consistent positive relationship leaf nitrogen content and photosynthetic capacity (see review in RUNDEL & YODER, 1998). The range of values in our study is within the range of those reported for temperate conifer species (REICH *ET AL.*, 1995).

Analyses of carbon isotope discrimination in the conifers studied showed three patterns of water use efficiency. Four species (*Cephalotaxus griffithii, Pinus merkusii, P. kesiya,* and *Dacrydium elatum*) had low $\delta^{13}C$ values of –29.3 to –30.4‰ (Table 1), signifying a relatively low water use efficiency. At the other extreme, *Podocarpus wallichianus* had a $\delta^{13}C$ value of –24.1‰, indicating a relatively high level of water use efficiency. This is surprising given the wet forest habitats where *P. wallichianus* characteristically occurs. The remaining two species, *Podocarpus imbricatus* and *P. neriifolius*, had intermediate

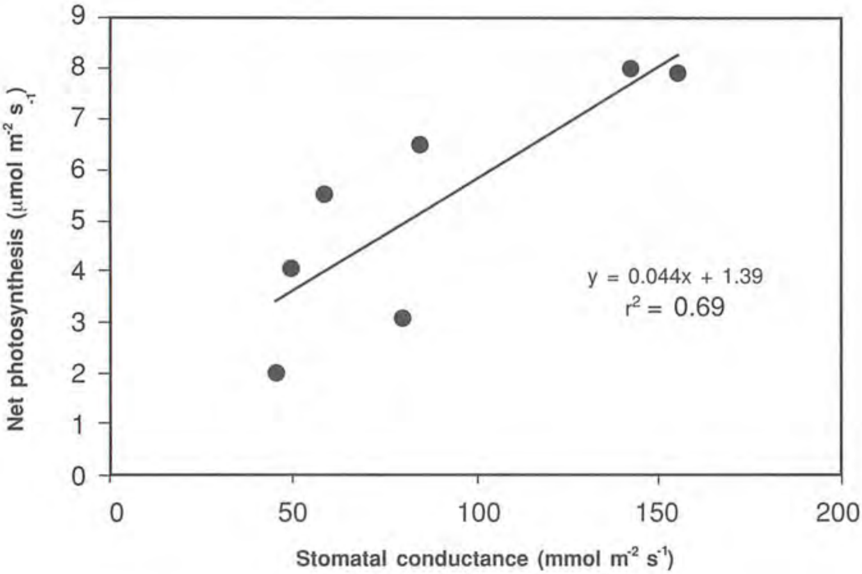

Figure 1. Relationship between net photosynthesis (µmol $m^{-2} \cdot s^{-1}$) and stomatal conductance (µmol $m^{-2} \cdot s^{-1}$) in 7 species of Thai conifers. See text for discussion.

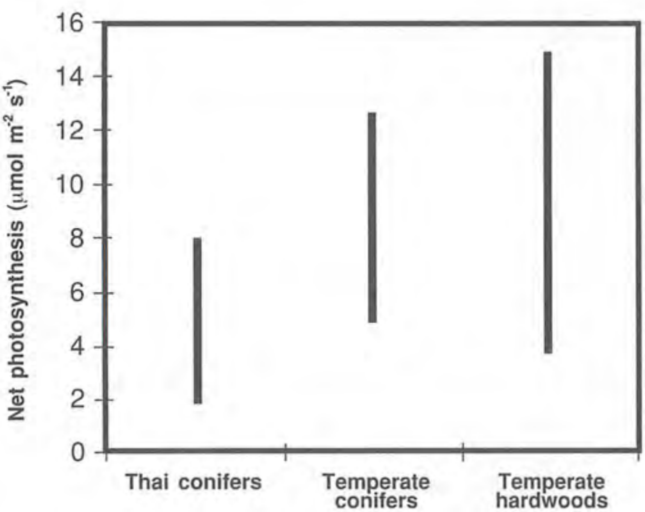

Figure 2. Comparative values of net photosynthetic (µmol $m^{-2} \cdot s^{-1}$) under optimal conditions in Thai conifers and in temperate conifers and hardwood trees from North America. Data on North American trees are from REICH *ET AL.* (1995).

values of $\delta^{13}C$ with −28.0 and −27.6‰, respectively. Thus, these species had intermediate levels of water use efficiency.

DISCUSSION

Our objectives in this paper have been to describe the photosynthetic capacity of a diverse group of these tropical conifers growing together under common garden conditions, and to compare values of maximum rates of photosynthetic assimilation with those reported in the literature for temperate conifers. If the tropics provided ideal conditions for conifer growth, one might expect photosynthetic rates higher than those of temperate conifers. However, if the structural characteristics of conifer override the potential for high rates of carbon fixation, then comparable rates would be expected.

Photosynthetic rates under field conditions for members of the Podocarpaceae have rarely been measured. Recent studies with *Podocarpus oleifolius* in the high Andes of Venezuela (CAVIERES *ET AL.*, 2000) and *P. coriaceus* in the West Indies (DUCREY, 1994) have reported relatively low rates of maximum net photosynthesis.

The range of relatively modest photosynthetic rates reported here are comparable or slightly lower than those that have been widely reported for temperate conifer species (see reviews in SMITH & HINCKLEY, 1995; RUNDEL & YODER, 1998). In pines for example, reported rates of photosynthesis in temperate species are commonly 6–14 μmol $m^{-2}.s^{-1}$ (RUNDEL &YODER, 1998), bracketing the rate of 8 μmol $m^{-2}.s^{-1}$ reported here. Figure 2 shows data on photosynthetic capacity for Thai conifers compared to ranges of values reported for temperate North American conifers and North American hardwoods. The range of values for the North American hardwoods is wide, but within this range most species have higher rates than those present in either Thai or North American conifers. Rates of stomatal conductance in Thai conifers are also comparable to those seen in temperate conifers, and generally lower than those measured in temperate hardwood leaves (REICH *ET AL.*, 1995). Our data suggest that inherent limitations in the structural characteristics of the photosynthetic and water transport systems in conifers are equally applicable to tropical as well as temperate conifers in mainland Southeast Asia. *Podocarpus wallichianus* with leaves up to 70 mm in width, likely the broadest of any conifer species in the world today, had the lowest photosynthetic rate of any species studied.

Although Thailand has a strongly seasonal monsoon climate, conifers with the exception of *Pinus merkusii*, are largely absent from lowland habitats. It is not clear whether low rainfall, strongly seasonal climates, high temperatures, or ecological competition with angiosperm trees limit their survival. The mean annual rainfall levels of 1100–1500 mm that characterize most of the lowlands of Thailand are well within the range of seasonal rainfall regimes where temperate pines thrive. Moreover, the low nutrient conditions present over the shallow lateritic soils that characteristically underlie deciduous dipterocarp forest might be expected to provide a competitive advantage to pines over hardwood species. *Pinus merkusii* is unique among Southeast Asian conifers in being adapted for survival in these low elevation deciduous dipterocarp forests as on the Khorat Plateau (WERNER, 1993; SANTISUK, 1997).

Cooler temperatures and higher rainfall in montane habitats, with no more than 3–4 months of functional dry season (compared to 5–6 months in most lowland habitats), provide conditions for the highest diversity of conifers. Pines in Thailand show their greatest dominance in lower montane habitats with low nutrient substrates. Relatively pure savannas of *Pinus kesiya* and/or *P. merkusii* with a grass or sedge understory are well developed on the tops of sandstone plateaus at 1000–1800 m elevation in Northeast Thailand, as at Phu Soidao and Phu Kradueng National Parks. The great majority of Thai conifer species are found in lower montane evergreen forests above the zone of dipterocarp-dominated forest communities where they may occur as tall canopy trees (e.g. *Podocarpus species* and *Dacrydium elatum*), or subcanopy shade-tolerant species (e.g. *Cephalotaxus griffithii*). This is similarly true throughout Southeast Asia. The Dalat Plateau in the Central Highlands of southern Vietnam supports 16 species of native conifers (LOC & HIEP, 1997; RUNDEL, unpublished data), and there are 12 conifer species present in the Fan Si Pan massif in northern Vietnam near the Chinese border (THIN & THOI, 1998).

Wet evergreen lowland forests such as those in the Malay Peninsula of southern Thailand have lower diversities of conifers than montane forest habitats. Only six conifer species are found in peninsular and southeastern Thailand in areas with high precipitation and relatively little rainfall seasonality. In addition to their tall forest growth forms, dwarf forms of *Dacrydium elatum* and *Podocarpus imbricatus* form major canopy dominants in boggy areas of the Cardamom and Elephant Mountains in Cambodia, and in Khao Yai National Park, Central Thailand, suggesting a high tolerance of water-logged soil conditions.

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REFERENCES

CAVIERES, L. A., F. RADA, A. AZOCAR, C. GARCIA-NUNEZ, AND H. M. CABRERA. 2000. Gas exchange and low temperature resistance in two tropical high mountain tree species from the Venezuelan Andes. *Acta Oecol.* 21: 203–211.

DUCREY, M. 1994. Influence of shade on photosynthetic gas exchange of seven tropical rain-forest species from Guadeloupe (French West Indies). *Ann. Sci. Forest. (Paris)* 51: 77–94.

FARQUHAR, G. D., M. H. O'LEARY, AND J. A. BERRY. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration of LEAVES. *Austr. J. Plant Physiol.* 9: 121–137.

HIEP, N. T., AND J. E. VIDAL. 1996. Gymnospermae. *Flore du Cambodge, du Laos et du Vietnam* 28: 1–166.

KRUSSMAN, G. 1985. *Manual of Cultivated Conifers.* Timber Press, Portland OR, USA, 361 p.

LOC, G. P. K., AND N. T. HIEP. 1997. Cac loai hat tran cua Viet Nam bi de doa tieu diet va su co mat cua chung trong cac khu bao ton. *Vietnam For. Rev.* 1: 18–19.

PHENGKLAI, C. 1972. Pinaceae, Cephalotaxaceae, Curessaceae, Podocarpaceae. *Flora of Thailand* 2: 193–203.

REICH, P.B., B. D. KLOEPPEL, D. S. ELLSWORTH, AND M. B. WALTERS. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104: 24–30.

RUNDEL, P. W., AND M. R. SHARIFI, 1993. Carbon isotope discrimination and resource availability in the desert shrub *Larrea tridentata.* Pages 173–185 *in* J. H. Ehleringer, A. E. Hall, and G. D. Farquhar (eds.) Stable isotopes and plant carbon-water relations. Academic Press, San Diego.

RUNDEL, P. W. AND B. J. YODER. 1998. Ecophysiology of pines. Pages 296–323 *in* Richardson, D. R. (ed.) *Biogeography and Ecology of Pinus.* Cambridge University Press, Cambridge.

SANTISUK, T. 1997. Geographical and ecological distributions of two tropical pines, *Pinus kesiya and Pinus merkusii* in Southeast Asia. *Thai For. Bull.* 25: 102–123.

SMITH, W. K. AND T. M. HINCKLEY (eds.) 1995. *Ecophysiology of Coniferous Forests.* Academic Press, San Diego, CA, USA. 338 p.

THIN, N. N. AND N. T. THOI. 1998. Diversity of vascular plants at high mountain area: Sa Pa-Phan Si Pan. Nhà Xuât Bân Dai Hoc Quôc Gia Hà Nôi, Hanoi, 115 p.

WERNER, W. 1993. Pinus *in Thailand.* Franz Steiner, Stuttgart, 286 p.

[illegible] 1993. Geographical and ecological [illegible]

[illegible] *Proc. Natl. Acad. Sci.* [illegible]

[illegible] 1974. [illegible]

[illegible] 1970. [illegible]

[illegible] *Tech.* [illegible] 113 p.

[illegible] 1975. [illegible]