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Nitrogen form preference of six dipterocarp species

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Abstract

We investigated the nitrogen form preference of six dipterocarp species: *Anisoptera costata* Korth., *Dipterocarpus obtusifolius* Teijsm. ex Miq., *Hopea odorata* Roxb., *Neobalanocarpus heimii* (King) P. Ashton, *Shorea faguetiana* Heim, and *Shorea roxburghii* G. Don. Seedlings were supplied with nitrogen as nitrate, ammonium, or both in sand culture in a controlled environment. Except for *N. heimii*, all species showed greater shoot growth when supplied with ammonium than with nitrate. Higher root mass ratios were observed in all species with nitrate, which would be an adaptive response to limited nitrogen uptake. The five species, which preferred ammonium, showed a higher light-saturated photosynthetic rate with ammonium supply. The lower light-saturated photosynthetic rate with nitrate supply was a result of lower photosynthetic capacity, as indicated by a lower CO_2-saturated photosynthetic rate. The lower leaf nitrogen content in seedlings supplied with nitrate would be the cause of the lower photosynthetic performance. Nitrate reductase activity in leaf and root of *D. obtusifolius*, *N. heimii*, and *S. roxburghii* showed generally low inducibility with nitrate.

Keywords: Nitrate; Ammonium; Growth; Photosynthesis; Nitrate reductase; Dipterocarpaceae

1. Introduction

The members of the Dipterocarpaceae are predominant tree species of the upper canopy of tropical rain forests in Southeast Asia (Symington, 1974; Whitmore, 1984). They are the most important timber species in the region, and depletion of the stock is now of concern as a result of overexploitation since their entrance on the international market in the 1950s (Richter and Gottwald, 1996). Examination of sustainable use and enrichment of existing resources has increased the need for knowledge of the environmental responses of the species.

Light and water are the two main factors covered in studies of the environmental responses of dipterocarp and other tropical tree species (Chazdon et al., 1996; Mulkey and Wright, 1996; Whitmore, 1996). These two factors have crucial roles in species distribution and thus the species richness of tropical forests. Studies of temperate tree species have shown a correspondence of the site preference of a species with its nutritional characteristics, so the nutrient regime

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likely will also be important for seedling establishment (Kronzucker et al., 1997). The nutritional characteristics of trees are of great importance in silviculture as well. Nevertheless, our knowledge of the influence of nutrient conditions on tropical tree species is less than that of light and water (Whitmore, 1996). Nutritional studies in dipterocarp species are mostly limited to some fertilizer experiments (e.g., Fetcher et al., 1996; Gunatilleke et al., 1997). However, a study by Bungard et al. (2000) showed the effects of nitrogen availability on the photosynthetic characteristics of four dipterocarp species under different light regimes and on responses of these characteristics to sudden changes of light regime. The results suggested the importance of variations in nitrogen availability in regeneration dynamics and in the distribution of canopy-dominating dipterocarp species.

Both the amount and the form of nitrogen affect tree growth by affecting nitrogen uptake. Nitrate and ammonium are the major inorganic forms of nitrogen taken up by plant roots (Marschner, 1995). Ammonium can be readily assimilated into amino acids, but nitrate has to be first reduced to ammonium via nitrate reductase followed by nitrite reductase. In studies of closed- and open-forest communities of Australian rainforests, Stewart et al. (1988, 1990) reported low levels of nitrate reductase in the roots and shoots of most of the closed-forest species examined but high levels in the leaves of pioneer species.

In the field, the soil nitrogen regime depends on climate, soil type, vegetation, and microenvironment (Vitousek and Matson, 1988; Maggs, 1991; Smith et al., 1998; Silver et al., 2000). The composition of nitrogen can vary over time (Maithani et al., 1998) and change in response to disturbances (Vitousek et al., 1989). Investigations of nitrogen composition changes with succession have found ammonium to dominate as a result of low nitrification at late successional stages (Attiwill and Adams, 1993). Studies of changes of nitrogen composition after burning or clear-cutting have reported an increase in nitrogen mineralization and nitrification, after such disturbances (Matson et al., 1987; Attiwill and Adams, 1993). Most of the limited studies of tropical tree species have examined the effects of quantity (e.g., Lawrence, 2001) but not quality of nitrogen. Consequently, responses of tropical tree species to qualitative changes in soil nitrogen remain to be shown.

Understanding of nitrogen characteristics of dipterocarps is essential for clarifying mineral cycling and species establishment in tropical forests in Southeast Asia and for development of silvicultural techniques. The effects of nitrogen on dipterocarps, however, have been reported only quantitatively (e.g., Mirmanto et al., 1999; Bungard et al., 2000, 2002), not qualitatively. Given that dipterocarps are climax-forest species, it would seem that they should prefer ammonium to nitrate, as in the case of Australian rainforest species. However, considering that the Dipterocarpaceae consist of nearly 500 species with a broad range of light demand (Symington, 1974), variation in nitrogen characteristics cannot be ruled out. Here, we report responses of growth and photosynthesis to ammonium, nitrate, or a mixture in six dipterocarp species: *Anisoptera costata* Korth., *Dipterocarpus obtusifolius* Teijsm. ex Miq., *Hopea odorata* Roxb., *Neobalanocarpus heimii* (King) P. Ashton, *Shorea faguetiana* Heim, and *Shorea roxburghii* G. Don. All the six species are distributed in Thailand and chosen because of the availability of seeds. The objective of the study was to clarify whether each species prefers ammonium to nitrate for shoot growth. Owing to the irregular fruiting habit of dipterocarps, we carried out two independent experiments with three species each. In Experiment II, we assessed in vivo nitrate reductase activities (NRA), growth, and photosynthesis.

2. Materials and methods

2.1. Plant materials and treatments

2.1.1. Experiment I

Seeds of three dipterocarp species—*A. costata*, *H. odorata*, and *S. roxburghii*—were collected in southern Thailand and sown in a greenhouse (28/25 °C, natural light) in Tokyo, Japan. One-year-old seedlings were transplanted into a 1/10000-a Wagner pot (100 cm^2 surface area and 18.5 cm depth) in sand. Two to three weeks after transplanting, 10 pots of each species were set in each of six watering systems. Seedlings were watered with a nutrient solution at the level of sand surface of pots, differing in nitrogen