Carbon Isotope ($\delta^{13}C$) Signatures of Rheophytic *Dipteris lobbiana*.—As with most plant groups, ferns show their highest diversity in the tropics (Mutke and Barthlott, Biol. Skr. 55:521–537. 2005). *Dipteris lobbiana* (Hook. *f.*) Moore is a fern species found commonly growing in riparian habitats throughout the tropical island of Borneo where it is often strongly attached to rocks along and within streams (Fig. 1). It belongs to the family Dipteridaceae which has two genera and nine species found only in the Palaeotropics (Kramer, *in* K. U. Kramer & P. S. Green eds. *The Families and Genera of Vascular Plants Vol. 1. Pteridophytes and Gymnosperms*: 99–101. Springer-Verlag, Berlin, Germany. 1990).

FIG. 1. *Dipteris lobbiana* growing adjacent to streams at (a) Bako National Park, Sarawak, Malaysia and (b) Barito Ulu, Central Kalimantan, Indonesia.

The maintenance of a positive carbon balance is important for the growth and survival of all plant species and is related to the amount of carbon fixed per unit of water lost (water use efficiency; WUE). As *D. lobbiana* grows as a facultative rheophyte and has access to large sources of water, I hypothesised that it would have a low WUE. A simple way to test this hypothesis is through analysis of its stable carbon isotope values.

Stable carbon isotope values ($\delta^{13}C$) of plant tissues are controlled by the primary carboxylating enzyme used in photosynthesis, the isotopic composition of the atmospheric CO_2 taken up by the plant, and the ratio of the internal to external concentration of CO_2 which is primarily controlled by stomatal opening (O'Leary, BioScience 38:328–336. 1988; Farquhar *et al.*, Annu. Rev. Plant Physiol. Plant Mol. Biol. 40:503–537. 1989). Measures of leaf $\delta^{13}C$, which integrate responses over the lifetime of the leaf, can be used as a measure of WUE. If we assume that the isotopic composition of the atmospheric CO_2 is the same at all sites studied, the foliar isotopic value is therefore dependent upon the relative importance of the leaf stomatal conductance (*G*s) and maximum rate of photosynthesis (A_{max}). When water levels are low, *G*s is reduced and there will be slower uptake of the heavier ^{13}C isotope; this will lead to leaves having less negative $\delta^{13}C$ values. Equally, where A_{max} is higher, ^{13}C will be taken up more readily and foliar $\delta^{13}C$ will be more negative. In sum, factors reducing the supply of CO_2 through, for example, stomatal closure lead to less negative $\delta^{13}C$ values.

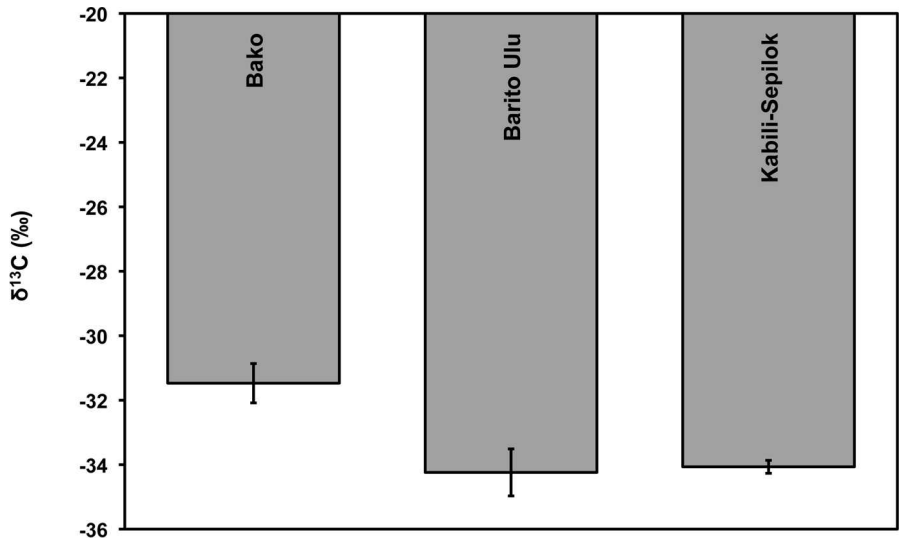

FIG. 2. Foliar carbon isotope ($\delta^{13}C$) values of *Dipteris lobbiana* from three sites in Borneo.

Flanagan *et al.* (Oecologia 111:481–489. 1997) showed that where water levels were not limiting there were more negative foliar $\delta^{13}C$ values in plants growing in mesic 'hanging garden' communities in Utah (USA) where water continually seeps through the porous rocks and is easily available for these plants. In contrast, plants from desert communities can have much less negative $\delta^{13}C$ values indicating the severe water stresses they face (Winter *et al.*, Oecologia 25:115–123. 1976; Ehleringer *et al.*, Rev. Chil. Hist. Nat. 71:79–86. 1998).

I examined foliar carbon isotope values to determine the WUE of *D. lobbiana* from three sites in Borneo. I hypothesised that as this fern is rheophytic it would have very negative $\delta^{13}C$ values and that there would be no difference in $\delta^{13}C$ values between the three sites.

Leaf samples were taken in 2006 from Bako National Park in Sarawak (1° 43′ N; 110° 28′ E), Barito Ulu in Central Kalimantan (0° 06′ S; 114° 0′ E) and Kabili-Sepilok Forest Reserve in Sabah (5° 51′ N; 117° 58′ E) from small- to medium-sized individuals ($n = 3$ per site). Voucher specimens from Bako and Kabili-Sepilok are in TCD with Kabili-Sepilok duplicates in SAN. Samples were dried, ground, and analyzed on a Finnegan Delta^{plus} IRMS interfaced with a Carlo Erba elemental analyser via a Conflo III.

The carbon isotope values were negative (mean value across all sites of −33.3‰; Figure 2) as expected for plants growing in forest environments due to the low light levels found around the shaded understorey streams (Farquhar *et al.*, Annu. Rev. Plant Physiol. Plant Mol. Biol. 40: 503–537. 1989) and also the incorporation of respired carbon dioxide which is depleted in ^{13}C relative to well mixed atmospheric conditions (Buchmann *et al.*, Oecologia 110:120–131.1997). This mean value of −33.3‰ is comparable to the mean value of

−33.8‰ for terrestrial fern species found at La Selva in Costa Rica by Watkins Jr. *et al*. (Oecologia 153:225–232. 2007). The value is not unusually negative and suggests that there are no major differences in WUE between this rheophytic fern species and many terrestrial fern species although analyses of other species from the Borneo study sites would allow confirmation of this suggestion. It also confirms the generally more conservative water use strategies of ferns when compared with angiosperms (Brodribb and Holbrook, New Phytol. 162:663–670. 2004).

Foliar samples from Bako had a significantly less negative foliar $\delta^{13}C$ values than samples from the other two sites ($F_{2,6} = 7.65$, $p = 0.022$; Fig. 2). This was somewhat surprising given that this site has the highest annual rainfall (Bako: 4025 mm, Barito Ulu: 3800 mm, Kabili-Sepilok: 3000 mm) but could be due to the desiccating winds of the more coastal environment. There is also a possibility that stream flow may be less regular at this site and is having an effect on the water relations of this fern species.

This study has shown that *Dipteris lobbiana* does not have a particularly low WUE and that, even for this potentially non-water stressed fern species, there are differences in $\delta^{13}C$ between sites suggesting that water limitation of rheophytic ferns may occur if stream flow is reduced.

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