RESPONSES OF *SHOREA CURTISII* AND *SHOREA LEPROSULA* SEEDLINGS TO SHORT-TERM FLOODING

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Shorea curtisii Dyer *ex* King which grows up to 70 m tall is the major tree species in the hill dipterocarp forest (300~750 m above sea-level) of Peninsular Malaysia (Soerianegara & Lemmens 1994). In the hill dipterocarp forests, it typically occurs on ridge crests of granite and rarely on valley bottoms. It also occurs on coastal hills just above sea-level. Site properties where it occurs are characterised by infertile soils with low water holding capacity (Whitmore 1984). A soil survey in a hill dipterocarp forest indicated that the soil of valley bottoms, where *S. curtisii* was absent, showed mottling and gleying which were absent on the ridges (Tange *et al.* 1998). Because these mottles form as a result of periodic reducing conditions in the soil, it is possible that the absence of *S. curtisii* on valley bottoms relates to its sensitivity to the anaerobic soil conditions induced by high soil moisture contents during the rainy season.

Although responses of plants to flooding are well studied (Kozlowski *et al.* 1991), little is known about such responses in tropical tree species. Flooding effects on photosynthetic activity are different between flood-tolerant and flood-sensitive tree species (Pezeshki 1993). Flood-sensitive species such as cherrybark oak (*Quercus falcata* var. *pagodaefolia*) showed significant stomatal closure and reduction of photosynthetic rate after a few days of flooding (Pezeshki & Chambers 1985). Flooding induces chlorosis and subsequent abscission of leaves of flood-sensitive species, such as *Betura platyphylla* var. *japonica* (Terazawa & Kikuzawa 1994) and *Betura papyrifera* (Tang & Kozlowski 1982). These results indicate that we can take some information on the level of flood-tolerance by observation of the responses of tree species to short-term flooding.

In the present study, in order to consider the physiological aspects for the absence of *S. curtisii* on valley bottoms, leaf gas exchange and chlorophyll contents of *S. curtisii* seedlings in response to flooding were compared with those of *S. leprosula*, which grows up to 60 m tall and occurs commonly on well-drained or swampy sites on clay soil below 700 m altitude in Peninsula Malaysia (Soerianegara & Lemmens 1994).

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Potted seedlings of *S. curtisii* and *S. leprosula* were raised from seeds under 50% relative light intensity (photosynthetic photon flux density) of artificial shading at the nursery of the Forest Research Institute of Malaysia, Kuala Lumpur. Seven-month-old seedlings were used for the experiment. The heights of the *S. curtisii* and *S. leprosula* seedlings were 30 ± 7 cm (mean ± SD) and 44 ± 7 cm respectively. They were transplanted to plastic pots (*c.* 10 litre) three days before the following treatment. Eight of 14 *S. curtisii* seedlings and 6 of 10 *S. leprosula* seed-lings were flooded for 8 days, and the remaining seedlings were watered once a day. Light condition was maintained at 50% relative light intensity.

One undamaged fully expanded mature leaf in the upper canopy of each seedling was taken for gas-exchange measurement. The measurement was carried out on the day before flooding treatment and on the 1st, 2nd, 4th and 8th days of flooding treatment with a portable gas-exchange analysis system (LCA-4, ADC Co., Ltd., UK). Photosynthesis and stomatal conductance were measured at the nursery in the morning (900–1100 h, Malaysian local time), when air temperature, vapour pressure deficit, ambient CO_2 concentration, and photosynthetic photon flux density were from 29 to 34 °C, 1.5 to 2.0 kPa, 370 to 400 µmol mol^{-1} and 500 to 1000 µmol m^{-2} s^{-1} respectively. Chlorophyll contents of two undamaged fully expanded mature leaves in the upper canopy of each seedling were measured on the day before flooding treatment and on the 8th day of flooding treatment using a chlorophyll meter (SPAD-501, Minolta Co., Ltd., Japan). SPAD value obtained by the chlorophyll meter is in proportion to foliar chlorophyll contents (Tadaki & Kinoshita 1988). For analysis of foliar nitrogen content, undamaged fully expanded mature leaves were sampled from six seedlings of each species. Nitrogen content was determined by dry combustion/gas chromatography (NA-1500 model, Carlo Erba Co., Ltd., Italy).

Before the treatment, stomatal conductance of *S. curtisii* was 93± 7 µmol m^{-2} s^{-1} (mean ± SE, n=14) and that of *S. leprosula* was 139 ± 15 mmol m^{-2} s^{-1} (n = 10). Though significant ($p < 0.01$), the difference in stomatal conductance between both species was not so large compared with the difference in net photosynthetic rate, 2.3± 0.2 µmol m^{-2} s^{-1} (n=14) and 7.1± 0.3 µmol m^{-2} s^{-1} (n=10) for *S. curtisii* and *S. leprosula* ($p < 0.01$) respectively. The corresponding foliar nitrogen contents on a dry weight basis (mean ± SE) were 1.24 ± 0.06% (n=6) and 2.32 ± 0.08% (n= 6). The nitrogen content of *S. curtisii* was not abnormally low in comparison with that of field-grown seedlings (1.6 to 1.7%; Grubb *et al.* 1994, Tange *et al.* 1998). SPAD value (mean ± SE) of *S. curtisii* (26.5 ± 0.7, n = 28) was slightly lower than that of *S. leprosula* (29.1± 1.0, n=20). The difference in photosynthetic rates of the two species seems to relate to the differences in foliar nitrogen contents and chlorophyll contents.

The flooded seedlings of *S. curtisii* showed significant reduction in net photosynthetic rate and stomatal conductance as compared to the control seedlings by four days of flooding, with no further reduction thereafter (Figure 1). In contrast, the flooded seedlings of *S. leprosula* showed no significant reduction either in the photosynthetic rate or in the stomatal conductance as compared to the control seedlings over the eight days of flooding. In terms of leaf chlorophyll contents, *S. curtisii* showed a slight, statistically significant decrease in response to the flooding, whereas *S. leprosula* showed no significant change ($p < 0.05$) (Figure 2).

Soil oxygen deficiency induced by flooding injures the root system, and causes additional physiological changes that lead to stomatal closure (Kozlowski *et al.* 1991). Flooding-induced changes could cause the observed reductions in photosynthetic rates through stomatal closure. The similarity in the curves for net photosynthesis and stomatal conduct-ance shown in Figure 1 suggests that this was indeed the case. Photosynthetic rates of flood-sensitive species showed rapid reductions in response to soil flooding and decreased to near zero in a few days of flooding (Pezeshki & Chambers 1985). It was also observed that flooding stress induced leaf senescence (Kozlowski *et al.* 1991). Chlorosis and sub-sequent abscission of leaves were induced on flood-sensitive species by a few weeks of flooding (Tang & Kozlowski 1982, Terazawa & Kikuzawa 1994). As *S. curtisii* did not show such a rapid and extreme reduction in photosynthetic rates and chlorophyll contents, we could not consider *S. curtisii* as a flood-sensitive species. However, because *S. curtisii* showed larger reduction in photosynthetic rates, stomatal conductance and chlorophyll contents than *S. leprosula*, it seems to be less tolerant to flooding stress than *S. leprosula*, which could be a disadvantage for competition on valley bottoms.

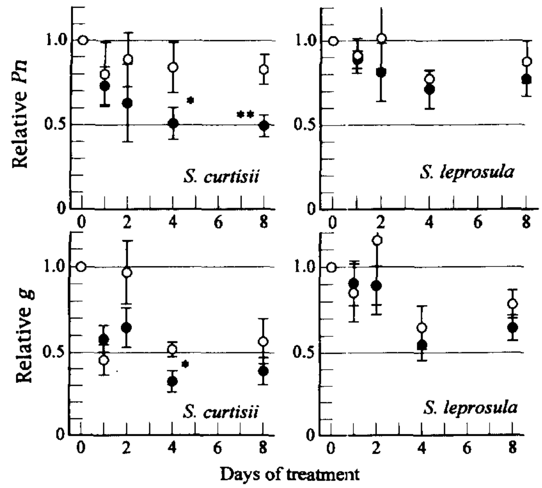

Figure 1. Changes in net photosynthetic rate (*Pn*) and stomatal conductance (*g*) after flooding treatment

Relative *Pn* and relative *g* are the ratios of values on each day to those before the flooding treatment. The ratios before the treatment were plotted at day 0. The values are means ± SE (n = 4 to 8). Asterisks indicate significant differences (Student's *t*-test: **,p < 0.01, *,p < 0.05) between the flooded and control seedlings. O; control, ●; flooded

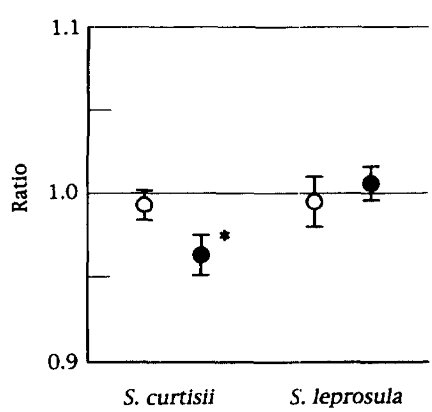

Figure 2. Changes in leaf chlorophyll content during the eight days of flooding treatment

Leaf chlorophyll contents were measured on two leaves of each of the 4 to 8 seedlings for each treatment. The values are means ± SE, and are presented as the ratios to the value before flooding treatment. An asterisk indicates significant difference (Student's *t*-test: *, p < 0.05) between the flooded and control seedlings. O; control, ●; flooded

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