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Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival

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Summary

1 Soil and plant–water relations were studied in a canopy opening and surrounding forest shade in a moist tropical forest in Ghana using seedlings of two tree species with different regeneration strategies, the pioneer *Terminalia superba* and the non-pioneer light demander *Entandrophragma utile*.

2 During two consecutive dry seasons, soil matric potential varied from –30 kPa at the end of the rainy season, to below –2.5 MPa in the middle of the dry season. During part of the first dry season soil matric potential was higher in the gap than in the surrounding forest. In the second dry season no differences were observed.

3 Leaf water potential varied from about –750 kPa at dawn for unstressed seedlings of both species to < -2.5 MPa when seedlings were permanently wilted. For both species, the maximum stomatal conductance of unstressed seedlings varied from 300 to 450 mmol m^{-2} s^{-1} for those in the gap centre to 150 mmol m^{-2} s^{-1} for those under forest shade. Maximum conductance decreased to between 10 and 30 mmol m^{-2} s^{-1} in drought-stressed seedlings during the middle of the dry season. The two species responded similarly to a drying soil profile but the decrease in leaf water potential and stomatal conductance was more rapid under forest canopy than in the centre of the gap.

4 Only 7% of the seedlings of *Terminalia superba* and 4% of *Entandrophragma utile* survived the dry season under forest shade. In contrast, 85% and 78%, respectively, survived of those growing in the centre of the forest gap. At all positions, seedlings of *T. superba* had larger relative height growth rates during the wet season than *E. utile* (29.6, 21.4 and 8.4% month^{-1} compared with 5.2, 20.0 and 1.6% month^{-1}, for gap centre, margin and forest shade, respectively).

5 The observed changes in leaf water potential and stomatal conductance indicated that despite the reduced irradiance, shaded seedlings experienced more drought stress during the dry season than seedlings growing in the forest gap. The reasons for this and possible consequences for trees which differ in leaf phenology and regeneration strategy are discussed.

Keywords: forest gaps, leaf water potential, seasonal droughts, soil matric potential, stomatal conductance

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Introduction

Most studies on growth and mortality of seedlings in tropical forests have concentrated on the effect of variation in irradiance, but recently attention has also been drawn to the importance of soil water. Seedlings in forest gaps have been reported to have a lower mortality during the dry season than seedlings in the understorey, while irrigation in the understorey enhanced survival (Fisher *et al.* 1991). Higher soil matric potentials have been observed in gaps (Becker

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et al. 1988) and Wright (1992) and Grubb (1995) have proposed that, in comparison to plants in gaps, understorey plants will be more affected by seasonal droughts.

It is however, unclear whether higher soil matric potentials in gaps would automatically lead to reduced drought stress, since increased canopy opening also leads to increased irradiance, higher temperatures and greater vapour pressure deficits on the forest floor and a more rapidly drying soil surface (Fetcher *et al.* 1985; Ashton 1992; Brown 1993). Also Robichaux *et al.* (1984) report lower predawn leaf water potentials in shrubs growing in gaps compared to the understorey, implying increased drought stress in gaps. There is thus a need for field studies in tropical rain forests that combine measurements on the soil water regime with plant–water relations.

Tree species differ in their regeneration strategy with regard to irradiance requirements. In Ghana, species have been divided into guilds (Hall & Swaine 1981; Hawthorne 1993). Some species regenerate exclusively in open habitats while others also regenerate under the forest canopy. On the basis of the reported differences in soil water regime between gaps and the understorey, it may be hypothesized that during periods of drought, the way in which water relations vary between plants growing in gaps, compared to the understorey will depend on the species' regeneration strategy.

In this paper we report observations, made in and around a large gap in a West African moist semideciduous forest, on the soil water regime and plant–water relations of tree seedlings of two species which differ in regeneration strategy. We test the hypothesis that tree seedlings regenerating in a forest gap have an enhanced plant–water status compared to tree seedlings regenerating in shade.

Materials and methods

PLANTING EXPERIMENT

The study site was located in Tinte Bepo Forest Reserve (7°04′N, 2°06′W) a moist semideciduous forest in Ghana. Rainfall is concentrated in the months May to June and September to October with the main dry season between December and February (Fig. 1). Soils at the site were acid (pH 5.5–6.5), reddish-brown sandy clays, with a free-draining profile on a slope of 0–3%.

A large gap ≈ 26 m in diameter was created by removing shrubs and trees until photosynthetically active radiation (*PAR*) in the centre of the gap reached 60% of ambient daily irradiance, as measured over weekly periods with Didcot integrating *PAR* sensors (DRP 02) (Agyeman 1994).

Three-month-old seedlings of *Terminalia superba* Engl. and Diels and *Entandrophragma utile* (Dawe and Sprague) Sprague were used in the study. *T. superba* belongs to the pioneer guild and requires high irradiance throughout its life, whereas *E. utile* is a nonpioneer light-demanding species and although it is found as a seedling (< 5 cm d.b.h.) under the forest canopy, it requires gaps to develop further (Hawthorne 1993).

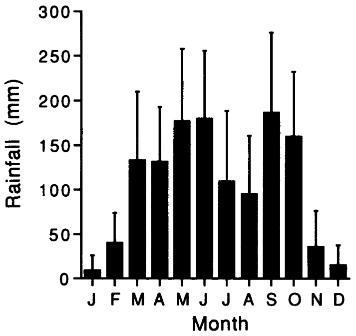

Fig. 1 Average monthly rainfall at Bechem (7°7′N, 2°3′W; 1970–93; long-term mean annual rainfall is 1288 mm; Error bar is 1 standard deviation. Source: Department of Meteorological Services, Accra.)

Plots (4 m wide) were established perpendicular to the gap boundary to the north, south, east and west. The plots stretched across the canopy margin and were divided into three sections (1) gap (at least 5 m into the gap from the margin) (2) gap margin (at most 3 m into the gap or into the forest) and (3) forest shade (under the forest canopy, at least 5 m from gap margin). In June 1992 tree seedlings were planted in the sections at a minimum spacing of 1 m, with seven plants for each species in each of the gap centre sections and eight plants in each gap margin and forest shade section. All plants were randomly allocated to their position. Height and diameter were recorded at planting time, again after the end of the rainfall season (December 1992) and at the start of the next rainfall season (May 1993) and used to calculate relative growth rate of height and diameter (Beadle 1993). Growth data at the end of the wet season and survival at the end of the wet and the dry season were analysed with Games & Howell's approximate test of equality of means because of heterogeneity of variances (Sokal & Rohlf 1981, pp. 408–412; note that strictly speaking samples are biased due to mortality). During the rainy seasons, vegetation around seedlings in the gap was cut down every two months.

SOIL WATER REGIME

Soil matric potential was measured using the filter paper technique (Deka *et al.* 1995). Random soil samples were taken with an auger from the centre of the gap, the gap margin and under tree canopy. Samples were taken from two or three pits in each site at depths of 20, 40 and 60 cm. Samples were equilibrated with filter papers from individually calibrated batches, in an insulated box at room temperature for 7–10 days. This procedure gives accurate results down to –2.5

MPa below which the method may lead to underestimation (Deka *et al.* 1995). After arcsine transformation to improve homogeneity of variance, water contents of the filter papers were used for two-way analysis of variance. Daily rainfall was measured with a manual rain-gauge on the forest edge, 3 km from the site.

PLANT–WATER RELATIONS

Leaf water potential was measured using the pressure bomb technique (Tyree & Hammel 1972). Measurements were made at dawn (between 06.30 and 08.00 hours) and at midday (12.30–14.00 hours) on plants selected from the gap centre, gap margin and under forest shade. One plant of each species was selected randomly from each section in the north, south, east and west blocks. In the second year, diurnal measurements were taken from three plants of each species remaining from the previous year, but only in the centre of the gap. Water potentials were measured in the fully expanded mature leaves from the top of the plants of *T. superba* and on distal leaflets of *E. utile*. Leaf water potential data were compared using analysis of variance.

Stomatal conductance, leaf temperature, photosynthetic photon flux density and relative humidity were measured with a transit-time diffusion porometer (model A.P.4, Delta T. Devices, Cambridge, UK) (Beadle *et al.* 1993). Plants were randomly selected in the same way as for the leaf water potential measurements. Stomatal conductance was measured in the first year on different plants from those used for leaf water potential. Measurements in the second year were made on the same plants. Use of the porometer to measure leaf temperature led on occasion to an underestimate of the actual leaf temperature of up to 1 °C for leaves growing in high irradiance. New sensor heads calibrated by the manufacturer were used in each year. Air temperature was recorded with a thermocouple temperature sensor and a Squirrel data logger (Grant Instruments). Vapour pressure deficit was calculated as in Jones (1993, Appendix 4).

Results

DRY SEASON 1992–93

Soil water regime

In 1992 the last rains of the rainy season fell on 12 November (Fig. 2) and apart from four light showers in January and February, totalling 11.5 mm, no further rain fell until the start of the following rainy season on 5 March. Measurements of soil matric potential were started on 21 November. Matric potentials declined over a period of 7 weeks to about –2 MPa. Matric potentials showed a large variability, but were generally highest in the gap and lowest in the gap margin. Statistically significant differences ($P < 0.01$) were found between both date and site at depths of 20 cm and 60 cm (Appendix 1). At these depths soil matric potential values were highest in the gap. By mid-January, matric potentials at all depths decreased to less than –2.5 MPa, below which experimental accuracy of the filter paper technique becomes limiting.

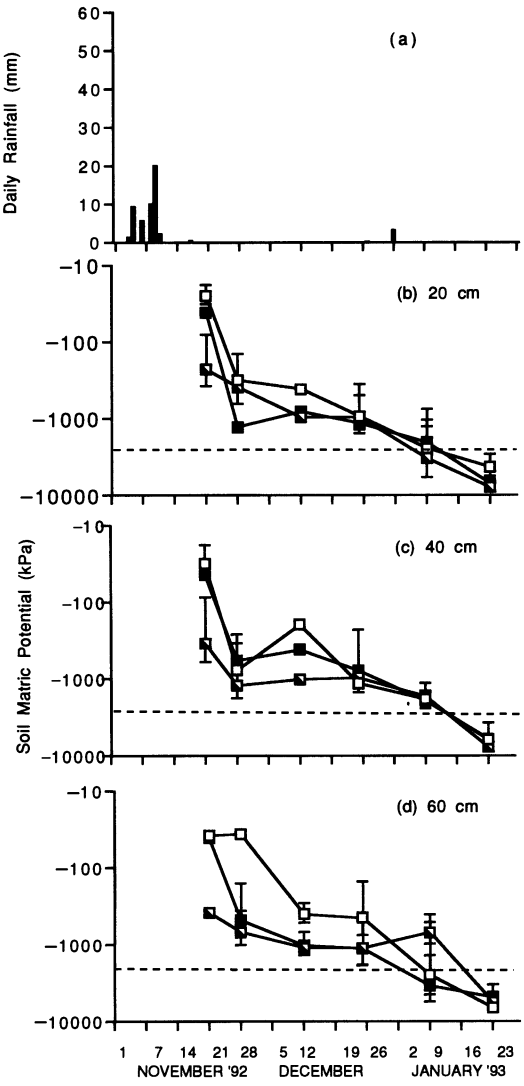

Fig. 2 Daily rainfall (a) and soil matric potential ($n = 2$) at depths of (b) 20, (c) 40 and (d) 60 cm in Tinte Bepo Forest Reserve (moist semi-deciduous forest) during the dry season 1992/1993 (open symbols, gap centre; half closed symbols, gap margin; closed symbols, forest shade. The broken line indicates the potential below which values are less reliable. Error bar is ± 1 standard error. If not shown, they are smaller than the symbol).

Plant–water relations

Observations on leaf water potential (Ψ) and stomatal conductance were made in the beginning (21 November), during the middle (12 December) and towards the end (22 January) of the dry season.

Initially Ψ_{dawn} varied between –0.75 and –1.0 MPa while Ψ_{midday} varied between –1.45 and –1.65 MPa

(Fig. 3). Differences between time of day were significant, but not between the two species or the location of the trees.

Three weeks later Ψ_{dawn} had dropped to –0.9 MPa in the gap and –2.6 MPa in the shade, with the gap margin intermediate. Ψ_{midday} varied between –2.3 MPa in the gap and –3.0 MPa in the shade. Differences between time of day and canopy shading were significant, but not between the two species. Ψ values in the morning were significantly higher in the gap than the other locations.

On 22 January only plants in the gap centre still had green leaves. Ψ_{dawn} and Ψ_{midday} did not differ significantly and had a mean value of –2.8 MPa.

Early morning stomatal conductance (g_s) on the first day of measurements (Fig. 4a) reached 300–450 mmol m^{-2} s^{-1} in both species in the gap and in the gap margin, and 150 mmol m^{-2} s^{-1} under forest shade at a time when photosynthetic photon flux density (*PPFD*) was below 100 μmol m^{-2} s^{-1} in the gap and below 15 μmol m^{-2} s^{-1} in the shade. By midday, when *PPFD* had reached 980 μmol m^{-2} s^{-1} in gap centre and 25 μmol m^{-2} s^{-1} under forest shade, some depression in g_s was present in both species in most sites. Vapour pressure deficit (*VPD*) varied between 0.4 MPa at 08.30 hours to 1.4 MPa at 21.00 hours and air temperature between 23 °C at 8.30 hours and 29 °C at midday. Midday leaf temperatures in plants in the gap centre were 2–4 °C and in the shade 1 °C higher than air temperature. *T. superba* plants in the centre of the gap showed visible signs of wilting by midday, but recovered in the afternoon.

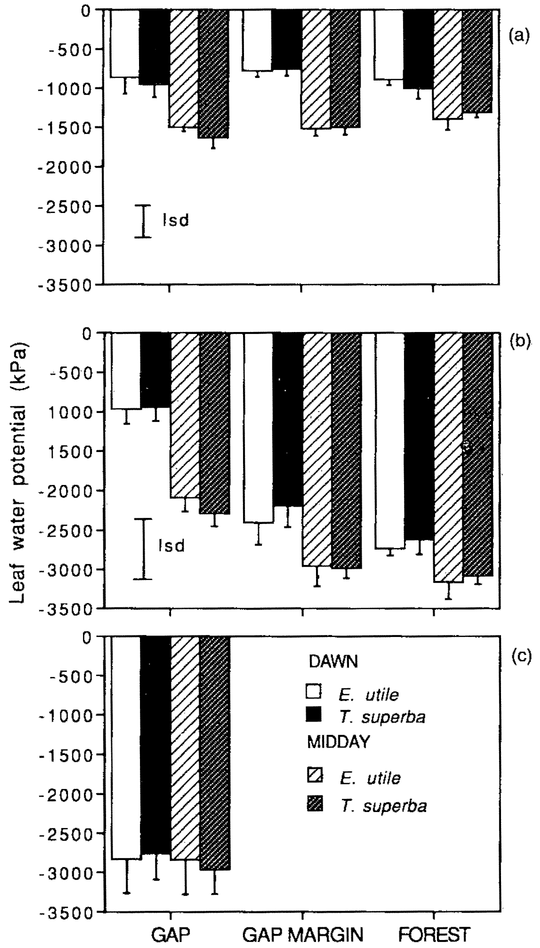

Fig. 3 Leaf water potential at dawn (06.30–08.30 hours) and at midday (12.30–14.30 hours) during (a) the early (21 November 1992), (b) middle (12 December 1992) and (c) late (22 January 1993) dry season in tree seedlings of *E. utile* and *T. superba* growing in different locations ($n = 4$. Error bar is 1 standard error).

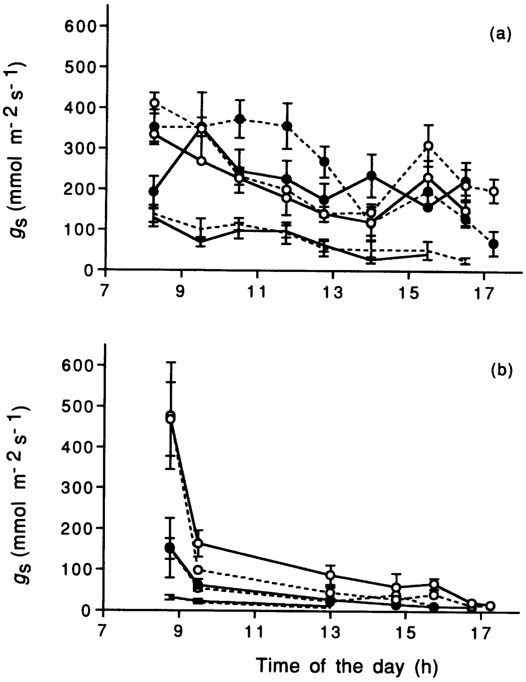

Fig. 4 Diurnal variation in stomatal conductance (g_s) in tree seedlings during (a) the early and (b) the middle dry season in different locations (open symbols, gap; closed symbols, gap margin; no symbols forest shade; solid lines, measurements on *E. utile*; broken lines, measurements on *T. superba*. $n = 4$. Error bar is ± 1 standard error. If not shown, they are smaller than the symbol.

Three weeks later the daily pattern of g_s was very different (Fig. 4b). In the early morning, g_s in plants in the gap centre reached values similar to those in November while in the gap margin g_s was reduced to 150 mmol m^{-2} s^{-1} and under forest shade to 30 mmol m^{-2} s^{-1}. After 09.00 hours stomatal conductance reduced strongly in both gap and gap margin plants. By midday, g_s of plants growing under forest shade had fallen below 10 mmol m^{-2} s^{-1} and measurements on these plants were discontinued. It was overcast so that by midday maximum *PPFD* in the gap centre was no more than 250 μmol m^{-2} s^{-1} in the gap centre, 100 μmol m^{-2} s^{-1} in the gap margin and 20 μmol m^{-2} s^{-1} under forest shade. Air temperature was on average 1 °C lower than the previous day of measurements. *VPD* varied between 0.7 and 1.8 MPa at midday and differences between leaf and air temperature were as before. In the gap, *T. superba* seedlings showed signs of wilting by 10.00 hours and were heavily wilted by 14.00 hours but by 17.30 hours plants showed signs of recovery. In the shade, *T. superba* seedlings were wilted throughout the day, while plants in the gap margin showed an intermediate status of wilting. In *E. utile*, a similar but less severe pattern of wilting was observed.

As the dry season progressed, diurnal patterns of wilting became more severe and by the end of January leaves of plants in the forest shade and gap margin had dried out and had started to change colour. Plants in the centre of the gap still maintained green leaves, but showed heavy wilting with early morning g_s below 30 mmol m^{-2} s^{-1}.

Seedling growth and survival

Analysis of variance of relative growth rate of height (*RGRH*) and diameter (*RGRD*) did not show significant differences between east, west, north and south blocks and the level block was omitted from further comparisons.

In surviving plants *RGRD* and *RGRH* were larger for *T. superba* than for *E. utile* (Table 1). For both species, largest values for *RGRH* and *RGRD* were obtained during the wet season in the gap centre and gap margin but these were only significantly ($P < 0.05$) higher than in the forest shade for the pioneer *T. superba*. During the dry season average *RGRD* was close to zero, but negative in both species, with the exception of *T. superba* in the gap centre.

Most seedlings survived through the rainy season, but both species survived least well in the shade (91% survival for *E. utile* and 78% for *T. superba*, Table 2). For *T. superba*, survival in the shade was significantly less than at the other locations. However, many seedlings had died by the end of the dry season, with greatest survival in the gap followed by gap margin and least under forest shade. The trend was the same for both species.

DRY SEASON 1993/1994

Soil water regime

In 1993 the last rains of the rainy season fell on 25 November and the next rainfall started on 12 February 1994 (Fig. 5). Soil matric potential measurements in the gap and the surrounding forest were started on 5 November (Fig. 5). Matric potentials declined to values below –2.5 MPa within 5–7 weeks from the end of the last rains depending on profile depth. Although potentials were variable, they were similar in all three locations. Soil matric potentials tended to be greater at greater depth. Analysis of variance indicated statistically significant differences between dates but not between locations (Appendix 1).

Plant–water relations

During the second dry season observations were only made in the gap on plants of both species, that had successfully established as seedlings in the previous year. The 1.5-year-old saplings had by now reached heights of 120–200 cm in *E. utile* and 120 cm to 300 cm in *T. superba* and were big enough to take leaf samples for diurnal Ψ_{leaf} patterns without disturbing the plant. At the beginning of November, with ample water supply, Ψ_{leaf} decreased in both species from between -0.5 MPa before dawn to –1.9 MPa for *E. utile* and -2.1 MPa for *T. superba* at midday (Fig. 6). By late afternoon Ψ_{leaf} increased again to predawn levels.

By 14 December $\Psi_{pre\text{-}dawn}$ decreased to below -0.5 MPa. Midday values for both species were below -2.0 MPa. Late afternoon values did not return to predawn values, but increased to -1.5 MPa for both species.

By 22 January $\Psi_{pre\text{-}dawn}$ had decreased to less than -2.0 MPa in *T. superba*, but was higher in *E. utile*. In both species Ψ_{midday} reached –3.0 MPa and did not recover during the rest of the day. All plants survived this dry season.

Stomatal conductances during the wet season were similar to those observed in gap plants in the previous year except that maximum g_s observed in *E. utile* was somewhat lower at 250 mmol m^{-2} s^{-1}. As the dry season progressed, g_s was highest in mid-December during the early morning reaching maxima of 300 mmol m^{-2} s^{-1} in *T. superba* and 200 mmol m^{-2} s^{-1} in *E. utile*. *T. superba* started leaf abscission at the beginning of January, while *E. utile* kept its leaves

Table 1 Relative height growth rate (*RGRH*) and relative diameter growth rate (*RGRD*) of surviving seedlings of *E. utile* and *T. superba* in different locations during the wet (June–December) and dry (December–May) season. December values sharing a superscript do not differ significantly ($P < 0.05$) according to Games & Howell's test for approximate equality of means

	RGRH (% month^{-1})		*RGRD* (% month^{-1})	
Location/species	December	May	December	May
Gap				
E. utile	5.2 ± 0.9^a	4.4 ± 1.0	6.5 ± 1.0^a	-0.3 ± 0.7
T. superba	29.6 ± 1.4^b	10.4 ± 2.3	22.6 ± 1.8^b	4.7 ± 1.2
Gap margin				
E. utile	2.0 ± 0.9^a	2.4 ± 1.2	3.4 ± 0.9^a	-1.2 ± 0.6
T. superba	21.4 ± 1.5^b	4.5 ± 2.3	15.0 ± 1.5^b	-0.4 ± 0.7
Forest shade				
E. utile	1.6 ± 0.8^a	-0.7 ± 2.6	2.4 ± 0.6^a	-0.5 ± 2.4
T. superba	8.4 ± 1.7^a	7.8 ± 5.0	3.5 ± 0.9^a	-4.4 ± 1.8

Table 2 Numbers of surviving of seedlings (with percentage survival in parentheses) of *E. utile* and *T. superba* in different locations during wet (June–December) and dry (December–May) seasons. Values in each column sharing a common superscript do not differ significantly $P < 0.05$ according to Fisher's exact test

	Seedlings surviving		
Location/species	Initial	June–December	December–May
Gap			
E. utile	28	27^{a} (96)	21^{a} (78)
T. superba	28	27^{a} (96)	23^{a} (85)
Gap margin			
E. utile	32	31^{a} (97)	12^{bc} (39)
T. superba	32	32^{a} (100)	18^{b} (56)
Forest shade			
E. utile	32	29^{ab} (91)	4^{d} (14)
T. superba	32	25^{b} (78)	7^{cd} (28)

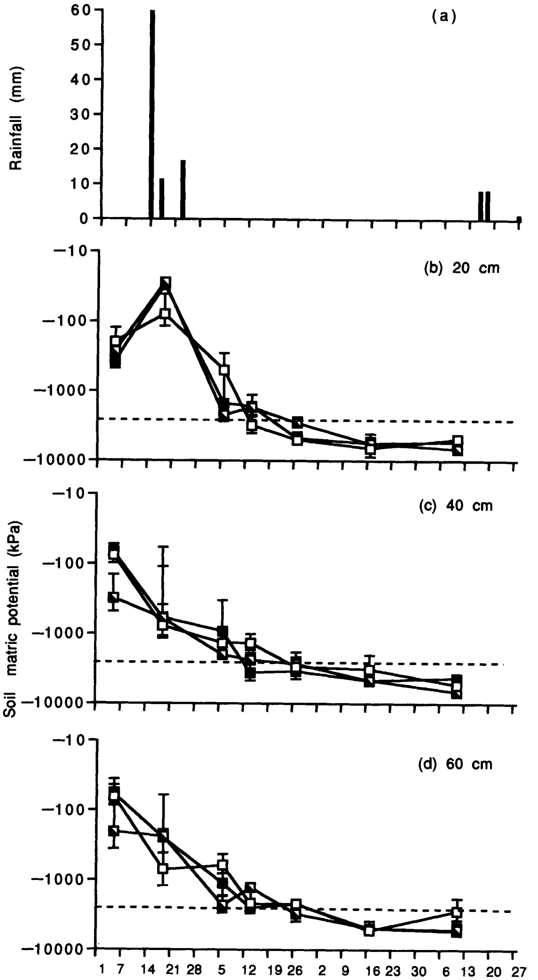

Fig. 5 Daily rainfall (a) and soil matric potential ($n = 3$) at depths of (b) 20, (c) 40 and (d) 60 cm in Tinte Bepo forest Reserve (moist semideciduous forest) during the dry season 1993–94 (open symbols, gap centre; half-closed symbols, gap margin; closed symbols, forest shade. Error bar is ±1 standard error. If not shown, they are smaller than the symbol).

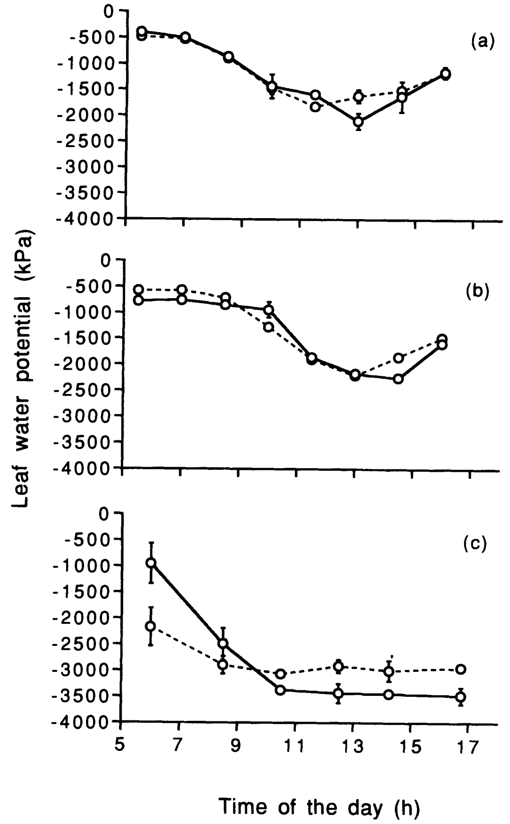

Fig. 6 Diurnal changes in leaf water potential in *E. utile* and *T. superba* saplings growing in the centre of a large gap during (a) the early (21 November 1993), (b) middle (12 December 1993) and (c) late (22 January 1994) dry season (solid lines, measurements on *E. utile*; broken lines, measurements on *T. superba*. $n = 3$. Error bar is ± 1 standard error. If not shown, they are smaller than the symbol).

throughout the dry season. By 21 January, *T. superba* was almost leafless. At this time, g_s in the morning was reduced to less than 100 mmol m^{-2} s^{-1} in both species.

Discussion

In the first dry season, soil matric potentials in the gap were higher than in the gap margin or in forest shade. In the second year, no significant differences were observed. Root density in newly formed gaps is initially decreased (Sanford 1990; Silver & Vogt 1993) and this, together with the loss of transpiring leaves, will contribute to a slower depletion of soil water in the centre of new gaps. However, as vegetation regrows, microclimatic conditions in gaps change rapidly (Fetcher *et al.* 1985). Our data confirm that differences in soil water regime between gaps and surrounding forest decrease over time. Because we discouraged re-growth by cutting down plants, soil matric potential differences may normally be smaller than found in this study.

In drying soils, plants growing in the centre of a gap may have access to small additional quantities of water through upward movement of water driven by the differences in day and night soil surface temperature (Marshall & Holmes 1988). The soil surface temperature during the day in gaps is greater than under forest shade (Lawson *et al.* 1970; Ashton 1992). Though small in absolute terms, this movement could be a contributing factor, where seedling survival is concerned.

In non-drought-stressed seedlings of both *E. utile* and *T. superba*, early morning g_s reached maxima of 300–450 mmol m^{-2} s^{-1} in the gap and the gap margin, and 150 mmol m^{-2} s^{-1} in the shade while *PPFD* was still low ($< 100\,\mu$mol m^{-2} s^{-1} in the gap and $< 10\,\mu$mol m^{-2} s^{-1} in the shade). Although this seems wasteful in terms of water use, it results in a decrease in stomatal limitation of photosynthesis during sunflecks (Pearcy 1990). The midday depression of stomatal conductance of seedlings in the gap is not surprising, as water vapour pressure deficits of more than 1.7 MPa are similar to those experienced by leaves in the upper canopy of rain forest trees (Aylett 1985; Koch *et al.* 1994).

As the dry season progressed, stomatal conductance showed the sharpest reduction in shaded plants followed by plants in the gap margin and the least reduction in plants growing in the gap centre (Fig. 4). This and the associated decrease in leaf water potentials (Fig. 3), particularly during the early morning in gap margin and shade, suggests that plants in the shade, despite lower water vapour pressure deficits, are subjected to greater drought stress than those in the gap. Part of the explanation is attributable to the differences in soil matric potential, but other aspects should also be considered. Deep shade conditions with less than 1% of ambient irradiance will result in morphological and physiological changes in leaves such as an increase in specific leaf area, reduced wax formation, reduced stomatal density and thinning of the cuticular membrane of the leaves (Givnish 1988; Kerstiens 1994). This makes shade leaves more vulnerable to water loss and could account for the decrease in leaf water potential and reduced stomatal conductance. Leaf temperatures were not high enough to be physiologically damaging, either in the gap or under forest shade.

Plant size and architecture may also have played a role. Relative growth rates of height and diameter in *T. superba* were significantly larger in plants growing in the gap and gap margin compared to those growing under the canopy. Similar, but insignificant differences were observed for *E. utile* (Table 2). Plants growing in shade are likely to show a reduced root: shoot ratio as a response to low irradiance, possibly reducing rooting depth, which may be important for the survival of understorey seedlings in dry forest (Mulkey *et al.* 1991). Growth and architecture combined will reduce the soil volume that can be exploited by the roots of plants growing under shade. In addition, shade plants will encounter more competition from the denser network of surrounding roots compared to plants establishing in gaps (Sanford 1990; Silver & Vogt 1993).

The more rapid decrease of leaf water potential and stomatal conductance indicate that plants growing in forest shade may experience drought stress 3–4 weeks longer than plants growing in the gap. Plants specialized to shaded habitats will have to be adapted to these drier conditions. Drought stress has been reported before as a factor in the mortality of seedlings (Turner 1990) and our findings support the suggestion that drought is an important stress factor for understorey vegetation in drier forests (Wright 1992; Grubb 1995).

In the first season, seedlings of *T. superba* and *E. utile* followed an evergreen strategy until the leaves died of desiccation. In the second season, the species differed strongly in leaf phenology. *T. superba* seedlings were deciduous and shed leaves by the end of January whereas *E. utile* remained evergreen and was able to take up water to retain some turgor during the early part of the morning, even in the middle of the dry season. Shade tolerant species are typically evergreen, which allows a longer pay-back time for leaf construction costs (Williams *et al.* 1989). Deciduous behaviour on the other hand is associated with a greater instantaneous nitrogen and water use efficiency (Sobrado 1991) and may help to avoid cavitation in the xylem vessels (Jackson & Grace 1994). It is interesting to note that many West African understorey species in drier forests have sclerophyllous evergreen leaves with a thick cuticular layer (personal observation) and it can be hypothesized that the leaves of these plants may be adapted not only to shade but also to the dry conditions experienced on the forest floor.

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Appendix 1

Analysis of variance of water contents of filter papers equilibrated against soil samples obtained from different depths

	Depth					
	20 cm		40 cm		60 cm	
Source of variation	d.f.	mean squares	d.f.	mean squares	d.f.	mean squares
1992/1993						
Date	5	0.138****	5	0.114****	5	0.082****
Location	2	0.029**	2	0.033NS	2	0.037***
Date × location	10	0.015*	10	0.011NS	10	0.016***
Error	16	0.005	18	0.010	18	0.003
1993/1994						
Date	6	0.287****	6	0.114****	6	0.287****
Location	2	0.006NS	2	0.013NS	2	0.003NS
Date × location	12	0.111NS	12	0.014NS	12	0.009NS
Error	35	0.181	36	0.024	35	0.005

*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$; ****$P < 0.001$.