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Full Length Research Paper

Influence of varying light regimes on photosynthesis and related variables on tree seedlings of *Warburgia ugandensis* Sprague and *Polyscias fulva* (Hiern) harms

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The physiology of seedlings of *Warburgia ugandensis* and *Polyscias fulva* were studied at varying light levels. Photosynthesis was significantly higher in *P. fulva* (1.4 μmols CO_2 m^{-2} s^{-1}) than in *W. ugandensis* (0.3 μmols CO_2 $m^{-2}s^{-1}$) when grown in full sunlight. However, photosynthesis was not significantly ($P > 0.05$) different under moderate and dense shades (PPFD about 600 μmols $m^{-2}s^{-1}$ and 350 μmols $m^{-2}s^{-1}$ respectively) for both species (and ranged between 0.4 and 0.5 μmols CO_2 $m^{-2}s^{-1}$). Generally, *P. fulva seedlings* had significantly ($P < 0.05$) greater reductions (from 1.0 to 0.4 μmols CO_2 $m^{-2}s^{-1}$) in photosynthetic rates in response to increasing shade than did *W. ugandensis* (0.6 to 0.4 μmols CO_2 $m^{-2}s^{-1}$). However, *W. ugandensis* attained significantly ($P < 0.05$) higher photosynthetic rates under shade conditions (0.6 μmols CO_2 $m^{-2}s^{-1}$) than full sunlight conditions (0.3 μmols CO_2 $m^{-2}s^{-1}$). Leaf temperatures were highest (30°C) in full sunlight and lowest (27°C) in dense shade for both species. Generally, stomatal conductance, transpiration and water use efficiency showed significantly ($P < 0.05$) higher values for shade grown *W. ugandensis* and full sunlight grown *P. fulva.* Water use efficiency for *P. fulva* (2.3 μmols CO_2 $mmol^{-1}$ H_2O) was significantly ($P < 0.05$) higher that for *W. ugandensis* (1.5 μmols CO_2 $mmol^{-1}$ H_2O) in full sunlight than. It was concluded that *P. fulva* was also less adapted to growth at low light intensity while *W. ugandensis* was better adapted to growth at low light levels because of its significantly greater ability to maintain higher rates of photosynthesis in low light intensity. Therefore in East Africa *P fulva* can be a better agroforestry species than *W. ugandensis.*

Key words: Net carbon exchange, forest tree seedlings, shade, *Warburgia ugandensis*, *Polyscias fulva.*

INTRODUCTION

Deforestation of tropical forests is increasing rapidly and this can have both global and local adverse consequences. Perhaps the single greatest cause for concern over the loss of tropical forests is the loss of the biological diversity that these forests contain (Raven, 1987). In Kenya, many areas of natural forests have been heavily disturbed through selective logging and clearing resulting in fragmentation and reduction in forest cover to less than 5% of land cover. These degraded areas vary in size from scattered canopy gaps to large abandoned clearings (Kigomo, 1990). There is a growing interest to rehabilitate the damaged areas by re-planting them, especially with indigenous tree species (Kigomo, 1990). However, there is little experience on silvicultural management of many of these species, in addition to the inadequate understanding of their ecological requirements. This is largely because their biological and ecological requirements are not well understood. Tree species differ in their requirements for light (Whitmore, 1984) and respond differently to environmental conditions associated with canopy gaps

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Abbreviations: PPFD, photosynthetic photon flux density, WUE, water use efficiency.

Table 1. Summary of the microclimatic conditions during the study.

Factor	Dense Shade (25% Full light)	Moderate Shade (65% Full light)	Partial Shade (42% Full light)	100% Full Sunlight
Mean daily photosynthetic photon flux density (PPFD) (μmols m^{-2} s^{-1})	347	588	918	1413
% Sunlight	25	42	65	100
Mean air temperature (°C)	27	28	29	30

of different sizes (Denslow,1980; Vincent, 2006).

Variation in the light environment in tropical forests affects plant germination, photosynthesis, growth, and reproduction (Longman and Jenik, 1987; Tokahashi and Rustandi, 2006) . Adequate data on photosynthesis are lacking for most forest species (Mooney et al., 1983). The capacity of plants to intercept and use radiant energy for photosynthesis determines the availability of photosynthates for growth. However, radiation is not only a source of energy, it is also a stimulus governing development, and occasionally also a stress factor (Larcher, 2003; Ogachi et al., 2006; Vincent, 2006).

The present study was intended as a contribution on the ecology of two economically important tree species of Kenya, *Warburgia ugandensis* Sprague and *Polyscias fulva* (Hiern) Harms grown under varying light regimes. *W. ugandensis* is a common forest tree in Kenya highland forests. The timber of this species does not develop any cracks and takes a high polish and the bark of the tree is of vital medicinal value (Kokwaro 1976). *P.* fulva is a highland forest tree and whose timber is easy to work and is odourless. It is a valuable timber for veneers and plywood. Ecophysiological responses to light were used to assess species characteristics that might be important for revegetation of disturbed forest areas or for use in agroforestry systems.

MATERIALS AND METHODS

The study was located at a nursery of the Kenya Forestry Research Institute, Muguga, Kenya. A randomised-block design of three replications was used. The four light treatments were randomised within the three blocks while the two species were randomised within the light treatments. A distance of 1m separated the blocks. The different light levels treatments (sub-plots) were 1m apart. Fourteen tree seedlings were planted in each sub-plot in a 2 x 7 arrangement. There were 12 subplots with a total of 168 seedlings for the two species.

The light conditions prevailing under the full sunlight represented a clearing in the natural environment and the dense shade a small gap. The partial and moderate shades represented large gaps in the forest.

Seeds of the two species (*W. ugandensis* and *P. fulva*) were acquired from the Seed Centre, Kenya Forestry Research Institute, Nairobi, Kenya. The seeds were sown separately in germination trays with sand as the medium and then transferred to the greenhouse for germination. After eight weeks, seedlings of the two species were transplanted separately into 20 cm height by 6.5 cm in diameter polythene pots which had been previously filled with forest topsoil, cow manure and gravel mixed into a ratio of 5:2:1 by volume, respectively. These were perforated at the bottom to allow easy draining of water. After transplanting, the seedlings were removed from the greenhouse and kept in the open for a period of one month to harden them. The seedlings were then randomized and transferred into the four different light regimes where they stayed for one month to acclimatise to the new environment before measurements were taken.

The shade levels were obtained by use of factory made artificial black shade materials. Each shade house was 1m long, 1m wide and 1m high. The artificial shades used in this experiment gave photosynthetic photon flux densities of 25% (dense shade), 42% (moderate shade), 65% of full sunlight (partial shade), and full sunlight (no shade).

Rates of photosynthesis, transpiration, stomatal conductance, and (photosynthetic photon flux density) PPFD were determined in the four different light regimes using an open system, portable, infra-red gas analyser (IRGA-ADC. model LCA-2, The Analytical Development Co. Ltd; Hertfordshire, England) fitted with a leaf chamber (model PLC). During measurements the analyser was used in a constant flow rate, variable differential mode (Long and Hällgren, 1985). Measurements were carried out from 09:00 h, after the leaves were free of dew and continued every hour until 17:00 h. Four different leaves of each species were used in the four different light regimes per measurement period on three clear days. CO_2 assimilation, transpiration and stomatal conductance of single leaves were calculated using flux equations adapted from von Caemmerer and Farquhar (1981) and Long and Hällgren (1985). Water use efficiency was calculated by dividing rate CO_2 assimilation by the rate of transpiration.

All data were analysed using a factorial ANOVA. When significant differences ($P < 0.05$) were found for either species, light treatments, or their interaction, Tukey's Multiple Range Test was used to separate significant ($P < 0.05$) means (Steel et al., 1997).

RESULTS

Photosynthetic photon flux density (PPFD)

The mean diurnal PPFD was about 350 μmols m^{-2} s^{-1} for dense shade, 600 μmols m^{-2} s^{-1} for moderate shade, 900 μmols m^{-2} s^{-1} for partial shade and 1400 μmols m^{-2} s^{-1} for full sunlight (Table 1). High PPFD characterized the full sunlight treatment, while all shaded microclimates show-ed reduced PPFD. There were significant ($P < 0.05$) differences in PPFD among the different light treatments.

Air temperature

The mean diurnal air temperatures recorded were: 30^oC in full sunlight, 29^oC in partial shade, 28^oC in moderate shade and 27^oC in dense shade (Figure 1). There was no significant ($P > 0.05$) difference among the shade treatments for temperature. However, higher temperatures characterized the full sunlight treatment while the shaded microclimates had lower temperatures.

Photosynthetic rate

Rates of photosynthetic assimilation for *P. fulva* were highest under full sunlight and lowest under dense shade treatments. However, *W. ugandensis* showed the highest rates of photosynthesis under partial shade and the lowest rates under the full sunlight treatment (Figure 2). Photosynthetic rates were significantly ($P < 0.001$) higher for *P. fulva* (1.4 μmols CO_2 m^{-2} s^{-1}) than for *W. ugandensis* (0.3 μmols CO_2 m^{-2} s^{-1}) when grown under full sunlight. Rates of photosynthesis for *P. fulva* grown under full sunlight were therefore 65% higher than in *W. ugandensis*. Full sunlight-grown *P. fulva* had a maximum photosynthetic rate of 3 μmols CO_2 m^{-2} s^{-1} compared with 0.4 μmols CO_2 m^{-2} s^{-1} for *W. ugandensis*.

In partial shade, the rate of photosynthesis for *P. fulva* was similarly higher ($P < 0.01$) than in *W. ugandensis*, at 1.0 μmols CO_2 m^{-2} s^{-1} and 0.6 μmols CO_2 m^{-2} s^{-1}, respectively. The photosynthesis range for *P. fulva* was 0.4 to 1.7 μmols CO_2 m^{-2} s^{-1} and 0.5 to 0.8 μmols CO_2 m^{-2} s^{-1} for *W. ugandensis* when grown under partial shade conditions. Shading enhanced the rate of photosynthesis in *W. ugandensis*, increasing it from 0.3 μmols CO_2 $m^{-2}s^{-1}$ in full sunlight to 0.6 μmols CO_2 m^{-2} s^{-1} in partial shade (a 50% increase). However, *P. fulva* had lower rates of photosynthesis in partial shade that was about 70% of that of the same specie in full sunlight. Rates of photosynthesis were not significantly ($P > 0.05$) different in the two species when grown under moderate and dense shade, with *P. fulva* exhibiting a range of 0.2 to 0.5 μmols CO_2 m^{-2} s^{-1} and 0.3 to 0.5 μmols CO_2 m^{-2} s^{-1} for *W. ugandensis* under these conditions.

Stomatal conductance

Seedlings of *P. fulva* exhibited the highest stomatal conductance in full sunlight ranging from 0.007 to 0.02 mols m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.003 to 0.009 mols $m^{-2}s^{-1}$ (Figure 3). Stomatal conductance in seedlings of *P. fulva* grown in full sunlight was therefore 55% higher than in seedlings of *W. ugandensis*. Stomatal conductances of the two species grown under moderate and dense shade were not significantly ($P > 0.05$) different. Like for photosyn-thesis, stomatal conductance decreased with increasing shade in *P. fulva*. However, in *W. ugandensis* stomatal conductance increased from dense shade to partial shade and was lowest in full sunlight.

Transpiration rate

P. fulva exhibited the highest rates of transpiration in full sunlight ranging from 0.3 to 0.8, mmols $m^{-2}s^{-1}$ while *W. ugandensis* exhibited values ranging from 0.2 to 0.3 mmols m^{-2} s^{-1} (Figure 4). Transpiration was greater ($P < 0.01$) for *P. fulva* in full sunlight and partial shade than for *W. ugandensis*. However, in dense and moderate shades the rates of transpiration for the two species were not significantly ($P > 0.05$) different.

Water use efficiency

P. fulva in full sunlight had significantly ($P < 0.01$) higher water use efficiency (WUE) than *W. ugandensis* in the morning hours (Figure 5). *P. fulva* exhibited a mean WUE value of 2.3 μmols CO_2 $mmol^{-1}$ H_2O in full sunlight while a mean value of 1.5 μmols CO_2 $mmol^{-1}$ H_2O was recorded in *W. ugandensis*. In partial shade, *P. fulva* exhibited a mean WUE value of 1.8 μmols CO_2 $mmol^{-1}$ H_2O, while *W. ugandensis* recorded a value of 2.0 μmols CO_2 $mmol^{-1}$ H_2O. Under moderate and dense shades the two species showed no significant ($P > 0.05$) differences in WUE. Highest values of water use efficiency, like rates of photosynthesis, were somewhat higher in the morning hours and lower in the afternoon hours for the two species.

DISCUSSION

The results of this study showed that temperature was PPFD dependent and similar results were found by Chazdon and Fetcher (1984) in forest gaps of various sizes. Results on photosynthesis showed that these tree species differed in their light requirements. *P. fulva* showed enhanced capacity to utilise high PPFD associated with the full sunlight treatment, attaining higher photosynthetic rates when grown under full sunlight than did *W. ugandensis*. This was especially so during the morning hours than afternoon hours of the day. The slow growth of *W. ugandensis* in its natural environment (Kigomo, 1990) may result from the extremely low photosynthetic rates observed in this species. Although *P. fulva* grew and survived in shaded habitats, though with relatively low photosynthetic rates, it is apparent that sun flecks may contribute significantly to photosynthesis in this species when growing in shaded environments. On the other hand, *W. ugandensis* was adversely affected by strong PPFD. This may have ecological implications in that the species may be unable to utilise strong sun flecks in the forest environment and hence not compete well with species such as *P. fulva*. Seedlings of *W. ugandensis* appear to do poorly under a high radiation environment. Impairment of photosynthesis in *W. ugandensis* with high light may result from chlorophyll decomposition or reduced photosynthetic quantum efficiency (Björkman, 1981). This can result from strong radiation in plants that readily reach maximum rate of photosynthesis at low light intensities (Kreibitzsch et al., 1997) and then a decline in photosyn-

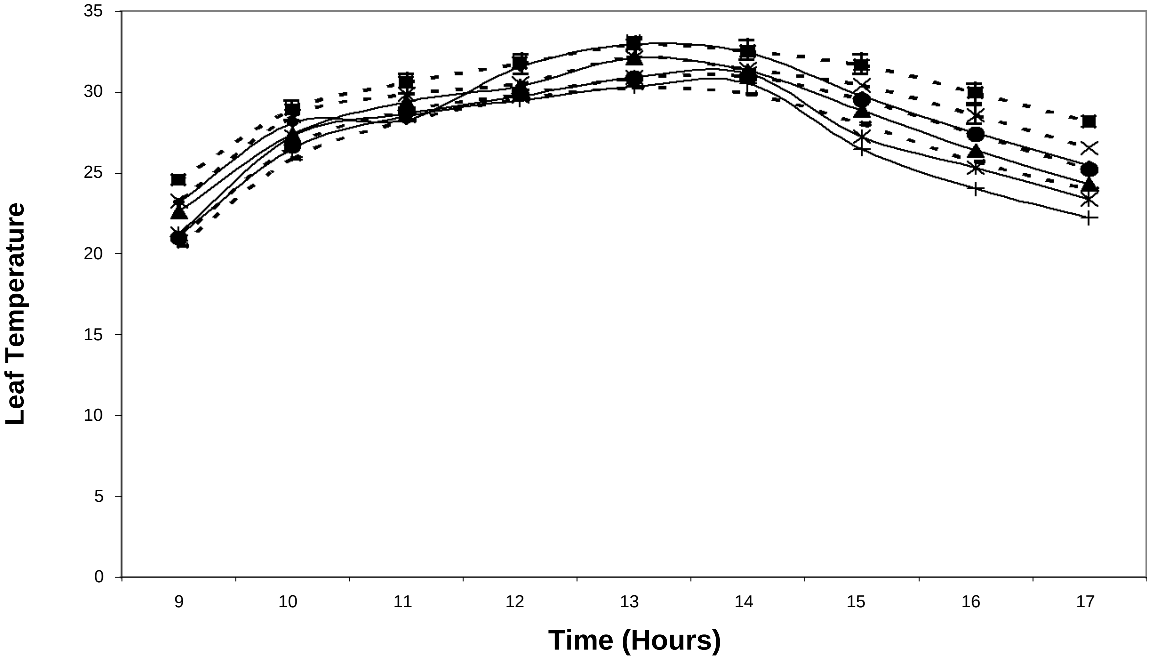

Figure 1. Mean diurnal trends in leaf temperature (°C).

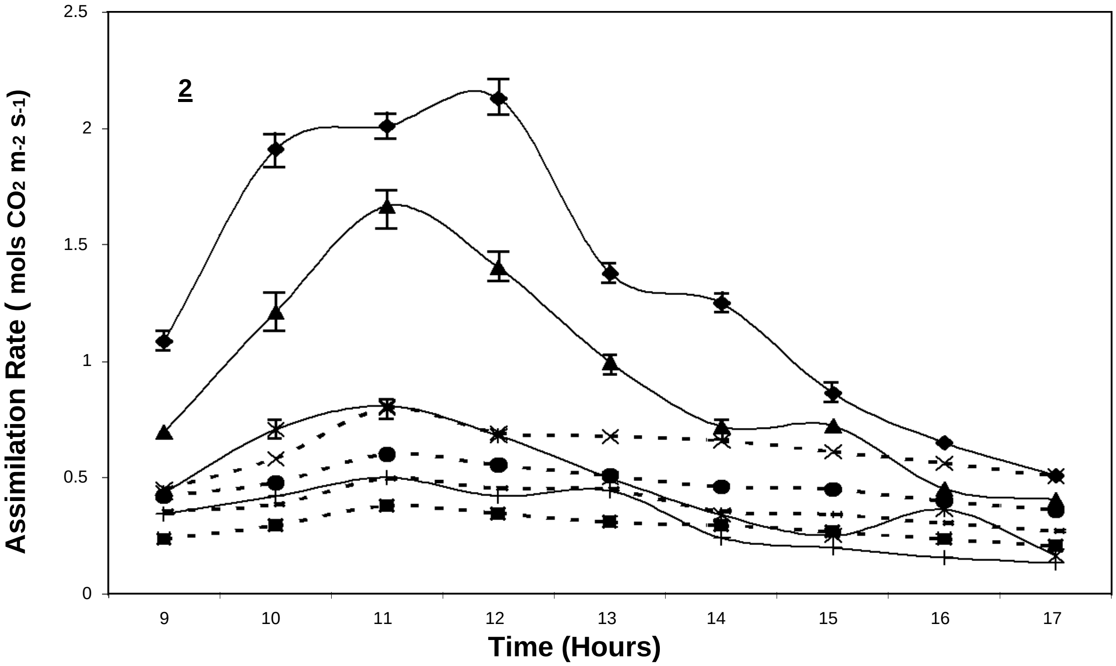

Figure 2. Mean diurnal trends in CO_2 assimilation rate (mols CO_2 m^{-2} s^{-1}).

thesis with increase in photon flux densities. This sensitivity is also found in many shade plants (Hariri and Prioul, 1978) although some are able to adjust their leaf photosynthesic rates to shade in natural canopies quite efficiently (Laisk et al., 2005). It appears that *W. ugandensis* responded to full sunlight exposure with tight stomatal closure, thus leading to low stomatal conductances and hence low rates of photosynthesis. The low photosynthetic rates of *P. fulva* under shade and the high photosynthetic rates under higher light levels show that seedling growth and photosynthesis in nursery and, therefore possibly in nature, is limited to some extent by light. It is

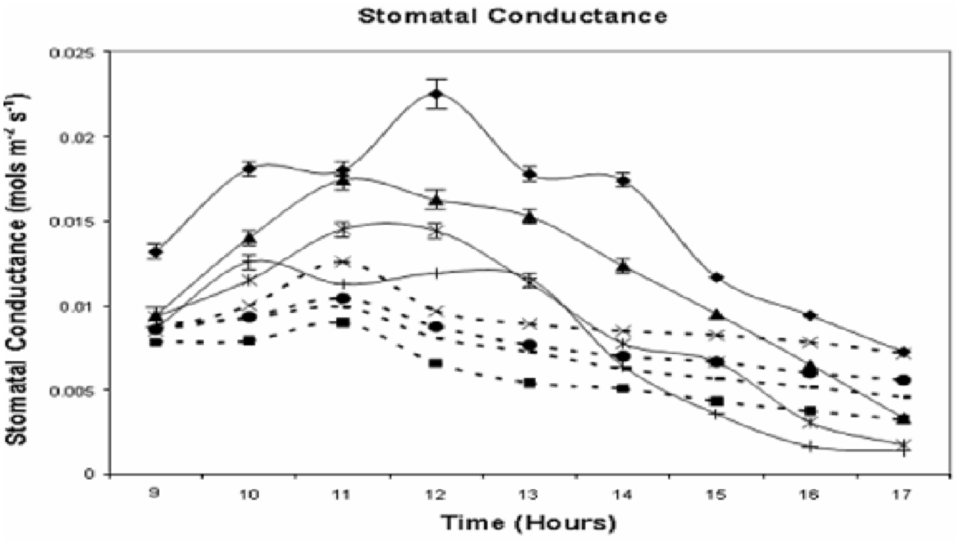

Figure 3. Mean diurnal trends in stomatal conductance (mols m^{-2} s^{-1}).

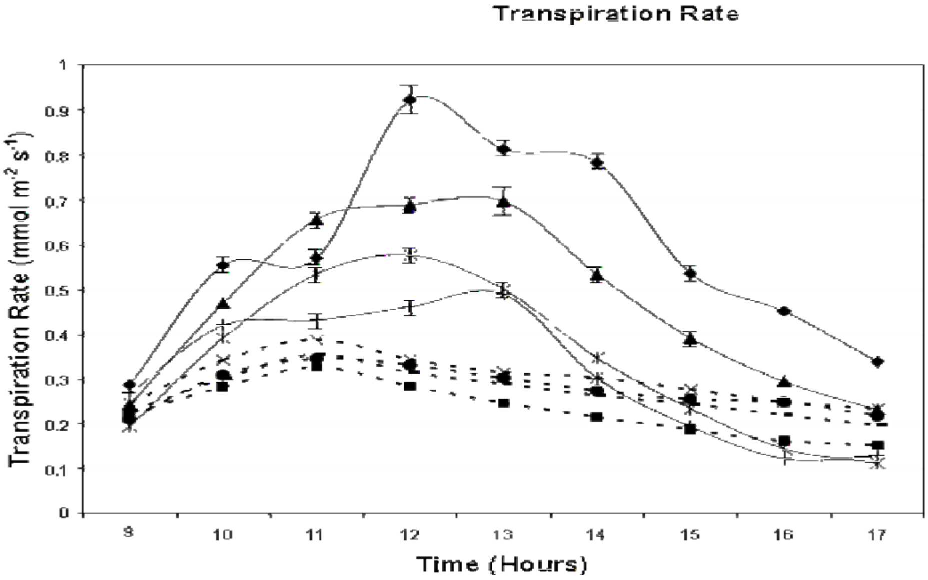

Figure 4. Mean diurnal trends in transpiration rate (mmol m^{-2} s^{-1}).

therefore possible that seedlings of *P. fulva* growing on the forest floor exist through sophisticated physiological and morphological adaptations for growth (plasticity) at low light levels (Vincent, 2006). This makes it possible for the seedlings to undertake efficient utilisation of a range of sun flecks for them to survive (Muraoka et al., 2003). Growth and survival of *P. fulva* in light levels below 1000 μmols m^{-2} s^{-1} light levels may indicate that apart from light, other factors in the field, especially competition for other resources, could also be important for establishment of this species. It is, therefore, necessary to carry out additional studies to determine other important limiting factors, particularly, the role of moisture and nutrients in determining the rate of seedling growth of this species in the forest. The adaptability of the maximum rate of photosynthesis to PPFD during growth of seedlings of *P. fulva* appears to have resulted from a change in stomatal conductance. *W. ugandensis* performed better under shade as supported by the higher rates of photosynthesis under the shaded regimes compared to full sunlight. Photosynthetic rates for *W. ugandensis* were reduced in full sunlight indicating that the species is shade tolerant. The suppressed CO_2 assimilation rates when *W. ugandensis* seedlings were exposed to full sunlight may have been

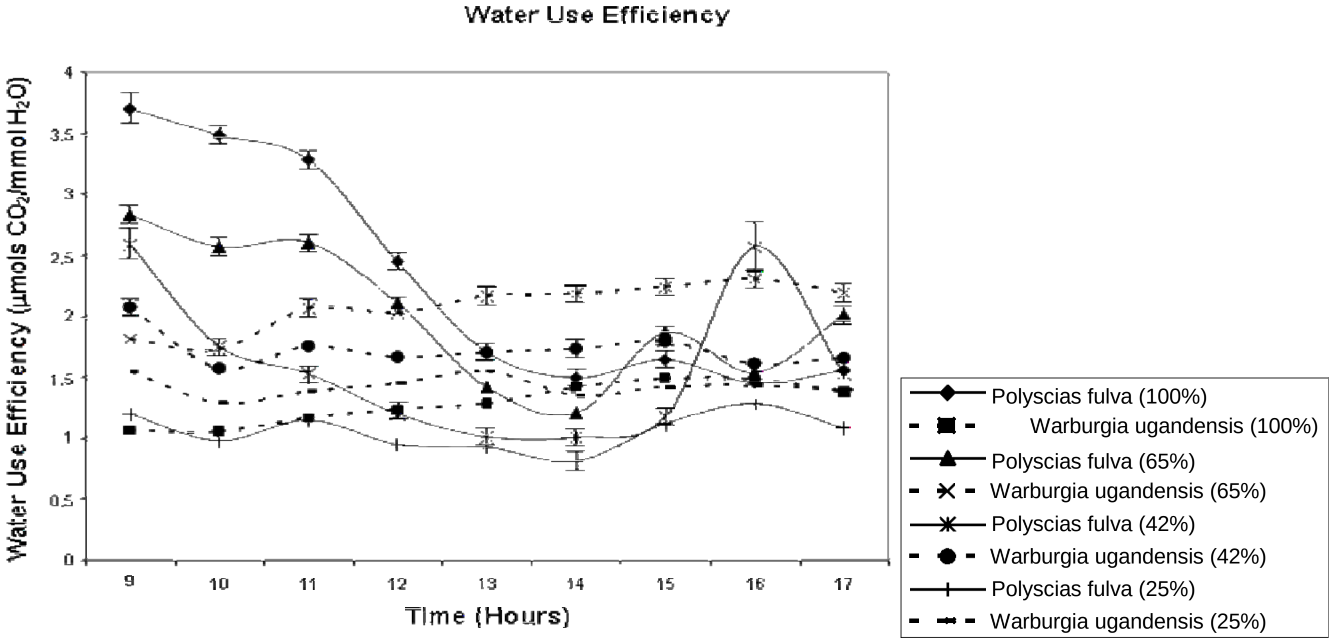

Figure 5. Mean diurnal trends in water use efficiency (µmols CO_2 $mmol^{-1}$ H_2O) for *Warburgia ugandensis* and *Polyscias fulva* seedlings under varying light regimes. Error bars represent 95% confidence interval of the mean.

been caused by high heat load, increasing leaf temperatures and respiration (Björkman, 1981; Terashima and Hikosaka, 1995) . High light may present the leaves of *W. ugandensis* with more photochemical energy than can be utilized for photosynthesis, overloading the photosynthetic process and resulting in lower CO_2 assimilation yield.

The ability of *W. ugandensis* to maintain a positive carbon balance in shade is not necessarily due to capacity to photosynthesize more rapidly than *P. fulva* in low light, but probably results from lower rates of respiration. For example, Loach (1967) found that shade tolerant and intolerant species have essentially equivalent rates of photosynthesis when grown in low light conditions. One study showed that a key to differential success in shade was a difference in dark respiration rate and therefore a lower light compensation point (Muraoka et al., 2003) allowing shade plants to maintain a positive carbon balance even at very low gross photosynthetic rates.

The transpiration rates of tree seedlings in our study were similar to those observed in other seedlings in south-east Asia grown under varying light regimes (Kriebitzsch et al., 1997). Although the two species showed no significant differences in WUE under moderate and dense shades, it is worth noting that *W. ugandensis* generally exhibited higher WUE than *P. fulva* under these conditions. This means that WUE in *W. ugandensis* may have been enhanced by shade. Therefore, *W. ugandensis* lost less water while fixing a mole of CO_2 under shade, but the reverse true for *P. fulva*. *W. ugandensis* appeared to close its stomata and had low rates of photosynthesis, stomatal conductance, transpiration rates and hence reduced WUE in full sunlight. The high WUE values observed in *P. fulva* when growing in full sunlight showed that this species is likely to out compete *W. ugandensis* in forest clearings and large gaps that are characterized by high PPFD and temperatures. Higher rates of photosynthesis and WUE in *P. fulva* than *W. ugandensis* in full sunlight indicate that *P. fulva* would accumulate more biomass with less water loss. It is, therefore, possible that seedlings of *P. fulva* would dominate those of *W. ugandensis* in clearings and large gaps of our forests. Based on these findings, *P. fulva* is recommended for planting in cleared forest areas and in agroforestry systems in East Africa where it occurs as an indigenous species..

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