PHOTOSYNTHESIS AND GROWTH OF SEEDLINGS OF TWO TREE SPECIES: *Polyscias fulva* AND *Warburgia ugandensis* UNDER DIFFERENT LIGHT REGIMES.

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DECLARATION

I DECLARE THAT THIS THESIS IS MY ORIGINAL WORK AND HAS NOT BEEN PRESENTED FOR A DEGREE IN ANY OTHER UNIVERSITY.

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DEDICATION

To my parents, John Theuri Wang'ombe and Magdalene Wanjiru Theuri for their moral, material, and spiritual support during my studies.

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Symbol	Parameter	Unit
A	CO_2 assimilation rate	μmol m^{-2} s^{-1}
E	Rate of transpiration	mmol m^{-2} s^{-1}
g_s	Stomatal conductance	mol m^{-2} s^{-1}
T	Temperature	^0C
SLA	Specific leaf area	cm^2g^{-1}
PPFD	Photosynthetic photon flux density	μmol m^{-2} s^{-1}
WUE	Water use efficiency	μmol CO_2 $mmol^{-1}H_2O$
DW	Dry weight	g
S/R	Shoot/Root ratio	gg^{-1}
LA	Leaf area	cm^2
Rubisco	Ribulose bisphosphate carboxylase/oxygenase	none

ABSTRACT

Seedlings of two indigenous tree species, *Warburgia ugandensis* Spraque subsp. Ugandensis (Canellaceae) and *Polyscias fulva* (Hiern) Harms (Araliaceae) were grown for five months at four different light regimes. The light levels were: dense shade (25% of full sunlight), moderate shade (42% of full light), partial shade (65% of full light). The full (100%) sunlight acted as the control. Measurements were made of assimilation rate (A), transpiration rate (E), stomatal conductance (g_s) and water use efficiency (WUE). Seedling height, leaf area changes of individual leaves, leaf survival and loss were determined after every fourteen days. Finally the seedlings were harvested and total dry weight (DW), leaf area (LA), specific leaf area (SLA) and shoot/root ratio (S/R) were estimated.

As expected the photosynthetic photon flux density (PPFD) varied in all the four light levels, with the control recording the highest. The mean diurnal PPFD in the four light levels were: dense shade 347 μmol m^{-2} s^{-1}, moderate shade 588 μmol m^{-2} s^{-1}, partial shade 918 μmol m^{-2} s^{-1} and full sunlight 1413 μmol m^{-2} s^{-1}. Leaf temperatures were higher in the full sunlight and lowest in dense shade. The mean leaf temperatures were: dense shade 27 ^{0}C, moderate shade 28 ^{0}C, partial shade 29 ^{0}C and full sunlight 30 ^{0}C. There was no significant ($P > 0.05$) difference in temperature for the two species in all the light regimes. The rate of photosynthesis was significantly ($P < 0.001$) higher for *P. fulva* than in seedlings of *W. ugandensis* when grown in full sunlight. The mean rate of photosynthesis in full sunlight grown seedlings of *P. fulva* was 1.4 μmol m^{-2} s^{-1} as compared with 0.3 μmol m^{-2} s^{-1} for *W. ugandensis*. Similarly in partial shade the rate of

photosynthesis for *P. fulva* was higher ($P < 0.01$) than in seedlings of *W. ugandensis*. The mean rate of photosynthesis in seedlings of *P. fulva* grown under partial was 1.0 μmolm^{-2} s^{-1}, while those of *W. ugandensis* recorded a mean value of 0.6 μmol m^{-2} s^{-1}. The rates of photosynthesis were not significantly ($P > 0.05$) different in seedlings of the two species when grown under moderate and dense shade. The mean rate of photosynthesis for *P. fulva* was 0.5 μmol m^{-2} s^{-1} and a similar value was observed for *W. ugandensis* under moderate shade. Under dense shade the mean rate of photosynthesis was 0.4 μmol m^{-2} s^{-1} for the two species. In general, seedlings of *P. fulva* reduced their photosynthetic rates in response to increasing shade. However, in seedlings of *W. ugandensis* photosynthetic rates increased under shade treatments.

Stomatal conductance, transpiration and water use efficiency were reminiscent of photosynthetic rates, showing high values for shade grown seedlings of *W. ugandensis* and full sunlight grown seedlings of *P. fulva*. Seedlings of *P. fulva* exhibited the highest stomatal conductances in full sunlight ranging from 0.007 to 0.02 mol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.003 to 0.009 mol m^{-2} s^{-1}. Stomatal conductances in *P. fulva* seedlings ranged from 0.003 to 0.002 mol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.007 to 0.01 mol m^{-2} s^{-1} under partial shade. Under moderate shade *P. fulva* seedlings showed stomatal conductance values ranging from 0.002 to 0.01 mol m^{-2} s^{-1}, while *W. ugandensis* gave values ranging from 0.006 to 0.01 mol m^{-2} s^{-1}. Stomatal conductance values under dense shade ranged from 0.001 to 0.01 mol m^{-2} s^{-1} and 0.005 to 0.01 mol m^{-2} s^{-1} for *P. fulva* and *W. ugandensis* respectively. Seedlings of *P. fulva* transpired more in full sunlight with values ranging from 0.3 to 0.8 mmol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.2 to

0.3 mmol m^{-2} s^{-1}. Transpiration rates ranged from 0.2 to 0.7 mmol m^{-2} s^{-1} for *P. fulva* as compared with 0.2 to 0.4 mmol m^{-2} s^{-1} for *W. ugandensis* under partial shade. In moderate shade *P. fulva* recorded transpiration values ranging from 0.1 to 0.6 mmol m^{-2} s^{-1} and 0.2 to 0.4 mmol m^{-2} s^{-1} for *W. ugandensis*. In dense shade *P. fulva* showed transpiration rates ranging from 0.1 to 0.5 mmol m^{-2} s^{-1} and 0.2 to 0.4 mmol m^{-2} s^{-1} for *W. ugandensis*. Seedlings of *P. fulva* showed higher water use efficiency in full sunlight than *W. ugandensis*. The mean WUE for *P. fulva* in full sunlight was 2.3 μmol CO_2 $mmol^{-1}$ H_2O and 1.5 μmol CO_2 $mmol^{-1}$ H_2O for *W. ugandensis*. In partial shade *P. fulva* exhibited a mean WUE value of 1.8 μmol CO_2 $mmol^{-1}$ H_2O, while it was 2.0 μmol CO_2 $mmol^{-1}$ H_2O for *W. ugandensis*. The mean WUE values were 1.6 and 1.3 μmol CO_2 $mmol^{-1}$ H_2O in moderate and dense shades for the two species respectively.

Seedlings of *P. fulva* exhibited the highest dry matter accumulation under full sunlight while the shade grown conspecifics recorded reduced dry weights. Seedlings of *P. fulva* showed a mean dry weight of 8.9 g in full sunlight as compared to 4.0 g for the dense shade grown conspecifics. Seedlings of *W. ugandensis* showed higher dry weights in shade treatments than in full sunlight. The mean dry weight was 0.6 g in full sunlight and 1.8 g in shade treatments for *W. ugandensis* seedlings.

In both species leaf number, leaf area, seedling height, shoot/root ratio and specific leaf areas were greater under shade treatments than in full sunlight. However, leaf loss was higher in the open than in the shade treatments for the two species. Leaf number was significantly ($P< 0.01$) higher in moderate and dense shade than in full sunlight and partial shade for the two species. The mean leaf number was 28 for *P. fulva* in full sunlight and 37 in dense shade. Seedlings of *W. ugandensis* gave a mean leaf number of 21 in full sunlight and 29 under dense shade. Leaf area of seedlings was significantly ($P< 0.001$) higher under shade treatments than in full sunlight for the two species. Seedlings of *P. fulva* recorded a mean leaf area of 238 cm^2 in the sunlight and 376 cm^2 under dense shade. *W. ugandensis* gave a mean leaf area of 33 cm^2 in full sunlight and 221cm^2 under dense shade. The mean shoot/root ratios for *P. fulva* were 0.97 and 1.8 gg^{-1} in full sunlight and dense shade respectively. For *W. ugandensis* the mean shoot/root ratios were 3.0 and 6.0 gg^{-1} in full sunlight and dense shade respectively. In *W. ugandensis* height increased by 36 mm in full sunlight as compared with 89 mm in dense shade. For *P. fulva* height increment was 20 mm in full sunlight and 38 mm under dense shade. Specific leaf area increased from 71 cm^2 g^{-1} in full sunlight to 198 cm^2 g^{-1} under dense shade for seedlings of *P. fulva*. For *W. ugandensis* specific leaf area was 106 cm^2 g^{-1} in full sunlight and 221 cm^{2}g^{-1} under dense shade. Increasing PPFD in *P. fulva* enhanced growth and photosynthesis, while shade promoted higher growth and photosynthesis in *W. ugandensis*. *P. fulva* was better adapted to growth in high PPFD than *W. ugandensis* because of its higher rates of photosynthesis at higher light intensities, above 1000 μmol m^{-2} s^{-1},while it was poorly adapted to growth at low light as a consequence of its lower rates of photosynthesis. *P. fulva* was also less well adapted to growth at low light intensity due to its relative inability to prevent a decrease in dry weight in low light intensity. *W. ugandensis* on the other hand was better adapted to growth at low light because of its significantly greater ability to prevent a decrease in its rates of photosynthesis and dry matter accumulation in low light intensity.

CHAPTER ONE

1.0 INTRODUCTION AND LITERATURE REVIEW

1.1.0 GENERAL DESCRIPTION OF TREES AND THEIR ENVIRONMENT

The tropical zone is biologically and ecologically the most productive region of the world. A high level of precipitation, abundant energy radiation, high temperatures and long growth periods ensure high net production of plant biomass. One characteristic is the many trees the region produces (Longman and Jenik, 1987).Tropical forests can no longer be taken for granted, whether as potential farmland, an exploitable reserve of timber or a source of new biological specimens. The tropical forests probably contain nearly half of all the world's animal and plant species, including many genera and families unknown in the rest of the world (Longman and Jenik, 1987). These forests also yield a multitude of useful products, ranging from saw logs and firewood to medicines and animal forage, which play substantial roles both in local economies and world trade. Thus, these remarkable assemblages of living organisms with their habitats are important to administrators, scientists, farmers and foresters.

Mankind has been destroying forests for millennia, ever since the discovery of agriculture (Williams, 1989). Forests are now being altered or being cleared more rapidly than at any time in the past. This is attributed to increase in population, and advanced technology worldwide. The Food and Agriculture Organization (FAO, 1988) reported that deforestation rates during the 1980s were higher than their earlier published accounts had suggested. Hence this relentless decline in the area of tropical forest has become more rapid, greatly exceeding natural regeneration plus replanting.

Deforestation of tropical lands can have both local and global consequences.

Locally, climate may become more extreme, soil may suffer physical and chemical deterioration, and hydrological balances may be disturbed. Massive deforestation, resulting in altered albedo and regional atmospheric water balances, could affect weather patterns, and there is particular concern at the possible contribution to global warming through the addition of green-house gases (for example carbon-dioxide, methane, etc) into the atmosphere from the burning or decomposition of the biomass (Myers, 1983). Perhaps the single greatest cause for concern over the loss of tropical forests is the considerable body of evidence that suggests that it is leading to unprecedented loss of the biological diversity that these forests contain (Myers, 1983; Ravan, 1987).

In Kenya, many areas of natural forests have been heavily disturbed through selective logging and clearing. The degraded areas vary in size from scattered canopy gaps to large abandoned clearings (Kigomo, 1990, Konuche; 1994). These areas need to be rehabilitated for both protective and productive purposes. There is a growing interest to rehabilitate the damaged areas by planting indigenous tree species (Kigomo, 1990; Konuche; 1994). However, there is little experience on silvicultural management of these species and there is also inadequate understanding of their ecological requirements (Konuche; 1994).

Indigenous, local species are native to a region or country. For example *Warburgia ugandensis* Sprague subsp. Ugandensis and *Polyscias fulva (Hiern)* Harms. are indigenous species in Kenya. Local species have numerous advantages: they are adapted to the local environment, provide habitat for wildlife and are able to regenerate naturally. Moreover, they have generally evolved considerable resistance to local insect pests and diseases. Therefore, in many circumstances they will be equal to or better than exotic species for the purposes specified.

Examples might include protective afforestation or situations where conservation of native flora and fauna is a major consideration (Evans, 1972). Indigenous species are also usually preferred by local people for subsistence, environmental, medicinal or cultural reasons (Bass, 1992).

Growth of planted indigenous species may be slower than exotic species, but this will not matter much if wood yield is not of primary importance. But this may change if it is necessary to attain soil cover rapidly, in which case, careful attention should be paid to initial site preparation and suppression of competing vegetation. If this is done, native species can show much faster growth than they would under their normal natural conditions. *Araucaria cunninghamii* and *Araucaria hunteinii* for instance, have been grown successfully in large plantations in Australia and Papua New Guinea, while species of *Terminalia* and *Triplochiton* have adapted well to plantation development in Africa (Shepherd, 1986).

In addition to being slow growing, many of the different genera of tropical hard woods are also very difficult to establish in production plantations. This is largely because their biology and ecological requirements are not well understood and silvicultural knowledge concerning how to handle them is inadequate (Zobel *et al.*, 1987). Furthermore, the tropical heavy hard wood species with desirable timber are late secondary or climax species, whereas for large-scale plantations the most useful species have so far tended to be invaders of gaps, pioneers, or early secondary species. Most pioneers and many secondary species are fast growing and therefore are important in agroforestry. This is because they retain nutrients and preserve watersheds. These species also help the recovery of forest structure after disturbance (Bazzaz *et al.*, 1984).

A dense forest canopy drastically modifies the quantity and quality of the solar energy incident on the forest floor (Kwesiga and Grace, 1986). The changes in spectral distribution of daylight that occur in vegetational shade and their effects on tree seedlings have rarely been studied experimentally, even though their probable importance has frequently been discussed by ecologists (Coombe, 1957; Evans, 1969). Canopy gaps and clearings are characterized by increased irradiance, temperatures and vapour pressure deficits (Fetcher *et al.*, 1984). Such areas are also rapidly invaded by weedy species, which may retard forest trees regeneration.

The rate of growth and pattern of development of seedlings depend on the light regime among other environmental factors (Kwesiga *et al.*, 1986; Kigomo, 1990, Olusegu *et al.*, 1992). In controlled experiments, plants grown in the absence of light but provided with a source of nutrients from storage organs (for example seed, bulb and tuber) are yellow and have greatly elongated spindly stems (Wareing and Phillips, 1981). The same plants, when provided with light, develop green colour associated with development of chlorophyll and the initiation of photosynthesis, and assume the normal stem structure. This means that light is an important factor for growth of a particular plant. The capacity of plants to intercept and use radiant energy for photosynthesis determines the availability of photosynthates for growth. Photosynthetic rates increase or decrease as radiant flux changes, consequently the growth of a plant, especially those that require or tolerate full sunlight, follows the solar radiant energy curve (Kwesiga and Grace, 1986). However, radiation is not only a source of energy (photoenergetic effect), it is also a stimulus governing development (photocybernetic effect), and occasionally also a stress factor (photodestructive effect) (Larcher, 1995).

1.1.1 Trees Light Requirements

Tree species differ in their requirements for light (Richards, 1952; Whitmore, 1984) and respond differently to environmental conditions associated with canopy gaps of different sizes (Denslow, 1980). Pioneer species show enhanced capacity to utilize high irradiance in gaps and clearings (Bazzaz and Picket, 1980). These species are highly amenable to silvicultural management and can help in recovery of forest structure after disturbance (Kigomo, 1990).

There are more than a quarter of a million species of higher plants, and very few of these have ever been the subject of detailed quantitative study (Bazzaz, 1984a). Although it is widely accepted that trees differ greatly in their light requirements, for example, there is little research, which has been done to determine the optimum light climate for seedling growth of specific species, for example, in the case of *Warburgia ugandensis* and *Polyscias fulva*. This is in fact common as far as the observations on the light response curves of seedlings, which have been raised in contrasting light regimes. Such observations will be useful if we are to interpret the pattern of succession that have been reported in tropical rain forests (for example Bazzaz and Carlson, 1984) and are vital in any attempts to construct mathematical models of standard development to be used in forest management.

Our knowledge on the response of seedlings to new light climate and their capacity to compete with each other is sparse in relation to their importance as timber trees, although foresters working in the tropics have long recognized "light demanders" and "shade tolerators" (Taylor, 1960). At a physiological level, two major groups of characteristics are likely to determine whether or not a tree seedling is a light demander or a shade tolerator. The first group relates to the effect of light on morphogenesis, including the growth of leaf number and the expansion of the stem and the leaf area. The second and more widely considered group of characteristics relates to photosynthesis. From work on herbaceous plants and trees it is known that light demanding plants generally display light-saturated rates of photosynthesis that are higher than those of shade tolerant species, and that the two types are distinct in several other respects (Boardman, 1977; Björkman, 1981). To some degree the morphogenetic and photosynthetic responses are related to each other. For example, leaves which have been grown at low photon flux density have an elevated specific leaf area, usually as a result of being thinner, and for this reason alone they are likely to display different photosynthetic characteristics (Björkman, 1981).

There are very few studies on the photosynthetic characteristics of tropical tree species. Growth analysis also has not been frequently used in the study of tropical trees. Some investigators (eg. Oberbauer and Strain, 1986; Fetcher *et al.*, 1983) have combined growth analysis with measurements of photosynthetic rates. These approaches will undoubtedly result in a better understanding of the control of productivity in tropical forests and the strategies of individual species.

1.1.2 The Forest Light Environment

Solar radiation is the primary source of energy on earth, and light is a directional resource, supplied from above, so that taller plants obtain a greater proportion of the light. The simplest indicator of the ability of trees to compete for light is their height at maturity (Givinish, 1982). Light attenuation occurs as light passes through the forest vegetation. The light regime of the tropical rain forest floor is characterised by a very low photon flux density and a low red:far-red ratio (Richards, 1952; Evans, 1956; Whitmore, 1965, 1975; Björkman and Ludlow, 1972; Longman and Jenik, 1974; Vazquez-Yanes, 1980). The attenuation of radiation in a stand of plants varies greatly and is determined mainly by leaf area index, leaf architecture, and leaf absorbance characteristics (Bazzaz and Pickett, 1980; Larcher, 1995). The attenuation of radiation in a forest is in accordance with the Lambert-Beer Extinction Law.

The strata that affect vertical light distribution are more recognizable in forests dominated by one or a few species (Richards, 1983). Kira *et al.*, (1969) found that, in a secondary forest in peninsular Thailand, the leaf area index was highest at 20-35m. In a young mixed dipterocarp forest at Pasoh in Malaysia there were two maxima: one at 20-35m and another below 5m above ground (Kira, 1978). Detailed analysis of the light energy profiles in tropical forest in the Far East can be found in Yoda (1974), Aoki *et al.* (1975), and Sasaki and Mori (1981). It important to note that such profiles of light energy distribution are unavailable for our Kenyan forests.

Chazdon and Fetcher (1984a) compared the light environments in a 0.5 ha clearing, a 400meters gap, and a heavily shaded understorey at La Selva, Costa Rica. Photosynthetic photon flux density (PPFD) reached a peak of over 1000 μmol m^{-2} s^{-1} in the clearing, but only 90 μmol m^{-2} s^{-1} in the understorey. However, in a dipterocarp forest, Sasaki and Mori (1981) showed that diffuse light remains relatively stable in spite of significant fluctuations in light levels in the open. Thus, the understory plants very likely function best when sunflecks contribute significantly to total daily PPFD. Total daily PPFD in clearings was generally higher in the dry than in the wet season. Many ecologists and physiologists have estimated relative illuminance in the under-growth to be lower than, even to a fraction of 1%. For example, Bünning (1947) found that the relative light intensity in the interior of an

Indonesian rain forest was only 0.2-0.7%; Carter (1934) reported very similar values in the Mora-forest of Guyana, as did Cachan (1963) in a rain forest in the southern part of Ivory Coast. Yoda (1974) gave 0.3% as a mean relative illuminance in an undisturbed rain forest of West Malaysia. Chachan and Duval (1963) and Chachan (1963) were among the first to record vertical gradients of illuminance in an entire profile of a tropical forest. They were able to measure the light intensity from the top of the emergent trees down to the forest floor. Their results showed a profound screening effect of the closed canopy in the middle layer, while the illuminance at 46m at the top of the forest was 1000 μmol m^{-2} s^{-1} it was 250 μmol m^{-2} s^{-1} at 33m, and only 8μmol m^{-2} s^{-1} at lm from the forest floor, 0.8% of that above the forest.

Another aspect of the forest's light environment is the shift in spectral quality as the light passes through the canopy. Direct solar irradiation, and the reflection, absorption and transmission processes of the foliage, twigs and stems affect the quality of the light within the canopy and near the ground in tropical forests. The foliage absorbs red over far-red light so that the light near the forest floor may have little red wavelength light. This filtering has been shown in several rain forests in neotropics, Africa, Australia, and Malaysia (Chazdon and Fetcher, 1984b; Sasaki and Mori, 1981; Pearcy, 1983 and Bazzaz and Pickett, 1980). Lee (1987) showed that the ratio of red to far-red light is closely correlated to the percent of full sunlight at different points in the forest. The low R/FR ratio occurring within the forest appears to be responsible for numerous morphogenetic processes, notably as a factor maintaining the dormancy of seeds in some colonising species. Vazquez-Yanes and Smith (1982) showed that R/FR ratio much more than the light intensity affect germination of *Cecropia obtusifolia* and *Piper auritum* seeds on the surface of the soil in the forest.

Sunflecks are another important source of diversity in the illuminance of the forest interior. Sunfleck-light is composed of direct sunlight, sunlight reflected from vegetation, diffuse skylight and diffuse skylight filtered by the vegetation (Morgan and Smith, 1981). The sunflecks move as the sun changes position, and as the wind or ascending air current disturbs the leaves. Their spectrum and flux density vary considerably over their ever-changing positions. Thus, the leaves must be adapted to utilising very low flux densities, but also tolerating and using the high fluxes in sunflecks from direct solar beams (Kwesiga, 1985). It has been reported, for example, that stomata in seedlings of *Shorea leprosula* and *Shorea maxwelliana* open within seconds of the arrival of a sunfleck (UNESCO, 1978). The light intensity near the forest floor thus depends partly on the structure of the canopy, but also on the angle at which the sun's rays are striking its surface.

Tropical forests are three-dimensional structures, their patterns of radiation and illuminance also vary horizontally. A dim phase occurs where there is 'normal' thickness of crowns, tree trunks, dwarf trees and seedlings. A light phase is found where there are small gaps created by fallen trees or broken limbs of emergent trees, with many seedlings germinating and sprouting. A dark phase is present where there are thickets of dying branches and living climbers which have fallen down from the upper layers without disrupting the canopy seriously (Longman and Jenik, 1987). The size of the light phase gap affects both the intensity and the spectral composition of the extra sunlight. For many tropical tree species light gaps are critical as establishment sites for seedlings (Richards, 1952; Whitmore, 1975; Denslow, 1980; Hartshorn, 1980 and Pickett, 1983). Light intensity and spectral composition also change seasonally for various reasons, such as the shedding of leaves and the incidence of hazy periods and particularly of clouds.

Mature tropical rain forests are dynamic communities with a high frequency of natural disturbances (Whitmore, 1978). The patchy and discontinuous nature of the canopy results in highly variable patterns of light availability in understorey and gap environments. Large disturbances, such as multiple tree falls, completely alter the microclimate. The canopy gaps created by treefalls are a major source of environmental heterogeneity of the tropical forest understorey (Brokaw, 1985a). The forest, therefore, may be considered a mosaic of patches in different stages of growth, with each stage receiving different amounts of light and other resources (Richards, 1952; Bazzaz and Pickett, 1980; Denslow, 1980).

In addition to increased incident light levels (Chazdon and Fetcher, 1984a), gap microclimates are generally characterised by lower humidity, higher temperatures (Schulz, 1960; Fetcher *et al.*, 1985), and higher moisture levels (Vitousek and Denslow, 1986, Uhl *et al.*, 1988) than the adjacent forest understorey. Tree-fall clearings are known to be important for growth and reproduction of many rain forest trees (Hartshorn, 1980; Clark and Clark, 1987b) and competition among seedlings and saplings within a gap may influence which species will occupy space in the canopy. Studies of sapling growth rates in gaps (Brokaw, 1987), growth responses in different light regimes (Bazzaz and Pickett, 1980; Pearcy, 1983, Chapin *et al.*, 1986; Chazdon, 1986), and the demography of tropical trees (Clark and Clark, 1985; Pinero and Sarukhan, 1982), suggest that species might partition establishment sites within this complex environmental mosaic through several different mechanisms. These mechanisms include (1) variation in propague dispersion through differences in seed longevity, abundance, and breadth of dispersal (Augspurger, 1984a, b, c) (2) variation in the relative allocation of resources to growth, reproduction, and defence (Chapin, 1980; Coley 1983, Coley *et al.*, 1985), and (3) variation in physiological adaptations for acquiring light and nutrients and tolerating heat and moisture stress (Bazzaz and Pickett, 1980; Pearcy, 1983; Chapin *et al.*, 1986).

Several important descriptions of the distribution of light in tropical rain forests throughout the world have been published (Evans, 1969; Ashton, 1978; Björkman and Ludlow, 1972; Yoda, 1974). Despite differential variations in the average under-storey PPFD of different tropical forests (Pearcy, 1983, Chazdon and Fetcher, 1984a; Chazdon, 1986), certain patterns are evident. The substantial three-dimensional variation in the light environment is largely due to the distribution of the vegetation. Different parts of individuals may simultaneously experience vastly different light environments. This is because of sunflecks, a shoot or a single leaf may experience rapid shifts from very low to very high light levels. This shift affects carbon-gain capabilities, and the growth and resource allocation of seedlings (Pearcy, 1983).

1.1.3 Role of Plant Morphological Factors on Primary Production.

The plants' architecture plays a significant role in the growth and production of tropical trees. The general growth form and branching patterns of tropical trees have been treated using the Halle and Oldeman growth models (Halle *et al.*, 1978). Different plant communities intercept different amounts of light depending on the density of the canopy. Chazdon (1985) worked on leaf display, canopy structure and the pattern of light interception in two understorey palms in Costa Rica. The study found that seedlings of the two species did not differ in light interception efficiency. However, adults of *Geonoma cuneata* had higher light interception efficiency than did those of *Asterogyne maritima* despite the fact that the latter had longer leaves, more leaves per plant and, therefore, a greater total leaf area than the former. The decreased efficiency of adult *A. maritima* crowns was largely due to increased proportion of pendent leaves relative to the adults of *G. cuneata*. In both species, there was relatively little self-shading because of the even distribution of leaves around the main axis. Studies of this kind, together with photosynthetic measurements and growth analysis, will be essential in the understanding of the mechanisms of adaptation of species to tropical forest environments.

Leaf area index (LAI) is a useful measure of canopy density and has been shown to be an important factor influencing primary production in several plant communities (Brougham, 1960; Loomis *et al.*, 1967). This influence is primarily due to the amount of light intercepted by the canopy and used in photosynthesis. High LAI values usually does not result in high production in most plant communities. This is because of light attenuation and self-shading within the plant canopy due to canopy depth and leaf architectural arrangements (Loomis *et al.*, 1967). Horizontally arranged leaves result in the greatest loss of PAR in the plant canopy due to absorption by the leaves in the upper plant canopy while vertically arranged leaves allow deeper canopy penetration of light.

The high photosynthetic rates and fast growth of pioneer species are generally associated with the development of low-density wood, this is one of the distinguishing characteristics of pioneers. Shukla and Ramakrishnan (1986) showed that fast growth over a longer period of time resulted in sparse branch arrangement and greater leaf exposure in two pioneer tree species in India. The higher proportion of far-red light in the understorey influences plant architecture as well. Sasaki and Mori (1981) showed that far-red stimulated internode elongation of some dipterocarp seedlings and restricted their root growth. Under low light conditions, internode elongation was greater relative to diameter growth. Thus, the ratio of height to diameter was higher than under high light conditions. Leaves from different canopy layers or heights exhibit light response curves of varying degree depending on the degree of shading by leaves in the upper layers. Boller and Nosberger (1985) and Theuri (1995) demonstrated that bottom leaves have low rates of net photosynthesis and light saturation, while unshaded upper leaves appeared not to be light saturated. Mid layer leaves showed an intermediate response. The distribution of irradiance over the individual leaves of the plant canopy and the photosynthetic response of these leaves to irradiance is known to influence CO_2 flux into a canopy (Sheely and Cook, 1977).

1.1.4 Light as an Ecological Factor.

Variation in the light environment in tropical forests affects plant germination, growth, and reproduction. The interaction between the vegetation and the environment generates a very complex and continually changing ecological setting. It is important to recognise that plants as individuals may experience much variation in the levels of resources, such as light, as they grow from small seedlings to mature, reproducing individuals, and that parts of the same individual may simultaneously experience different environments (Longman & Jenik, 1987). The short-wave solar radiation is important in photosynthesis, especially the region between 400 and 700nm known as photosynthetically active radiation (PAR). The PAR plays a major role in the growth, survival, and regeneration of tropical rain forest plants (Richards, 1952; Schulz, 1960; Longman and Jenik, 1974; Whitmore, 1975). Data on photosynthesis and growth are lacking for most rain forest species (Mooney *et al.*, 1983). Ecologically both the spectral quantity and quality are important. Visible radiation sources in general have been a powerful factor in the evolution of forest plants, with broad differences in growth form and physiological adaptations between light demanding (heliophilous) and shade-bearing (sciophilous) species (Richards, 1983). The euphotic layer of the forest bears heliophilous epiphytes such as orchids, bromeliads and lichens. It is the most productive part of the forest. The oligophotic layer is characterized by low relative illuminance. In the lower tree layer, epiphytes are either less numerous or are represented by sciophilous species, such as ferns, mosses and liverworts. In the oligophotic layer strong competition for light takes place and various adaptations of plants are found. The minimal light supply near the ground surface is reflected in the low development of plant biomass and in the stunted growth form of seedlings, saplings and pigmy trees in this layer (Longman and Jenik, 1987).

A viable seed is one which will germinate and develop into a plant given favourable conditions, provided any dormancy that may be present is removed (Ellis, 1984). Upon germination, success in establishment depends on the prevailing environmental conditions. Among these is the amount of light available at the time of germination and thereafter. Seedlings are a sensitive stage in the plant life cycle, yet we do not have a good understanding of how specific traits of individual species and characteristics of the environment affect seedling growth (Jurik and Pleasants, 1990).

The response of a plant to its environment often includes changes in its morphology or physiology in addition to changes in the size or the number of its parts. Many species have the ability to produce thin "shade leaves" when growing under a forest canopy, and smaller, thicker "sun leaves" when growing in the open. Increased levels of carboxylating enzymes usually match this morphological response and decreased concentration of chlorophyll in sun leaves (Kwesiga and Grace, 1986).

Few studies have documented the light requirements of the seedlings stages of tropical species (Nicholson, 1960; Lebron, 1979; Sasaki and Mori, 1981; Augspurger, 1984; Fetcher *et al.*, 1983, Konuche, 1994). Murray and Nichols (1966) investigated the effects of different levels of artificial shading and full sunlight on growth of cocoa (*Theobroma cocao*) seedlings under field conditions. They observed that the relative growth rate was highest under moderate shade with irradiance levels of 25% to 50% of full sunlight. Light levels below and above these resulted in reduced growth and plants tended to be bushy. Huxley (1969) reported similar observations for coffee seedlings.

Inove (1976) examined the growth behaviour of *Cedrela odorata* L. and *Cedrela fissilis* (Vell.) in the young stage of development as a function of light. The investigations revealed that the growth of the valuable shade tolerant wood of the tropical and sub-tropical rain forests of Latin America is clearly dependent on the amount of radiant energy. This factor can be influenced by silvicultural measures, for example, by growing under shade. As the radiant energy increase the amount of shade should increase if the same growth is to be achieved as when there is little radiant energy. For this reason the two *Cedrela* species, for example, are suitable as additions to secondary tropical and sub-tropical forests if planted in the shade.

Tomboc and Basada (1978) found that *Shorea contorta* survived better under the canopy but grew faster and had more leaves in the open. In their extensive experiments with dipterocarp seedlings in shade houses, Mori (1980) and Sasaki and Mori (1981) showed how different species responded differently to light and its alteration. For most species the maximum height, shoot weight, stem diameter and root weight was attained at progressively greater illuminance.

Seedlings raised in a nursery for transplanting were heaviest and tallest at 35-60% relative light intensity, varying between species. But the shoot/root weight ratio dropped continuously with increasing illuminance and 50-70% was necessary to produce a seedling with big enough root relative to shoot to have a high chance of surviving the shock of being transplanted to the forest.

One of the greatest hindrance of successful natural regeneration in tropical forests lies in somewhat obscure field of germination (Ellis,1984).Inter-relationships between environmental factors affects the young plants ability to gain a foot hold, which means that only in rare cases is there natural regeneration. Artificial regeneration is then essential. It is precisely here that the lack of knowledge of the ecophysiological behaviour of individual tree species and of the dynamics of natural tropical forest is particularly felt. As regards the cultivation of indigenous species almost all questions that need to be answered to ensure optimum development of the plant in the nursery and successful transplanting, for example, level of shading, type and composition of substrate, age of transplanting, plant containers, depending on the particular individual species remain unanswered. This is true in case of *Warburgia ugandensis* Sprague subsp. ugandensis and *Polyscias fulva* (Hiern) Harms.

The quantity and quality of solar radiation received by a plant community influences primary production (Idso and Baker, 1968; Macharia, 1981; and Brewster, 1982). Due to the fundamental role of photosynthesis in plant metabolism, light is one of the most important environmental factors. Brewster (1982) found that in onions dry matter yields were linearly related to the total radiation intercepted during bulb growth. In general, species preferring open and sunny habitats have higher maximum photosynthetic rates than species preferring shady habitats. Within a species, shade-growing seedlings generally have lower light saturated photosynthetic rates than do sun-grown seedlings. Exceptions do occur, for example, *Hymenea parviflora* and *H. courbaril* (Langenheim *et al.*, 1984). This is also true for leaves on the same individual (Oberbaurer and Strain, 1986). Bazzaz and Pickett (1980) and Bazzaz (1984a) have reported that understorey species have lower photosynthetic rates than do primary canopy species and those in turn have lower rates than pioneers.

Langenheim *et al.* (1984) worked with five species from tropical forests grown at 100% and 6% of full sunlight. They found that the shade-grown seedlings had lower compensation points, higher quantum yields and lower respiration rates per unit area than did those grown in full sun. Light saturated photosynthetic rates of the seedlings grown in sun were not significantly different (except for one species) from seedlings grown in the shade. In the forest, both sun and shade leaves may be found on the same individual. Their carbon-gain capacities and contribution to the total carbon budget of that individual are probably different. Oberbauer and Strain (1986) compared seedling leaves to leaves from three heights in the canopy of *Pentaclethra macroloba*. They found that changes in leaf characteristics along the canopy gradient paralleled changes that could occur in seedlings grown on a light gradient. Individuals of the same species grown in full and 25% sun had equal biomass. Switching seedlings between these two light environments had no effect on growth. However, individuals switched from full and 25% sun to 1% sun had a negative CO_2 exchange rate and suffered leaf abscission resulting in negative growth. Plants switched from 1% to full sun showed severe photoinhibition and leaf damage.

Oberbauer and Strain (1984) studied the photosynthetic capacity of seven tree species in a Costa Rican rain forest. They found that light-saturated photosynthetic rates were related to preferred light environment in the field. Plants preferring heavy shade had a mean photosynthetic rate of 6.8 µmol m^{-2} s^{-1}, those in canopy gaps 11.3 µmol m^{-2} s^{-1} and the species from large clearings 27.7 µmol m^{-2} s^{-1}. Light saturation of plants from the clearings occurred at PPFD greater than 1000 µmol m^{-2} s^{-1}, while those from shadier environments reached light saturation at much lower PPFD. Leaf-level and whole-plant carbon gain is influenced by leaf life span. The leaf life span is estimated to be 6 to 9 months in deciduous species and little more than 1 year in evergreen ones. Phenology of leaf expansion ranges from almost continuous in some pioneer species to discontinuous flushes in mature phase species (Coley, 1983).

1.1.5 Growth and Environment

The term growth is applied to quantitative changes occurring during plant development and it may be defined as the irreversible change in the size of a cell, organ or whole organism (Wareing and Phillips, 1981). Plants grow, reproduce and die within an environment defined by both biotic and abiotic parameters. Their phenologies, forms, biomass and seed yields can be explained as responses to their environment. Plant form cannot be divorced from the dynamic processes of growth that generate it. All plant growth derives from highly localised meristems, where there is rapid cell division and tissue differentiation. Primary growth results from the activity of terminal meristems, which extend the root and the shoot axes.

In primary growth, the root and shoot meristem give rise to an axis and an array of lateral primordia. In trees these lateral primordia differentiate into leaves and their associated axillary meristems, arranged in a characteristic, geometric pattern known as 'phyllotaxy' The axillary meristem either begins creating new shoots immediately (as in many tropical trees), or they first lie dormant within scale leaves, forming a bud (as in temperature tree).

The points on the stem where leaves and their buds are located are known as internodes. The elongating terminal meristem of a woody dicot shoot leaves behind it a ring of dividing cells, which allow the twig to increase in girth. These lateral meristems form two cylindrical zones of cell division termed the vascular cambium and the bark cambium, which produce tissue collectively known as secondary growth (Esau, 1977).

Different species of plants differ in their responses to their environment over a wide range, and in many different ways (Hughes and Evans, 1962). It is, therefore, not a priori reason to suppose that conditions, which produce optimum growth in *Warburgia*, are the same for *Polyscias*, despite the fact that the two species are found in nature both growing in the same climatic regions. It is also important to note that the conditions for optimum growth of a particular species are not necessarily the same at all parts of the life cycle (Esau, 1977). The relationship between the different environmental factors and the reactions of the plant are rarely linear, although one does find a very close approach to linearity over a specific range. For example, Hughes (1965) found a linear relationship between rate of increase of the total dry weight of a plant per unit leaf area and total daily visible radiation when working with *Impatiens parviflora*. But in most cases a complex relationship, which may take a variety of forms, is observed. For example, Hughes and Evans (1962) observed a sigmoid relationship between mean total daily visible radiation and unit leaf rate. Therefore, a study of some aspects of growth such as the rate of increase of dry weight per unit leaf dry weight would show that it changes relative little with total daily visible radiation, a fall in one component compensating for a rise in the other.

1.1.6 Growth of Leaves.

Many species have demonstrated considerable capacity to vary morphology and physiology of leaves provided in different light environments (Fetcher *et al*., 1983, 1987; Langenheim *et al*., 1984). Growth rates of leaves are often rapid, especially at the time when they are about half their final size. Leaflets of *Amherstia nobilis* can increase in length by 18mm per day, and petioles by 41mm per day (Schimper and Von Faber, 1935). The rachis of the large fern *Angiopteris evecta* can extend at 90mm per day. Coster (1929) found that leaf growth rates of *A. nobilis* and *A. evecta* two species were lower in the day than at night when the weather was sunny, but not on a cloudy day.

In the great majority of species, leaf growth is determinate, so that the duration of its period of expansion is limited. Nevertheless, in some species with large compound leaves, each one may take several weeks to complete its growth. In a few cases, such as *Guarea guidonia* and *Chisocheton* spp, the leaf tips remain meristematic, producing new leaflets continuously or periodically over a longer period of time (Steingraeber and Fisher, 1986). Leaf growth usually involves both cell division and cell enlargement, and the final size reached, and sometimes also the leaf shape, can be affected by a range of external, internal and genetic factors (Longman and Jenik, 1987).

Shading commonly influences leaf development, generally increasing the rates of growth and final sizes, and sometimes modifying leaf shape. In cocoa and coffee, for example, the leaves that expand in full sunlight are often smaller and yellowish-green, those growing in shade tend to become larger and darker green (Longman and Jenik, 1987).

1.1.7 Leaf Senescence and Abscission

A leaf typically reaches a peak of photosynthetic capacity around the time that expansion ceases, thereafter showing a gradual decline. Sooner or later a point is reached when it suddenly begins to turn yellow, brown, or less commonly red, and is then actively shed from the tree by completion of a separation layer in the abscission zone at its base. This change of colour is termed senescence, and it appears to be mediated by alterations to the balance of several endogenous growth substances. It is the terminal irreversible phase in the functioning of the leaf (Addicott, 1982), which signals the wholesale breakdown of chlorophyll, ribonucleic acid and protein, and the rapid translocation out into the stem of some but not all of its organic and inorganic nutrients.

A very wide range of factors appear to promote leaf-fall in trees, including lowered light intensity, changed temperature and photoperiod, mineral nutrient deficiency and water stress. Older leaves are much more likely to be abscised than those that have recently expanded are. Leaf fall have many ecological implications, for example, regarding the nutrient and water status of the soil, the photon flux densities reaching lower tree layer, and the amount available to herbivores (Longman & Jenik, 1987. The partial or complete loss of old foliage represents an important change in photosynthetic, transpiring and respiring tissue (Jansen and Wilson, 1974).

The minimum life span for undamaged leaves is likely about three months, as recorded for the wood climber *Grewia caspinifolia* in Ghana (Swaine *et al*., 1984). Although the majority of leaves probably do not last more than about fifteen months, there as some well-documented cases, such as the understorey trees *Drypetes Parvifolia*, *Vepris heterophylla*, and canopy species *Diospyros abyssinica* and *D. mespiliformis*, and conifers of montane forests, in which the life-span is at least 2-3 years (Swaine *et al.*, 1984; Grubb, 1977).

1.1.8 Rate of Stem Elongation

The rate of stem extension can be affected by light, shade, temperature, water status, nutrient availability as well as by others such as the force of gravity and the presence of atmospheric pollutants (Damptey, 1964). Two processes are involved in the production of new stems: the formation of additional nodes and the elongation of the internodes between them. The photon flux density is an important factor in stem extension both directly and indirectly through carbon assimilation. It is important to note that differences may not always be due to light itself, since treatments may also produce modifications of light quality, leaf temperatures and water potential (Longman and Jenik, 1987).

The rate of stem elongation in some tropical woody plants can be extraordinarily high. Certain species of bamboo may even elongate pre-formed tissue at almost 1m per day, and vines and lianas can also grow very fast (Longman and Jenik, 1987). Lebrum and Gilbert (1954) working on early growth rates of young trees under natural conditions in Zaire found that three climax species increased in height at an average rate of 0.3-1.2m per year, and three pioneers at 1.2-3.7m per year.

In their study of over 1500 trees during early succession of cleared forest in Ghana, Swaine and Hall (1983) found that some secondary species reached a height growth of up to 4m yr^{-1} forty-five individuals, mostly *Harungana madagascariensis* and *Frema orientalis*, exceeded 10m in 5 years with one individual of *Trema* reaching 17m. Primary species such as *Albizzia adianthifolia*, *A. zygia*, and *Antiaris toxicaria* achieved 5m or more in 5 years.

Brokaw (1985b) reported even higher values. The study measured 13.5m height extension in 2 years in *Trema micrantha* and 4.9 and 5.0m in one year by *Cecropia insignis* and *Zanthoxylum* species respectively. Some individuals of the primary species also grow rapidly in gaps. *Simarouba amara* grew 3.0m per year, *Viola sebifera* 2.4m per year, and *Protium panamensis* 2.3m per year.

Exceptionally high stem extension rates have also been reported in other tree species. For example, Nicholson (1965) found 8-9m rates in the first year in *Albizia falcataria*. NAS (1979) reported similar rates in *Sesbania grandiflora*, while Mabberley (1983) recorded the same rates in Eucalyptus deglupta and *Trema micrantha*, the latter exceeding 30m in 8 years. A comprehensive long-term study of tree growth in tropical forests has been reported by Lieberman *et al.* (1986). Growth of 46 common species in a Costa Rican tropical forest was measured on plots established in 1969-1970. They used both canopy and subcanopy species and measured annual diameter at breast height (dbh), age and life span. They made trajectories of maximum, minimum and median growth, rates and life span. The results of the study show that: (a) shade - intolerant canopy and subcanopy species have maximum growth rates and are short-lived; (b) shade-tolerant subcanopy trees live about twice as long as understorey trees and grow at approximately the same maximum rate; (c) canopy and subcanopy trees that are shade tolerant but respond opportunistically to increased light levels have long life span and high maximum growth rates; and (d) understorey species have low maximum growth rates and short life spans.

1.2.0 *WARBURGIA UGANDENSIS* SPRAGUE SUBSP. UGANDENSIS

Warburgia ugandensis belongs to the family Canellaceae (Battiscombe, 1936; Kokwaro, 1976). Locally this tree is known as Apacha (Kakamega), Muthiga (Kikuyu), Olosogon (Masai), Soget (Kipsigis), Sogo-maitha (Luo), Soke (Tugen) and Musunui (Meru). It is a large timber-tree, which grows up to 25m with a girth of up to1m. The tree produces the so-called "Kenya Greenheart" timber.

Warburgia ugandensis is common in Kenya especially in forests above an altitude of 1300m. These include Kikuyu, Eldalat, and Elburgon, Londiani, Kamasia and Southwest Kenya forests. The bark of the tree is rough and almost black in appearance. The leaves are dark green, shinning, entire and ovate. Small green flowers are produced at the axis of the leaves. The fruits are egg-shaped and green in colour. The timber of this tree has a high oil-content, and of yellowish colour but that of old over-mature trees assumes a fine green colour. The timber is not durable in the ground, and is eaten by white ants. The timber does not develop any surface cracks, it takes a high polish and turns brown on exposure to the light (Battiscombe, 1936).

Locally the tree is of vital medicinal value. Dried bark is chewed and the juice swallowed, thus acting as a remedy for stomach-ache, constipation, coughs, fever, toothache, muscle pains, weak joints and general body pains (Kokwaro, 1976). The bark may be scrapped off, dried and ground into a powder. The roots are used by the Kikuyu in preparing soup, and for prevention of diarrhoea. Leaves are boiled in bathing water for curing several unspecified diseases. A decoction of the bark or leaves is taken as a cure of malaria, but causes violent vomiting. The leaves and seeds are used as 'chilli' substitute in curries and its resin acts as a glue to fix tool handles (Kokwaro, 1976).

1.3.0 *POLYSCIAS FULVA* (HIERN) HARMS.

Polyscias belongs to the family Araliaceae. The tree is known as Mutati (Kikuyu), Mukunukunu (Meru), Ol-yalilingi (Masai), Saiyet (Nandi) and Aul (Kamba). It is a tall timber-tree, which grows up to 25m with a diameter of1.5m. It is widely distributed in the highland forests wherever there is a good rainfall at an altitude of 200-2500m. It thrives in Limuru, Kericho, Kakamega, Elburgon, Londiani and other highland forests. The tree has pinnate leaves with dark green leaflets. The branches and young stems are marked with leaf scars. The branches are self-pruning and the crown open. The timber is white and lightweight, not durable but easy to work and entirely odourless. For these reasons the timber is used to make butter-boxes, veneers and plywood. The wood is not a good fuel, though it can be used as such (Battiscombe, 1936).

1.4.0 Justification and Significance of the Research

In Kenya forest destruction is occurring at an alarming rate and this is mainly attributed to increase in human population. The impact is felt not only in natural forests but also in plantation forests. This means afforestation and re-afforestation programmes are vital if what is remaining of our natural heritage is to be saved. This is possible if suitable seedlings for planting either in plantation or in the natural forest are produced.

A forest will not regenerate if seedlings are not available and if the favourable environmental conditions are absent. Bearing in mind that tropical deforestation has reached a historical maximum during the last decade and attracted considerable public attention, it is therefore important to restock old woodlands or create new forests by planting nursery grown seedlings.

Foresters have usually restocked natural forests or created new forests by planting nursery grown seedlings. Once the total area of woodland is increased, natural regeneration may become more reliable and be used more frequently to restock woodlands. The establishment, survival and growth of natural seedlings depends to some extent upon the system of forest management since forest management can influence such site factors as soil conditions, density of herbaceous cover and micro climate. If natural regeneration is to be encouraged, information is needed on the effects of site conditions and their effects on seedling growth. Studies of species response to canopy gaps with different levels of PPFD will yield very useful information both for management purposes and for basic biology about the diversity of forest. The effect that sudden changes in environmental resources, like light, have on carbon-gain capacity, water-use efficiency, growth and allocation of resources in seedlings will yield much useful information about differential species response to the creation of gaps or selective cutting of large trees. Few studies have been conducted to determine the photosynthetic and growth characteristics of tropical tree species, and especially lacking are observations on the light response curves of seedlings, which have been raised, in contrasting light regimes. Such observations will be useful to forest management programmes.

1.5.0 OBJECTIVES AND HYPOTHESIS

The aim of the experiment was to determine the responses of seedlings of *Warburgia ugandensis* and *Polyscias fulva* to different levels of light in terms of photosynthetic rates, growth and morphogenetic characteristics. The two species are important for various tree-planting activities in Kenya. The present study was intended as a contribution on the autecology of the two economically important tree species of Kenya. The analysis of growth of these two tree species at different light regimes was based on measurements of dry weight, morphological parameters and photosynthesis. In order to evaluate the response of species to a range of light conditions, it is necessary to know their reaction in terms of CO_2 assimilation, growth, stomatal conductance, leaf area and transpiration. Toward this end, the current experiment was set out to evaluate the morphological, growth and physiological responses of seedlings of the two species grown under varying light regimes simulating what may occur in the natural ecosystem.

Hypothesis

The hypothesis was that the two species show similar response to different light regimes and that they display the greatest growth and photosynthetic rates under full sunlight conditions.

Specific research objectives

This work aimed at achieving the following main objectives:

(1) To determine the effect of different light regimes on carbon assimilation, transpiration, stomatal conductance and water use efficiency in *Warburgia ugandensis* and *Polyscias fulva* with the aim of establishing the best light level for growth in terms of physiological parameters.

(2) To determine the responses of each species to the varying light levels in terms of leaf area, specific leaf area, leaf number, leaf loss and height. This will help in determining the adaptation strategies of each species to the different light regimes, and

(3) To determine resource allocation in terms of aboveground and belowground biomass. The shoot/root ratio will help in determining resource allocation.

CHAPTER TWO

2.0.0 MATERIALS AND METHODS

The study was located at the Kenya Forestry Research Institute (KEFRI) nursery, Muguga.

2.1.0 Treatments, experimental design and layout.

The study was a split plot experiment with four levels of light (i.e. three shade levels and full sunlight) as main treatments. The sub-treatments were seedlings of two species (*Warburgia ugandensis* and *Polyscias fulva*). A randomised-block design of three replications was used. The light treatments were randomised within the blocks while the species were randomised within the light treatments. A distance of 1 metre separated the blocks. The different light levels were 1 metre apart. Fourteen seedlings were planted in each sub-plot in a 2x7 arrangement. There were 12 subplots with a total of 168 seedlings.

2.1.1 Plant Material

The experimental seedlings were *Warburgia ugandensis* and *Polyscias fulva*. Seeds of the two species were acquired from the Seed Centre, Kenya Forestry Research Institute (KEFRI), Muguga on 21st of January 1997. The seeds were sown 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 into 20 cm-long (diameter 6.5 cm) polythene pots perforated at the bottom. The pots were filled with forest topsoil, cow manure and gravel mixed into a ratio of 5:2:1 by volume respectively. After transplanting the seedlings were removed from the greenhouse and kept in the open for a period of one month in order to harden. The seedlings were later transferred into the different light regimes where they stayed for one month to acclimatise to the new environment before measurements were taken.

2.1.2 Light Treatments

The shade levels were obtained by use of factory made artificial black shade materials. The materials were of different light transmission capacities. Each shade house was 1m long, 1m wide and 1m high. The light treatments were:

(1) 100% full light,

(2) 60-70% of the full light,

(3) 40-45% of the full light and

(4) 20-30% of the full light.

Seedlings of the two species were transferred to the different light regimes on 23rd of May 1997. The following parameters were determined: height and number of living and dead leaves. A leaf was considered dead if a proportion of yellow/brown tissue exceeded 50%.

2.1.3 Measurement of photosynthesis and other related physiological processes.

The rates of photosynthesis, transpiration, stomatal conductance, and PAR 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). The principle of infrared gas analysis relies on the fact that hetero-atomic gas molecules absorb radiation at specific infrared wavebands each gas having a characteristic absorption spectrum.

The major absorption band of CO_2 is at 4.25nm with secondary peaks at 2.66, 2.77 and 14.99nm. The only hetero-atomic gas normally present in air with an absorption spectrum overlapping that of CO_2 is water vapour (both molecules absorb infra-red in the 2.7m region). Since water vapour is usually present in air at much higher concentration than

CO_2, this interference is significant. The problem of water vapour during this experiment was overcome by drying the air using silica gel, which was fitted to the air supply unit (Figure 1). During measurements the analyser was used in a constant flow rate variable differential method. In this method air of determined CO_2 concentration was passed at a known flow rate (400ml/min) using the air supply unit into a leaf chamber. Air was drawn from 5.0 meters height through a sampling tube (Normark BMP 500 type). The air was then drawn through the air supply unit and divided into two streams. The reference stream was passed directly to the analyser while the out stream was passed through the leaf chamber where temperature and humidity sensors were located. After passing through the leaf chamber the air entered the analyser as the analysis stream where it was analysed for CO_2 concentration. Differential reading was obtained when analysis and reference air streams were compared.

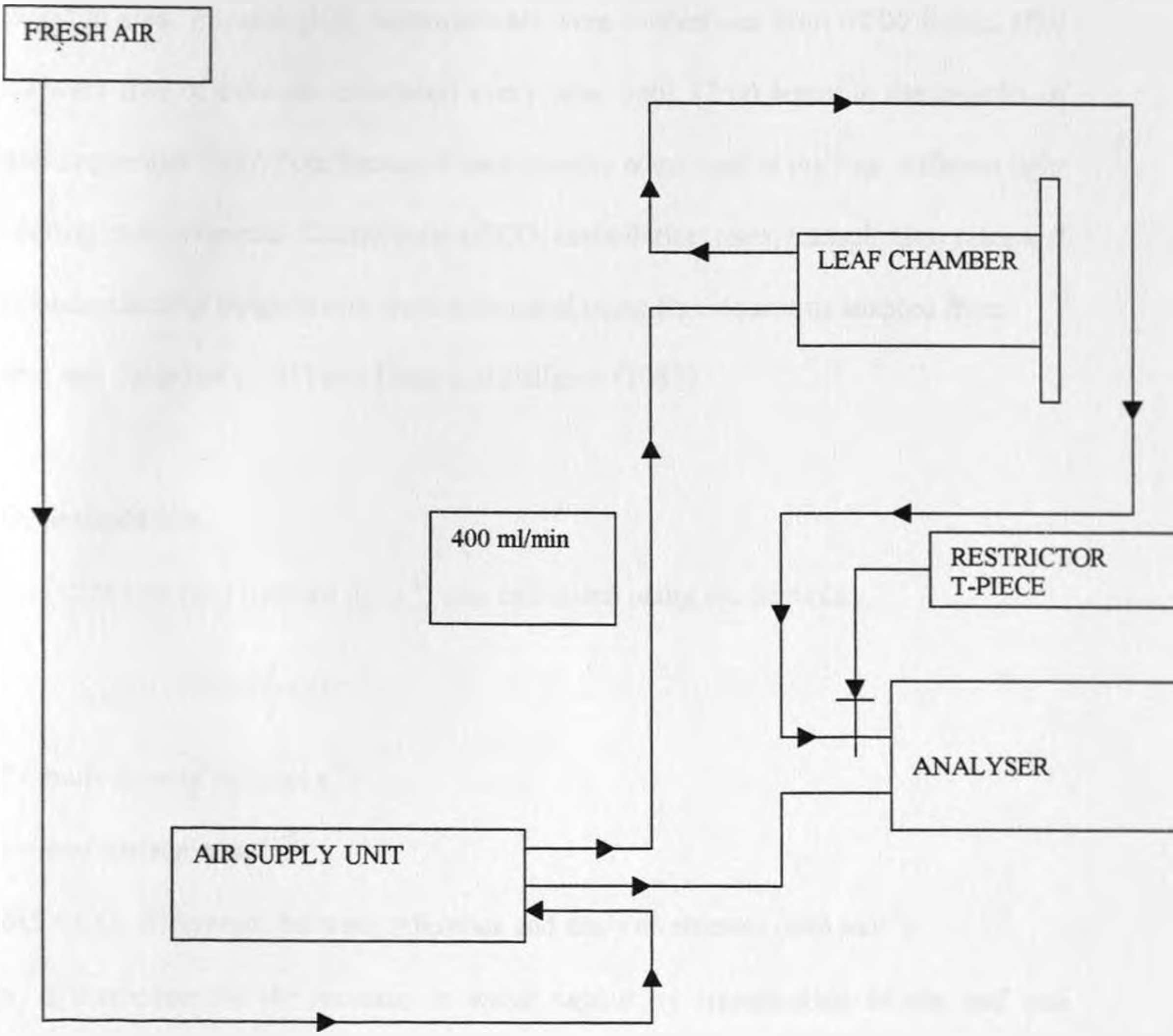


Figure 1.

Schematic presentation of flow of air in the IRGA system.

In the case of *P. fulva* a fully expanded and exposed leaf was placed into the leaf chamber so that it covered the area of 6.25cm^2. For *W. ugandensis* the leaf area of an expanded leaf was determined after placing the leaf into the leaf chamber because most of the leaves were less than 6.25cm^2 in area. Physiological measurements were carried out from 09:00 hours, after the leaves were free of dew and continued every hour until 17:00 hours in the months of August and September 1997. Four leaves of each species were used in the four different light regimes during measurements. Calculations of CO_2 assimilation rates, transpiration rates and stomatal conductance of single leaves were calculated using flux equations adapted from Caemmerer and Farquhar (1981) and Long and Hällgren (1985).

2.1.4 CO_2 assimilation

CO_2 assimilation rate (Fc) (µmmol m^{-2} s^{-1}) was calculated using the formula:

$$Fc = \frac{f}{s} \times \Delta C$$

Where,

f = mole flow of air (mol s^{-1})

s = leaf surface area (m^2)

ΔC = CO_2 differential between reference and analysis streams (mol mol^{-1})

However, a correction for the increase in water vapour by transpiration of the leaf was required: Therefore,

$$Fc = \frac{f}{s} \times \Delta C \times \frac{(1 - Xe)}{(1 - Xo)}$$

Where,

Xe = Mole fraction of water vapour at leaf chamber inlet (mol mol^{-1})

Xo = Mole fraction of water vapour at leaf chamber outlet (mol mol^{-1})

Xe and Xo are calculated from saturation vapour pressure (Xs) at the measured leaf temperature, given the relative humidity (RH) from the analyser:

$$Xo / Xe = Xs \times \frac{RH}{100}$$

Since all the above equations were in moles, the following equation was used to convert the measured volumetric flow to mole flow of air:

$$f = \frac{fv}{1000} \times \frac{1}{22.4} \times \frac{273.15}{273.15 + T} \times \frac{P}{101.3} \times \frac{1}{60}$$

Where,

f = mole flow of air (mol s^{-1})

fv = volumetric flow of air cm^3 min^{-1}

22.4 = volume in dm^3 of one mole of air at S.T.P.

T = temperature recorded during measurement (^0C)

P = atmospheric pressure during measurements (KPa)

2.1.5 **Transpiration Rate** (E) (mmol m^{-2} s^{-1})

Transpiration rate (E) was calculated using the following equation:

$$E = \frac{f}{s} \times \frac{(Xo - Xe)}{(1 - Xo)}$$

Where,

E = Transpiration rate (mmol m^{-2} s^{-1})

2.1.6 Stomatal Conductance (g_s) (mol m^{-2} s^{-1})

$$gs = \frac{E}{Xs \times (T1 - Xo)}$$

Stomatal conductance (g_s) was calculated following the equation:

Where,

g_s = Stomatal conductance (mol m^{-2} s^{-1})

T1 =Chamber temperature (°C)

Xs = mole fraction of water vapour at saturation

Assuming the leaf is saturated with water vapour pressure at actual leaf temperature, T1.

2.1.7 Water use efficiency WUE (μmol CO_2 $mmol^{-1}$ H_2O)

Water use efficiency was calculated by dividing CO_2 assimilation rate by the rate of transpiration.

2.2.0 Growth measurements

The growth measurements determined included seedling height, leaf area, dry weights, specific leaf area, shoot/root ratio and leaf numbers.

2.2.1 Seedling height

Seedling heights of all the seedlings in each plot were determined by taking measurements from the stem base to the apical meristem. Heights were measured after a fortnight.

2.2.2 Leaf area determination

In situ leaf areas were determined by tracing the leaves on paper. The area covered on paper was carefully cut out and the area was determined using an automatic leaf area meter (Hayashi Denkoh Co. Ltd model AAC-400). In this instrument the leaves passed between small light source and light detectors. The meter related the amount of light cut off from the detectors by the leaf to the area of the leaf. Calibration was done by running a metal disc of known area (100 cm^2) through the machine.

2.2.3 Seedling harvesting

One harvest was made to determine the final leaf areas, and dry weights and also specific leaf areas and shoot/root ratios. The harvested seedlings were divided into leaves, stems and roots and kept in polythene bags to minimise water loss.

2.2.4 Dry weight determination

The seedlings were dried separately in a well-ventilated oven at around 80 degrees centigrade for 24 hours, and their dry weights of each plant part were determined using a sensitive electrical balance. Total dry weight of the whole plant was then computed.

2.2.5 Leaf area (LA) and Specific leaf area (SLA)

The leaf areas of the harvested seedlings was determined using the automatic leaf area meter. Using the dry weights and the leaf area the specific leaf area was computed thus:

$$SLA = \frac{SA}{LM}$$

Where,

SLA= specific leaf area ($cm^2\ g^{-1}$)

SA= leaf surface area

LM= leaf mass

2.2.6 Leaf number

The number of both living and dead number of leaves was determined every week. A leaf was considered dead if a proportion of yellow/brown tissue exceeded 50%.

2.2.7 Data analysis

The data was analysed using ANOVA and level of significance determined using Turkey's Multiple Range Test (Zar, 1986).

CHAPTER THREE

3.0 RESULTS AND DISCUSSION

3.1 THE MICROCLIMATIC FACTORS OF THE FOUR LIGHT REGIMES

3.1.1 Photosynthetic Photon Flux Density (PPFD)

The artificial shades used in this experiment gave photosynthetic photon flux densities of 25% of full sunlight, 42% of full sunlight and 65% of full sunlight. The open (100% full sunlight) acted as the control. (The 25% of full sunlight will henceforth be referred to as dense shade, 42% of full sunlight as moderate shade, 65% of full sunlight as partial shade and 100% as full sunlight).

The photosynthetic photon flux density varied in all the four light regimes. This variation was important because the seedlings of both tree species were exposed to distinct light microclimates and hence any morphological and physiological differences in each species were due to light available at each light regime. The PPFD intercepted by the leaves of the two species depended on the available light in each regime with the open recording the highest values and the dense shade the lowest. The mean diurnal PPFD were: dense shade 347 μmol m^{-2} s^{-1}, moderate shade 588 μmol m^{-2} s^{-1}, partial shade 910 μmol m^{-2} s^{-1} and full sunlight 1413 μmol m^{-2} s^{-1} (Table 1). The amount of PPFD received in the full sunlight was 75% higher than that received in the dense shade, 58% higher than in moderate shade and 35% higher than in the partial shade. The PPFD received in full sunlight was significantly ($P< 0.001$) higher than in the dense shade. The partial shade received more PPFD ($P< 0.01$) than the dense shade. The moderate shade also received higher ($P< 0.05$) PPFD than the dense shade. There was no significant difference ($P> 0.05$) between the two species in terms of PPFD in the four light regimes (Figures 2 and 3). The PPFD range for full sunlight was

1000-1680 µmol m^{-2} s^{-1}, 600 – 1000 µmol m^{-2} s^{-1} for partial shade, 400 – 700 µmol m^{-2} s^{-1} for moderate shade and 250 – 400 µmol m^{-2} s^{-1} for dense shade. In the four light regimes the highest PPFD values were recorded at or around mid-day and the lowest in the morning or late in the afternoon (Figures 2 and 3).

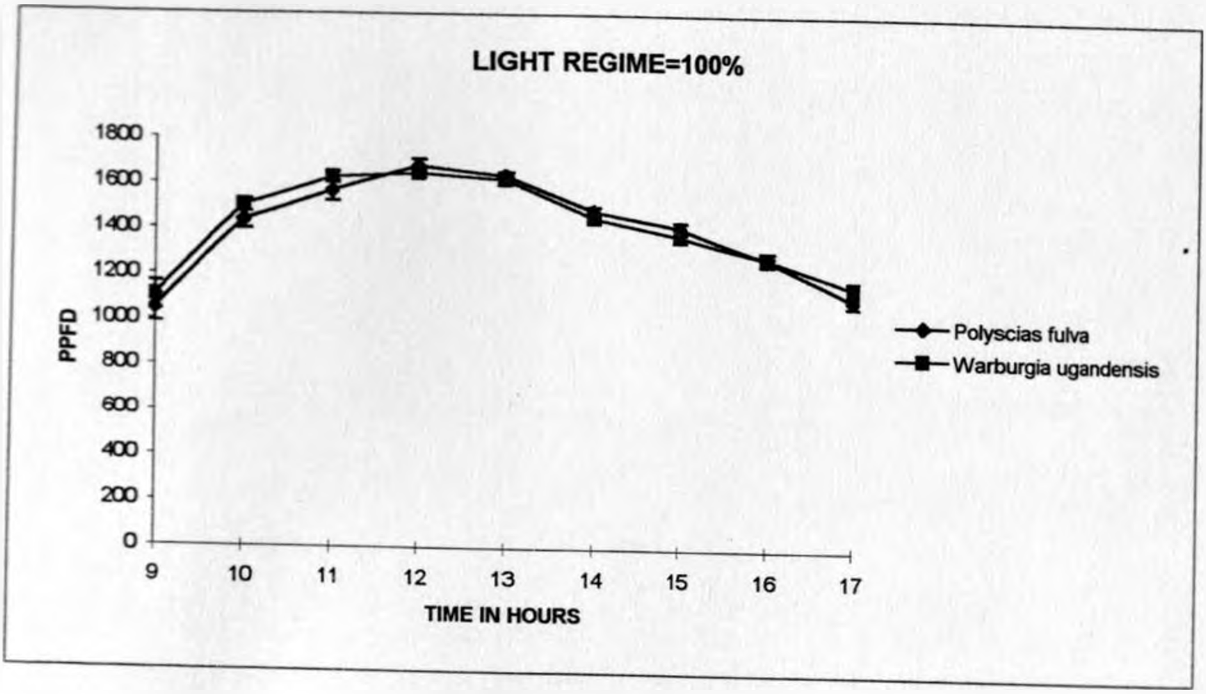
Table 1. Summary of the microclimate produced by the three shade materials in terms of PPFD and temperature.

LIGHT REGIMES

Microclimatic factors	Dense shade	Moderate shade	Partial shade	Full sunlight
Mean daily PPFD (µmol m^{-2} s^{-1})	347	588	918	1413
% Full sunlight	25	42	65	100
Mean daily temperature (^{0}C)	27	28	29	30

Figure 2

Mean diurnal changes in photosynthetic photon flux density (PPFD μmol m^{-2} s^{-1}) in 'sun' leaves of *P. fulva* and *W. ugandensis* raised in full light (100% sunlight) and partial shade (65% of full light). Vertical bars are standard error (S.E.) of means.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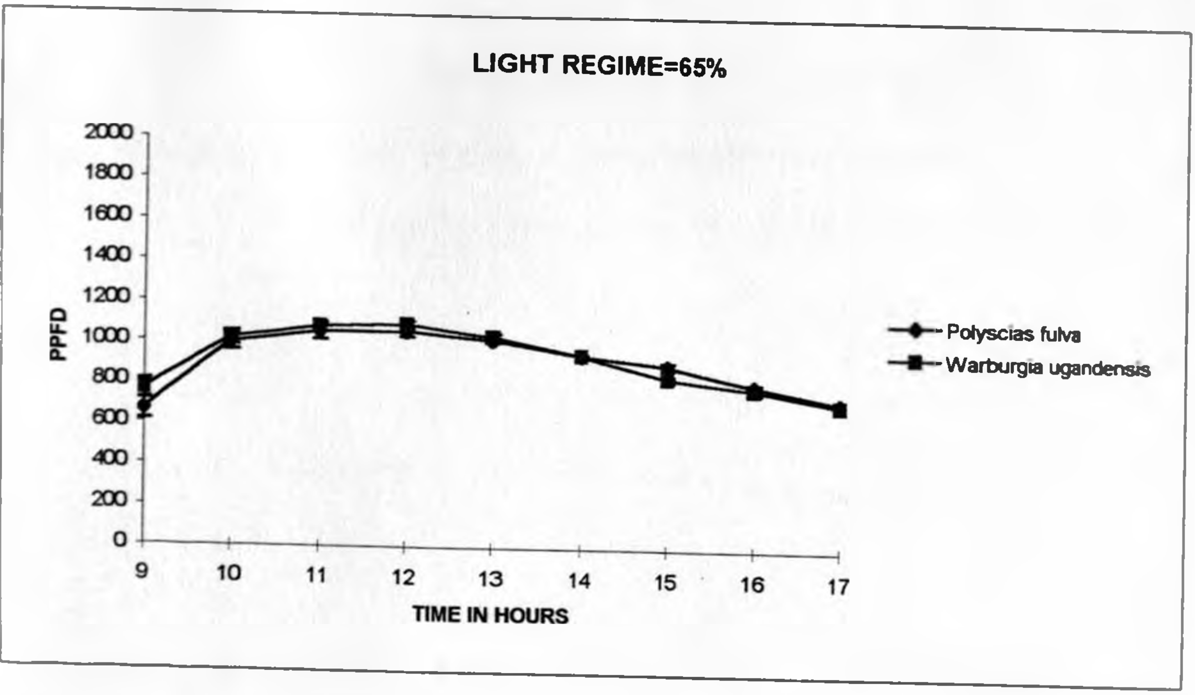
1600
1400
1200
1000
800
600
400
200
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis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PPFD
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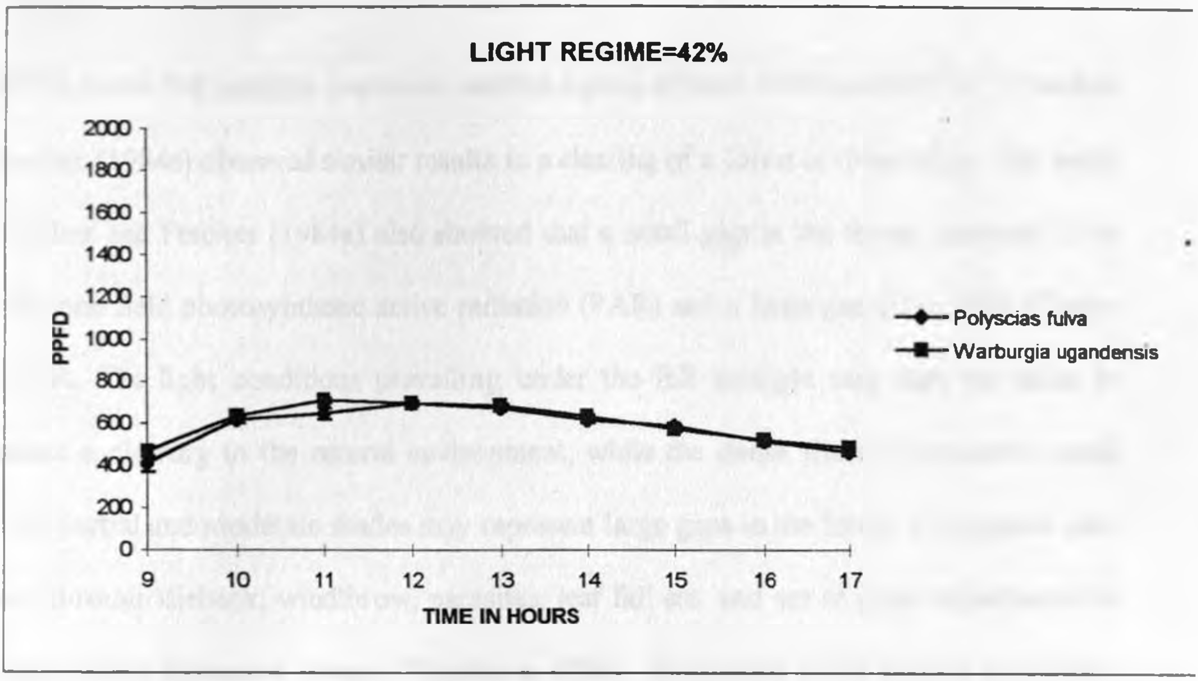
1800
1600
1400
1200
1000
800
600
400
200
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

Figure 3

Mean diurnal changes in photosynthetic photon flux density (PPFD μmol m^{-2} s^{-1}) in ‘sun’ leaves of *P. fulva* and *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of full light). Vertical bars are S.E. of the means.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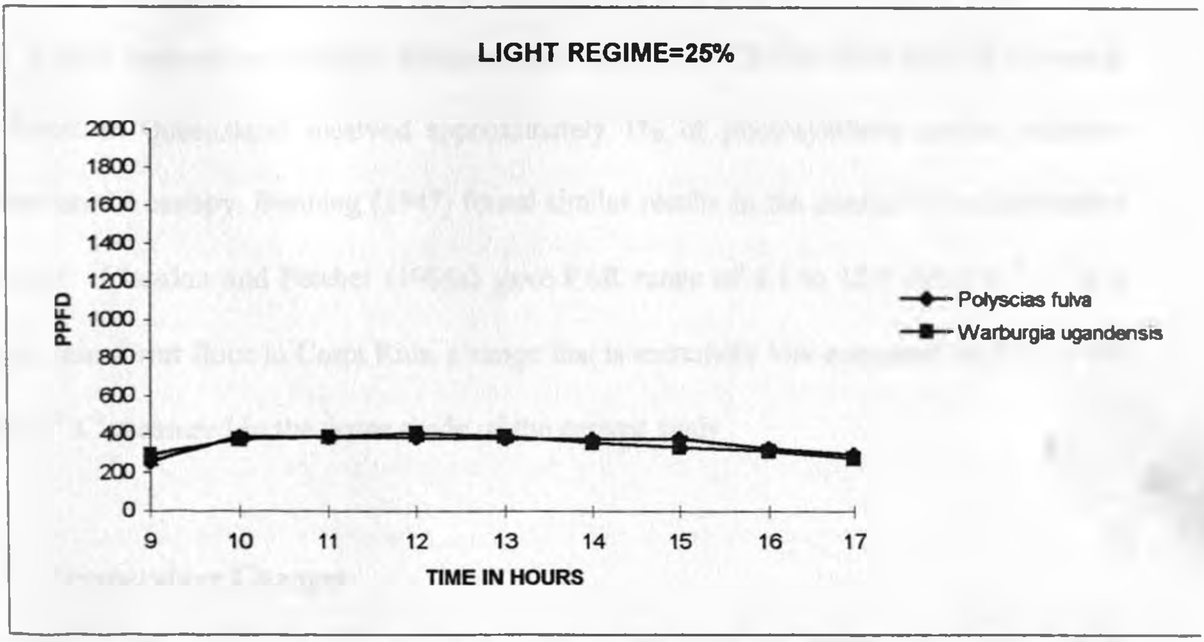
PPFD
2000
1800
1600
1400
1200
1000
800
600
400
200
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis


LIGHT REGIME=25%
PPFD
2000
1800
1600
1400
1200
1000
800
600
400
200
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

The PPFD in the full sunlight treatment reached a peak of over 1000 µmol m^{-2} s^{-1}. Chazdon and Fetcher (1984a) observed similar results in a clearing of a forest in Costa Rica. The study by Chazdon and Fetcher (1984a) also showed that a small gap in the forest received 10 to 20% of open field photosynthetic active radiation (PAR) and a large gap 20 to 50% of open field PAR. The light conditions prevailing under the full sunlight may thus be taken to represents a clearing in the natural environment, while the dense shade represents a small gap. The partial and moderate shades may represent large gaps in the forest. The natural gaps develop through dieback, windthrow, parasites, leaf fall etc. and are of great importance for the rejuvenation of tropical forests (Whitmore, 1978). The results in the current experiment also showed that none of the three shade levels could be a true representative of the forest floor. This is because according to Björkman and Ludlow (1972) the forest floor in a tropical rain forest in Queensland received approximately 1% of photosynthetic active radiation incident on the canopy. Bünning (1947) found similar results in the interior of an Indonesian rainforest. Chazdon and Fetcher (1984a) gave PAR range of 4.1 to 12.7 µmol m^{-2} s^{-1} at a tropical rain forest floor in Costa Rica, a range that is extremely low compared to 250 to 400 µmol m^{-2} s^{-1} measured in the dense shade of the current study.

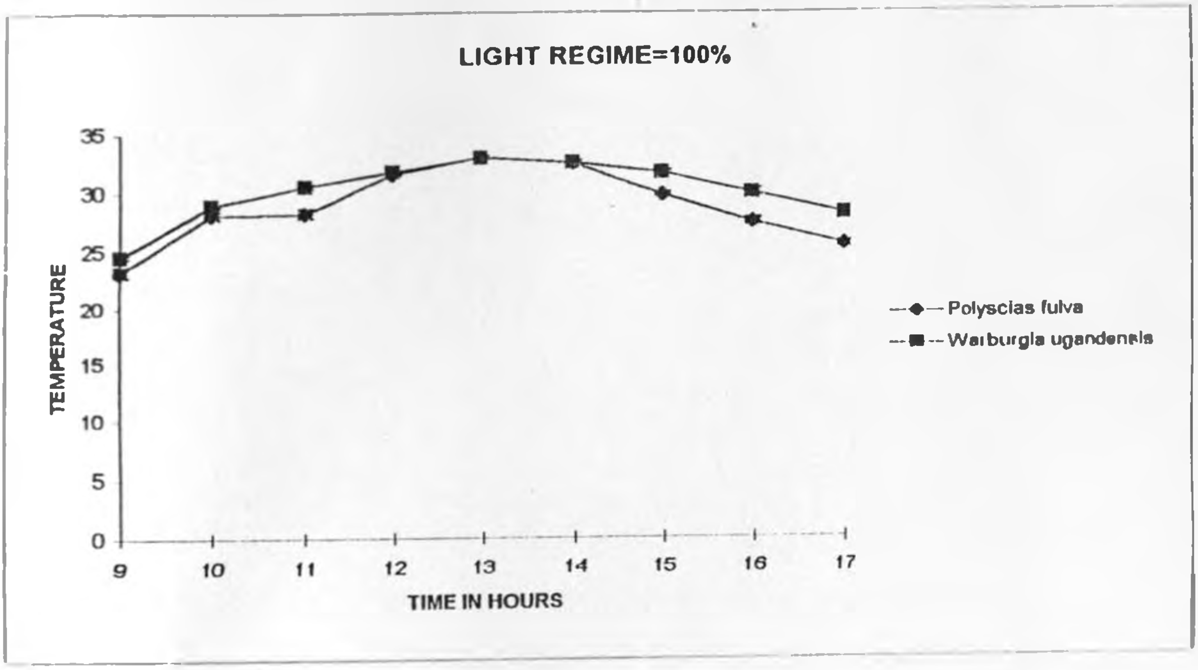
3.1.2 Temperature Changes

Temperature measurements were taken simultaneously with the PPFD and were used to characterise the microclimates of the four light regimes. The mean diurnal temperatures were: full sunlight 30 °C, 29 ^{0}C in partial shade, 28 °C in moderate shade and 27 °C in dense shade (table 1 above). The temperature ranges were: 24 to 33 °C in full sunlight, 21 to 31 °C in partial shade, 20 to 31 °C in moderate shade and 20 to 30 °C in dense shade. Like PPFD the highest temperatures were recorded in full sunlight and the lowest in the dense shade. There was no significant difference (P> 0.05) between species in each light regime in terms of temperature (Figures 4 and 5). The highest temperatures, like PPFD, were measured at or around mid-day and the lowest in the morning or late in the afternoon (Figures 4 and 5). High PPFD and temperatures characterized the full sunlight treatment while the shaded microclimates showed reduced PPFD and temperatures. The results showed that temperature was PPFD dependent that is, the higher the PPFD the greater the temperature and vice versa, similar results were found by Chazdon and Fetcher (1984a) in forest gaps of various sizes where the gaps with the highest light levels were also characterized by higher temperatures.

When interpreting the data in the current study one should bear in mind that the level of shading used gave PPFD values that were greater than those measured in the deepest shade of tropical rain forest (Björkman and Ludlow, 1972). The values were still higher than those measured on the floor of the Costa Rica forest (Chazdon and Fetcher, 1984a). It is also important to note that light quality under artificial shade differs from that under a canopy (Morgan and Smith, 1981). Humidity and temperature control in the shade enclosures was poor, probably exposing the seedlings of the two tree species to lower relative humidity and high temperatures than may be experienced in the forest atmosphere. This could be one reason why no significant differences were observed in the seedlings of the two species in terms of temperature (Figures 4 and 5). The net effect of these shortcomings is that the various responses in sun and shade-grown seedlings may have been underestimated. The results, therefore, can only speculate on the responses of tree seedlings following gap formation in our forests. Long-term monitoring of these seedlings in the field would be necessary to draw more definite conclusions.

Figure 4

Mean diurnal changes in temperature (^{0}C) in ‘sun’ leaves of *P. fulva* and *W. ugandensis* raised in full light (100% sunlight) and partial shade (65% of full light). Vertical bars are S.E of the means.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TEMPERATURE
35
30
25
20
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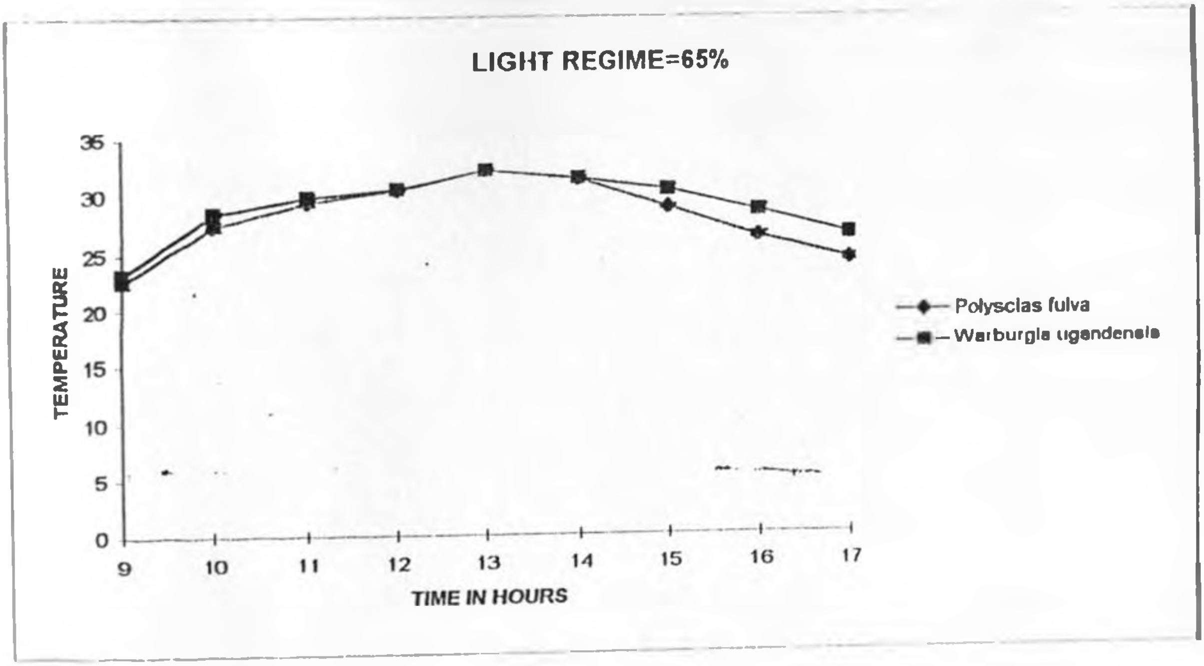
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis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TEMPERATURE
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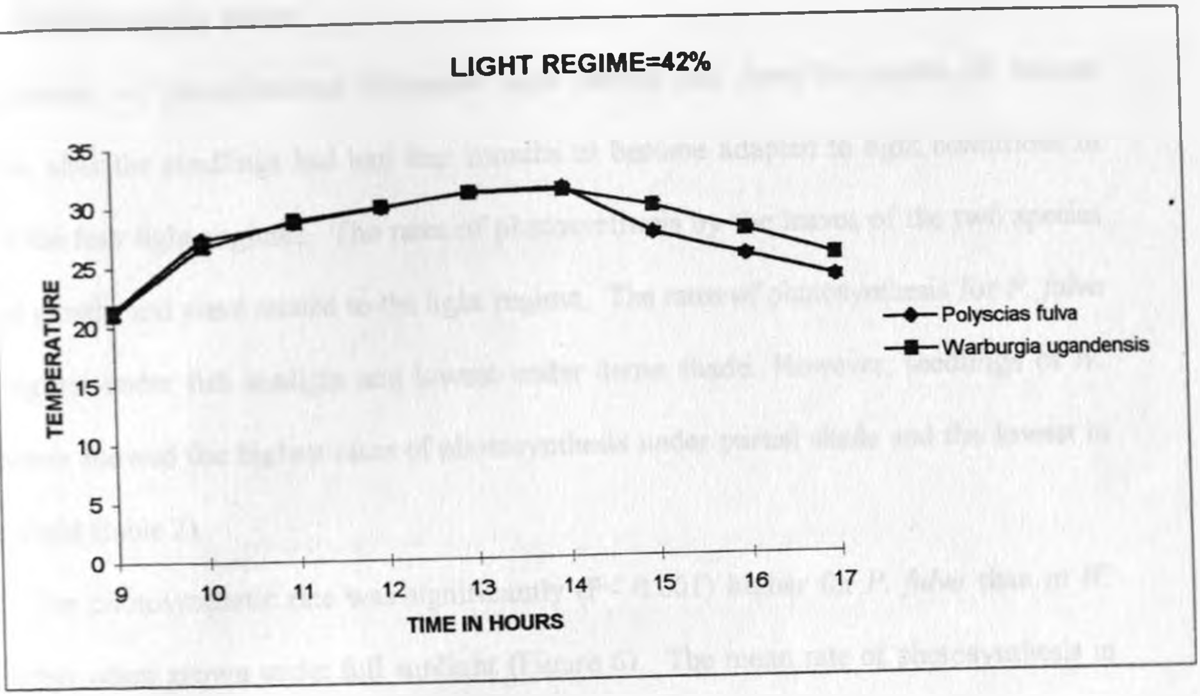
20
15
10
5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

Figure 5

Mean diurnal changes in temperature (^{0}C) in 'sun' leaves of *P. fulva* and *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of full sunlight). Vertical bars are S.E. of the means.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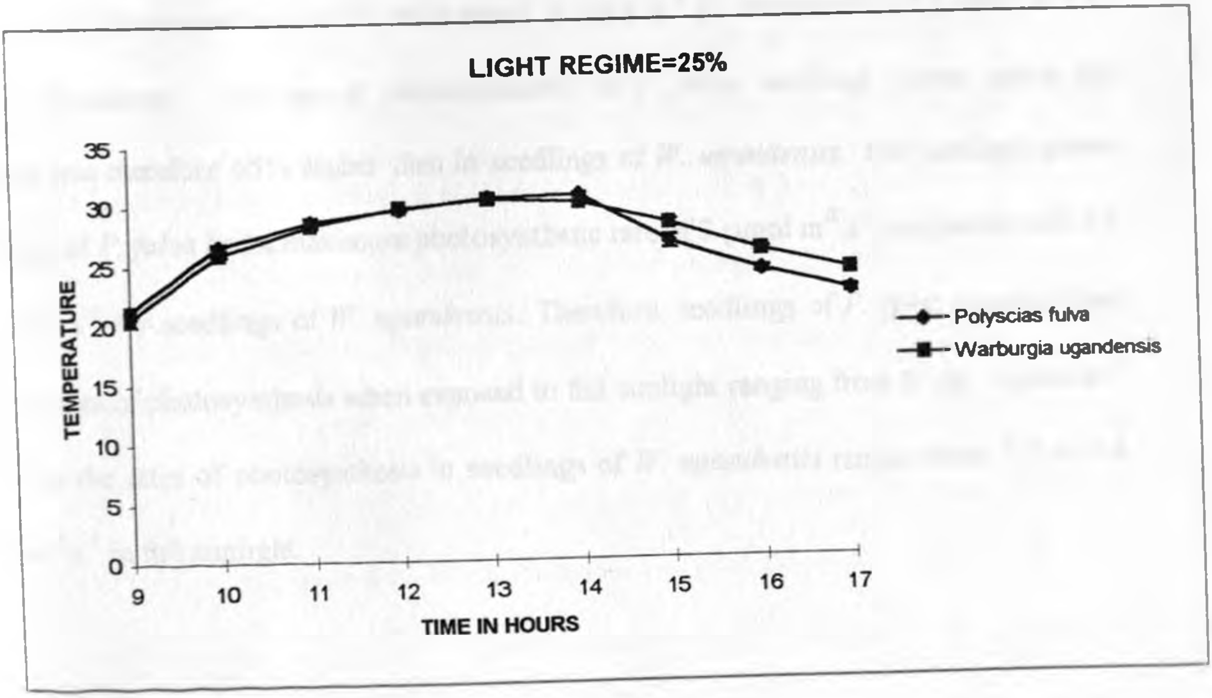
TEMPERATURE
35
30
25
20
15
10
5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis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TEMPERATURE
35
30
25
20
15
10
5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

3.1.3 Photosynthetic Rates

Measurements of photosynthetic responses were carried out from the month of August onwards, after the seedlings had had four months to become adapted to light conditions in each of the four light regimes. The rates of photosynthesis by the leaves of the two species differed greatly and were related to the light regime. The rates of photosynthesis for *P. fulva* were highest under full sunlight and lowest under dense shade. However, seedlings of *W. ugandensis* showed the highest rates of photosynthesis under partial shade and the lowest in full sunlight (table 2).

The photosynthetic rate was significantly ($P< 0.001$) higher for *P. fulva* than in *W. ugandensis* when grown under full sunlight (Figure 6). The mean rate of photosynthesis in full sunlight grown seedlings of *P. fulva* was 1.4 µmol m^{-2} s^{-1} compared to 0.3 µmol m^{-2} s^{-1} for *W. ugandensis*. The rate of photosynthesis for *P. fulva* seedlings grown under full sunlight was therefore 65% higher than in seedlings of *W. ugandensis*. Full sunlight-grown seedlings of *P. fulva* had a maximum photosynthetic rate of 3 µmol m^{-2} s^{-1} compared with 0.4 µmol m^{-2} s^{-1} for seedlings of *W. ugandensis*. Therefore, seedlings of *P. fulva* reached their highest rates of photosynthesis when exposed to full sunlight ranging from 0.5 to 3 µmol m^{-2} s^{-1}, while the rates of photosynthesis in seedlings of *W. ugandensis* ranged from 0.2 to 0.4 µmol m^{-2} s^{-1} in full sunlight.

Table 2. Mean rates of photosynthesis (in µmol CO_2 m^{-2} s^{-1}) in seedlings of the two species growing under four different light regimes.

LIGHT REGIMES

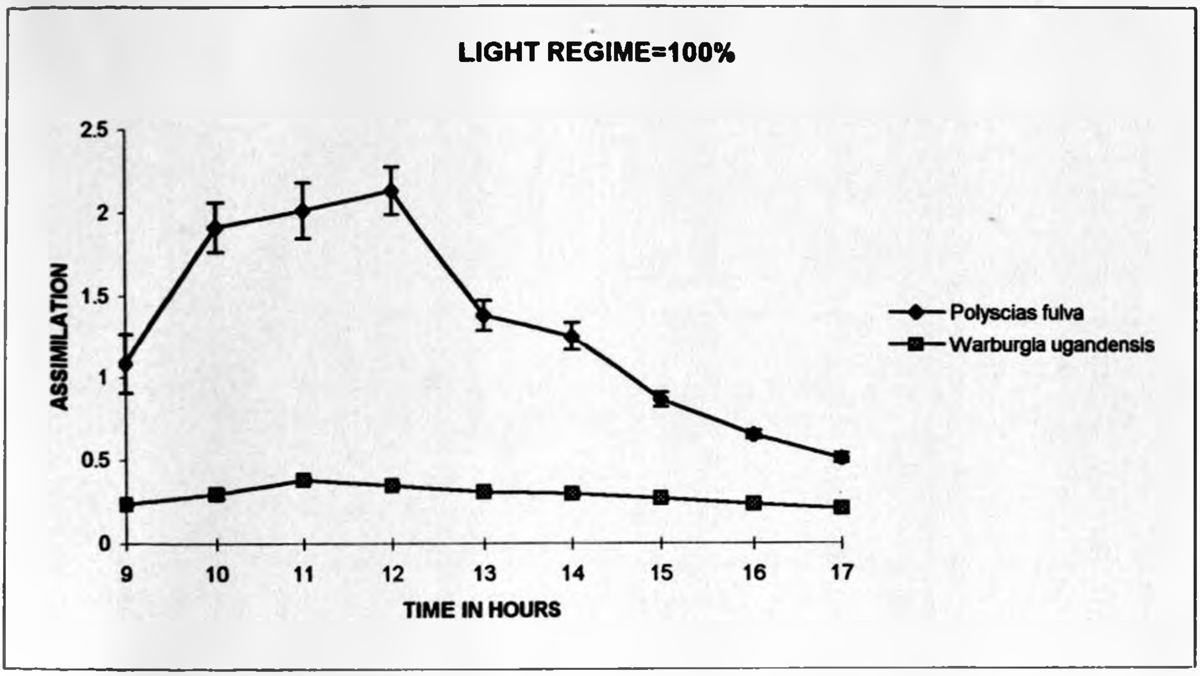
Species	Dense shade	Moderate shade	Partial shade	Full sunlight
P. fulva	0.4	0.5	1.0	1.4
W. ugandensis	0.4	0.5	0.6	0.3

In partial shade the rate of photosynthesis for *P. fulva* was similarly higher ($P<0.01$) than in seedlings of *W. ugandensis* (Figure 6). The mean rate of photosynthesis in seedlings of *P. fulva* grown under partial shade was 1.0 µmol m^{-2} s^{-1}, while those of *W. ugandensis* recorded a mean value of 0.6 µmol m^{-2} s^{-1} (see Table 2). The photosynthesis range for *P. fulva* was 0.4 to 1.7 µmol m^{-2} $s^{-1}$and 0.5 to 0.8 µmol m^{-2} s^{-1} for *W. ugandensis* when growing under partial shade. Shading increased the rate of photosynthesis in *W. ugandensis*. The rate of photosynthesis increased from 0.3 µmol m^{-2} s^{-1} in full sunlight to 0.6 µmol m^{-2} s^{-1} partial shade (a 50% increase). However, *P. fulva* lowered its rate of photosynthesis from 1.4 µmol m^{-2} s^{-1} in full sunlight to 1.0 µmol m^{-2} s^{-1} in partial shade. The rates of photosynthesis were not significantly ($P>0.05$) different in the seedlings of the two species when growing under moderate and dense shade (Figure 7). Under moderate shade seedlings of *P. fulva* had a mean rate of photosynthesis of 0.5 µmol m^{-2} s^{-1} and a similar value was observed for *W. ugandensis* (table 2). Seedlings of *P. fulva* gave a photosynthetic range of 0.2 to 0.8 µmol m^{-2} s^{-1}, while those of *W. ugandensis* recorded a range of 0.4 to 0.6 µmol m^{-2} s^{-1} under moderate shade. The two species showed similar rates of photosynthesis when grown under dense shade (Table 2) with *P. fulva* giving a range of 0.2 to 0.5 µmol m^{-2} s^{-1} and 0.3 to 0.5 µmol m^{-2} s^{-1}

for *W. ugandensis*. The diurnal trend in photosynthesis for *P. fulva* was characterized by high values between 9:00 hours and mid-day and low values towards 17:00 hours when grown under full sunlight (Figure 6). At 9:00 hours the mean rates of photosynthesis were 1.09 µmol m^{-2} s^{-1} and 0.23 µmol m^{-2} s^{-1} for *P. fulva* and *W. ugandensis* respectively, under full sunlight, rising to 2.4 µmol m^{-2} s^{-1} and 0.24 µmol m^{-2} s^{-1} before 12:00 hours respectively and reducing towards 17:00 hours (Figure 6). In the dense shade the mean diurnal photosynthetic rates for the two species were similar. In seedlings of *W. ugandensis* the mean rates of photosynthesis were 0.36 µmol m^{-2} s^{-1} and 0.46 µmol m^{-2} s^{-1} at 9:00 hours and 12:00 hours respectively. For *P. fulva* the mean rates of photosynthesis were 0.35 µmol m^{-2} s^{-1} and 0.42 µmol m^{-2} s^{-1} at the same times of the day (Figure 7). The diurnal trends in photosynthetic rates for the two species under partial shade and moderate shade are shown in figures 6 and 7 respectively.

Figure 6

Diurnal course in CO_2 assimilation rates (μmol m^{-2} s^{-1}) in leaves of *P. fulva* and *W. ugandensis* grown in full light (100%) and partial shade (65% of full light). Vertical bars are the S.E. of the means.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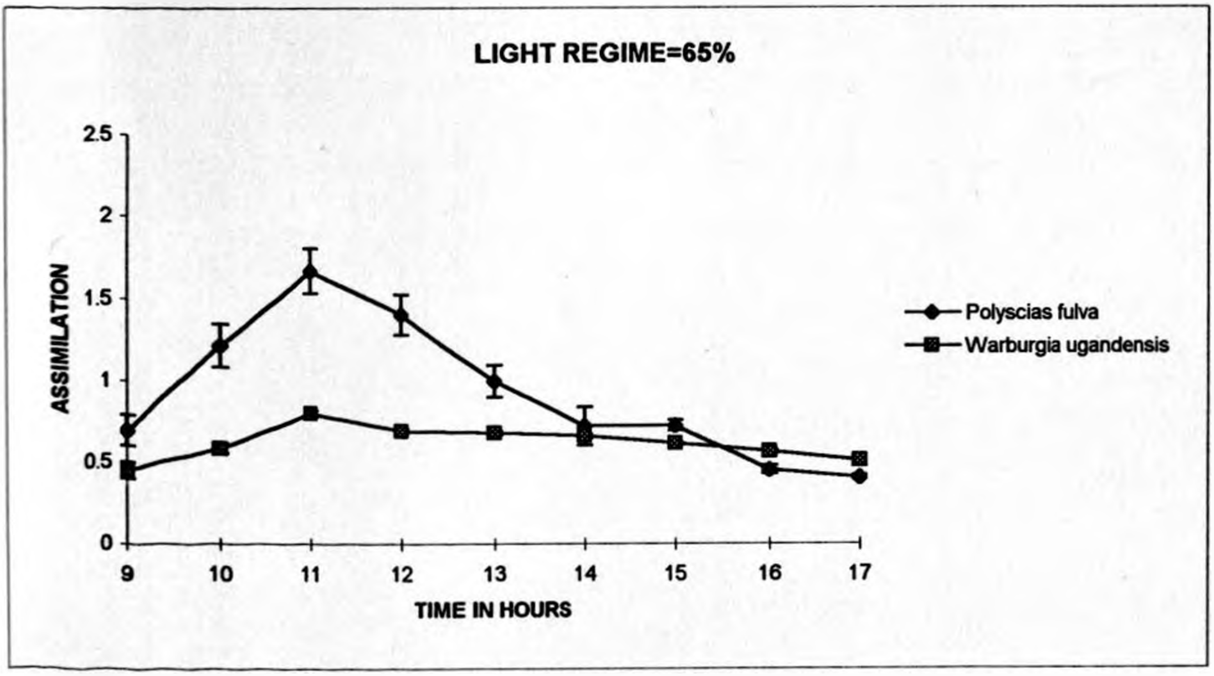
ASSIMILATION
2.5
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis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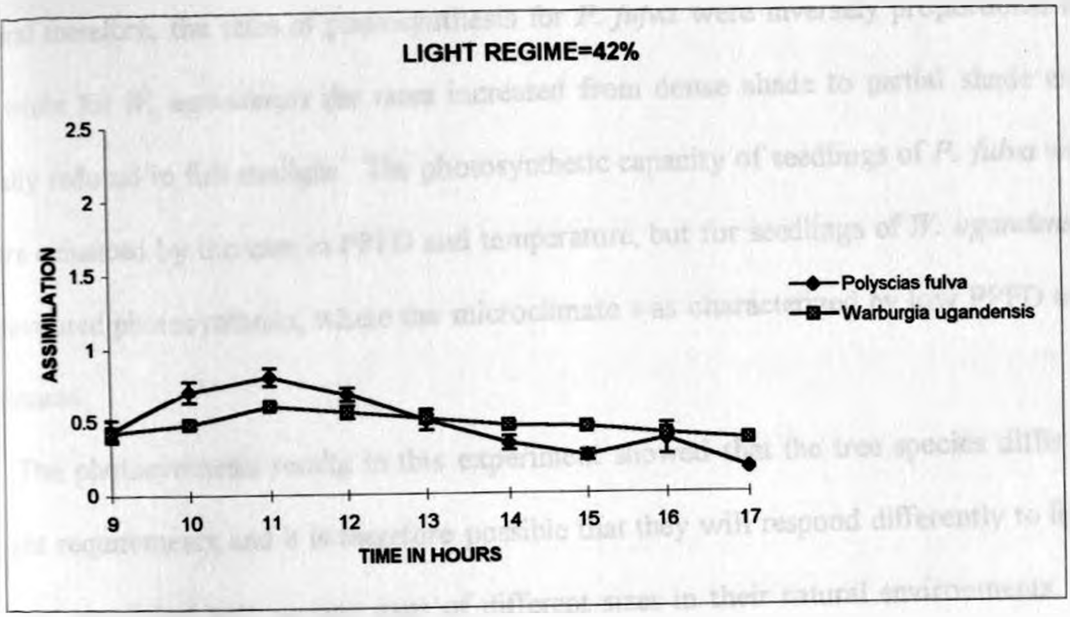
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

Figure 7

Diurnal course in CO_2 assimilation rates (µmol m^{-2} s^{-1}) in leaves of *P. fulva* and *W. ugandensis* grown in moderate shade (42% of full sunlight) and dense shade (25% of full sunlight. Vertical bars are the S.E.of the means.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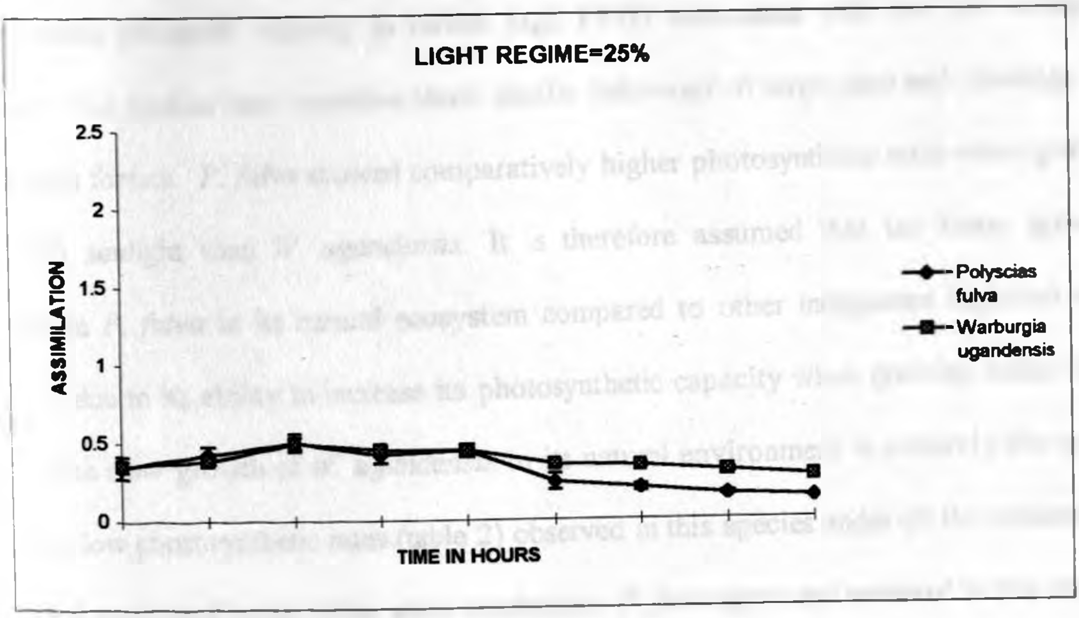
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis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2
1.5
1
0.5
0
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

In general therefore, the rates of photosynthesis for *P. fulva* were inversely proportional to shade while for *W. ugandensis* the rates increased from dense shade to partial shade and drastically reduced in full sunlight. The photosynthetic capacity of seedlings of *P. fulva* was therefore enhanced by increase in PPFD and temperature, but for seedlings of *W. ugandensis* shade favoured photosynthesis, where the microclimate was characterized by low PPFD and temperatures.

The photosynthesis results in this experiment showed that the tree species differ in their light requirements and it is therefore possible that they will respond differently to light conditions associated with canopy gaps of different sizes in their natural environments. *P. fulva* showed enhanced capacity to utilise high PPFD associated with the full sunlight treatment. The species may therefore show similar behaviour in large gaps and clearings in our Kenyan forests. *P. fulva* showed comparatively higher photosynthetic rates when grown under full sunlight than *W. ugandensis*. It is therefore assumed that the faster growth observed in *P. fulva* in its natural ecosystem compared to other indigenous highland tree species is due to its ability to increase its photosynthetic capacity when growing under high PPFD. The slow growth of *W. ugandensis* in its natural environment is probably due to its extremely low photosynthetic rates (table 2) observed in this species under all the treatments, although it performed better under shade treatments. *P. fulva* grew and survived in the shaded habitats though with relatively low photosynthetic rates. It is therefore apparent that sunflecks may contribute significantly to photosynthesis in this species when growing in shaded environments. *W. ugandensis* was adversely affected by strong PPFD. This may have ecological implications on the species because it may be unable to utilise sunflecks in the forest environment and hence being out completed by other species like *P. fulva*. The leaves of *P. fulva* growing under shade must be adapted to utilising very low flux densities, and the ability of tolerating and utilising the high fluxes in sunflecks from direct solar beams. This would enhance the ability of this species to compete with seedlings of other species in the shade. It appeared that in case of tree-fall clearings the photosynthetic rates of *P. fulva* may increase and hence the species competitive advantage among other seedlings and saplings would be enhanced within the gap which may favour the species in occupying space in the canopy.

Light demanding species display higher rates of photosynthesis when growing under high light intensities than under shade. These species are also able to adjust their maximum photosynthetic capabilities to utilise the light regime in which they are grown (Kwesiga and Grace, 1986). Bazzaz and Carlson (1984) made similar observations in fourteen early, middle and late succession species grown in full sunlight and under the shade of a mulberry canopy. In the current study higher rates of photosynthesis were observed in *P. fulva* when grown in full sunlight than in shaded habitats (Table 2). The species also showed more adaptability to shade of varying degree by adjusting its photosynthetic capacity. The maximum photosynthetic rate for *P. fulva* was 3 μmol m^{-2} s^{-1} in full sunlight, this reduced to, 1.7 μmol m^{-2} s^{-1} in partial shade, 0.8 μmol m^{-2} s^{-1} in moderate shade and a mere 0.5 μmol m^{-2} s^{-1} in the dense shade. Similar behaviour was observed in *Hopea odorata* grown under full sunlight and shade (Kriebitzsch *et al.*, 1997). According to the study, the maximum rate of photosynthesis for *H. odorata* was 4 μmol m^{-2} s^{-1} in full light and 2 μmol m^{-2} s^{-1} in the shade. Evidence from other work on sun and shade species (Björkman, 1981) suggests that obligate shade plants have an intrinsically low potential for photosynthetic light acclimation and particularly a low ability to increase their capacity for effective utilization of high PAR. *W.*

ugandensis responded like an obligate shade plant in that it showed the highest rates of photosynthesis under shade and the lowest in full sunlight. However, the rates of photosynthesis remained similar in partial shade, moderate and dense shades. This species showed a reduced ability to increase its capability for effective utilisation of high PPFD. Although these observation are evident in case of *W. ugandensis*, its rates of photosynthesis, both at dense shade and full sunlight, are almost similar. Thus it is not clear whether the seedlings of *W. ugandensis* are to be regarded as obligate shade plants. MacGregor (1934) concluded that obligate shade plants derive considerable benefit from shade, but in the controlled environment the species grow best in bright light (Kwesiga and Grace, 1986). The existence of obligate shade plants among tropical tree species seems in doubt following the demonstration by Augspurger (1984) that all species studied benefited from being in the more open sites. Studies by Kriebitzsch *et al.* (1997) showed that the maximum rate of photosynthesis in *Intsia palembanica* was 0.9 μmol m^{-2} s^{-1} in full light and this increased to 3 μmol m^{-2} s^{-1} under shade. The behaviour of *I. palembanica* is similar to that of *W. ugandensis* which showed a maximum rate of photosynthesis of 0.3 μmol m^{-2} s^{-1} in full sunlight rising to 0.8 μmol m^{-2} s^{-1} under shade. Oberbauer and Strain (1984) found that sciophilous plants had a mean photosynthetic rate of 6.8 μmol m^{-2} s^{-1}, those in canopy gaps 11.3 μmol m^{-2} s^{-1} and the species from large clearings 27.7 μmol m^{-2} s^{-1}. The values found in the above study are extremely high compared to the values observed for *P. fulva* and *W. ugandensis* in the current study (see table 2). According to Riddoch *et al.* (1991) climax species of tropical rain forests reach their low maximum rates of photosynthesis of less than 4 μmol m^{-2} s^{-1} at PAR values below 200 μmol m^{-2} s^{-1}. Ducrey (1994) in a study on predominant tree species of tropical rain forests distinguishes heliphilous species that are shade-intolerant form sciophilous species with maximum rates of photosynthesis values of up to 5 µmol m^{-2} s^{-1}. According to Ducrey (1994) forest-floor species have maximum photosynthesis values in the range between 1.6 and 2.1 µmol m^{-2} s^{-1}. The maximum rates of photosynthesis observed in *P. fulva* and *W. ugandensis* are thus of the same order as those of tropical shade trees as given in the literature. Shade plants are characterized by low photosynthetic rates (Björkman, 1981). The low photosynthesis rates observed in *W. ugandensis* seedlings grown under shade can therefore be interpreted to mean that the species is probably shade-loving. The low rates of photosynthesis observed in shade-grown seedlings of *P. fulva* can be regarded as an adaptation to shade.

Seedlings of *W. ugandensis* appear to suffer under strong radiation. Impairment of photosynthesis in this species may be due to chlorophyll decomposition or reduced photosynthetic quantum efficiency. According to Björkman (1981) impairment of photosynthesis through strong radiation occurs in plants whose maximum rate of photosynthesis is already reached at low light intensities. This sensitivity is found in typical shade plants (Hariri and Prioul, 1978) as well as in shade-grown heliophilous plants (Björkman and Holmgren, 1963), and additional stress can increase the tendency towards photoinhibition. In *W. ugandensis* photosynthetic rates increased from 0.4 µmol m^{-2} s^{-1} in dense shade to 0.6 µmol m^{-2} s^{-1} in partial shade and this reduced to 0.3 µmol m^{-2} s^{-1} in full sunlight (table 2). The decline in photosynthetic rate in W. ugandensis at high PPFD may therefore, have resulted from specific damage of light harvesting pigments (Gauhl, 1979) This pattern of increased photosynthesis with increased light during growth up to intermediate levels and then a decline at high levels has been shown for shade tolerant species (Loach, 1967; Chabot and Chabot, 1977).

It is therefore probable that *W. ugandensis* is shade tolerant. The rates of photosynthesis observed in *P. fulva* and *W. ugandensis* were low compared to those found in leaves of herbs, shrubs, grasses and some trees from other environment (Larcher, 1995). Mooney and Gulmon (1982) pointed out that assimilation rates in evergreen leaves are generally low, and possibly correlated with year round photosynthesis and leaf longevity.

3.1.4 Stomatal Conductance

Stomatal conductances were greater ($P<0.01$) in seedlings of *P. fulva* grown in full sunlight and partial shade than in seedlings of *W. ugandensis* (Figure 8). Seedlings of *P. fulva* exhibited the highest stomatal conductances in full sunlight ranging from 0.007 to 0.02 mol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.003 to 0.009 mol m^{-2} s^{-1}. Stomatal conductances in seedlings of *P. fulva* grown in full sunlight were therefore 55% higher than in seedlings of *W. ugandensis*. In partial shade the stomatal conductances in seedlings of *P. fulva* were similarly higher than those of *W. ugandensis*. The stomatal conductances in seedlings of *P. fulva* ranged from 0.003 to 0.02 mol m^{-2} s^{-1}, while seedlings of *W. ugandensis* exhibited values ranging from 0.007 to 0.01mol m^{-2} s^{-1} in partial shade. Stomatal conductances in seedlings of the two species grown under moderate and dense shade were not significantly ($P>0.05$) different (Figure 9). Under moderate shade *P. fulva* seedlings showed stomatal conductance values ranging from 0.002 to 0.01 mol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.006 to 0.01 mol m^{-2} s^{-1}. The stomatal conductance values under dense shade ranged from 0.001 to 0.01 mol m^{-2} s^{-1} and 0.005 to 0.01 mol m^{-2} s^{-1} for *P. fulva* and *W. ugandensis* respectively. Like rates of photosynthesis, stomatal conductances in seedlings of *P. fulva* decreased with increasing shade. However, in seedlings of *W. ugandensis* stomatal conductances increased from dense shade to partial shade and were lowest in full sunlight (table 3). The stomatal conductances were reminiscent of the photosynthetic rates in both species, showing the highest values for full sunlight grown seedlings of *P. fulva* and shade-grown seedlings of *W. ugandensis*. It appeared that *W. ugandensis* responded to full sunlight exposure with tight stomatal closure, this leading to low stomatal conductances and hence low rates of photosynthesis.

There have been reports of extremely high stomatal conductances in tropical trees (Whitehead *et al.*, 1981; Grace *et al.*, 1982). Grace *et al.* (1982) measured stomatal conductance of 1.4 mol m^{-2} s^{-1} for *Tectona grandis* in the wet season. Similar values were measured by Whitehead *et al.* (1981) in *T. grandis* and *Gmelina arborea* in the field in Nigeria. The highest value for *G. arborea* was 1.2 mol m^{-2} s^{-1} and 3.5 mol m^{-2} s^{-1} for *T. grandis*. In the present study the conductances were not extremely high, and similar to those reported for *Triplochiton scleroxylon* by Ladipo *et al.* (1984) and also by Kwesiga and Grace (1985) in four tropical tree species. It is possible that stomatal density increased with light intensity in seedlings of *P. fulva*. This resulted in high stomatal conductances observed in this species in high PPFD. In *W. ugandensis* stomatal conductances were reduced probably due to stomatal closure and also reduced stomatal density. Several studies have demonstrated that stomatal density increases with light intensity (for example, Holmgren, 1968 and Willmot and Moore, 1973).

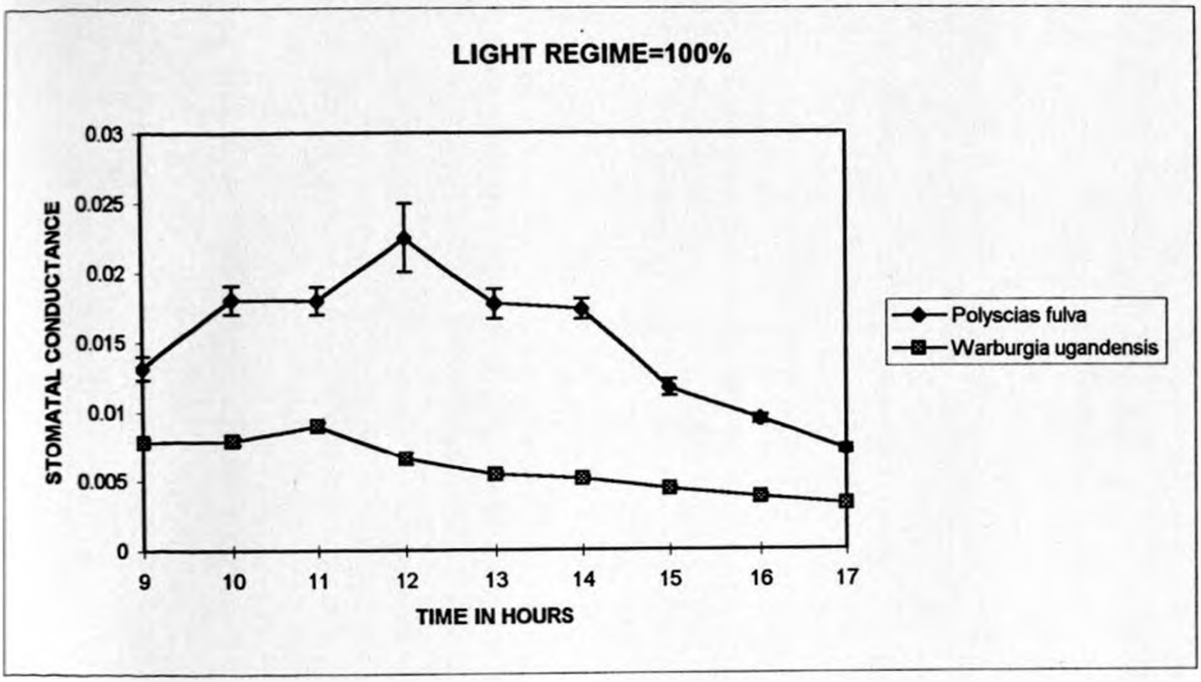
Table 3. Summary of physiological parameters: Mean photosynthetic rate (A in μmol CO_2 m^{-2} s^{-1}), transpiration rate (E in mmol H_20 m^{-2} s^{-1}), stomatal conductance (g_s in mol m^{-2} s^{-1}) and water use efficiency (WUE in μmol CO_2 mmol $^{-1}$ H_2O) in seedlings of *P. fulva* (P) and *W. ugandensis* (W) grown in four light regimes.

LIGHT REGIME

Photosynthetic parameters	Full Sunlight	Partial Shade	Moderate shade	Dense Shade
A				
P	1.4	1.0	0.5	0.4
W	0.3	0.6	0.5	0.4
E				
P	0.6	0.5	0.3	0.3
W	0.2	0.3	0.3	0.3
g_s				
P	0.02	0.01	0.009	0.008
W	0.06	0.009	0.008	0.007
WUE				
P	2.3	1.8	1.6	1.3
W	1.5	2.0	1.6	1.3

Figure 8

Diurnal course in stomatal conductances (mol m^{-2} s^{-1}) in exposed leaves of *P. fulva* and *W. ugandensis* raised in full sunlight (100% sunlight) and partial shade (65% of full sunlight) Vertical bars are the S.E. of the means.


LIGHT REGIME=100%
STOMATAL CONDUCTANCE
0.03
0.025
0.02
0.015
0.01
0.005
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

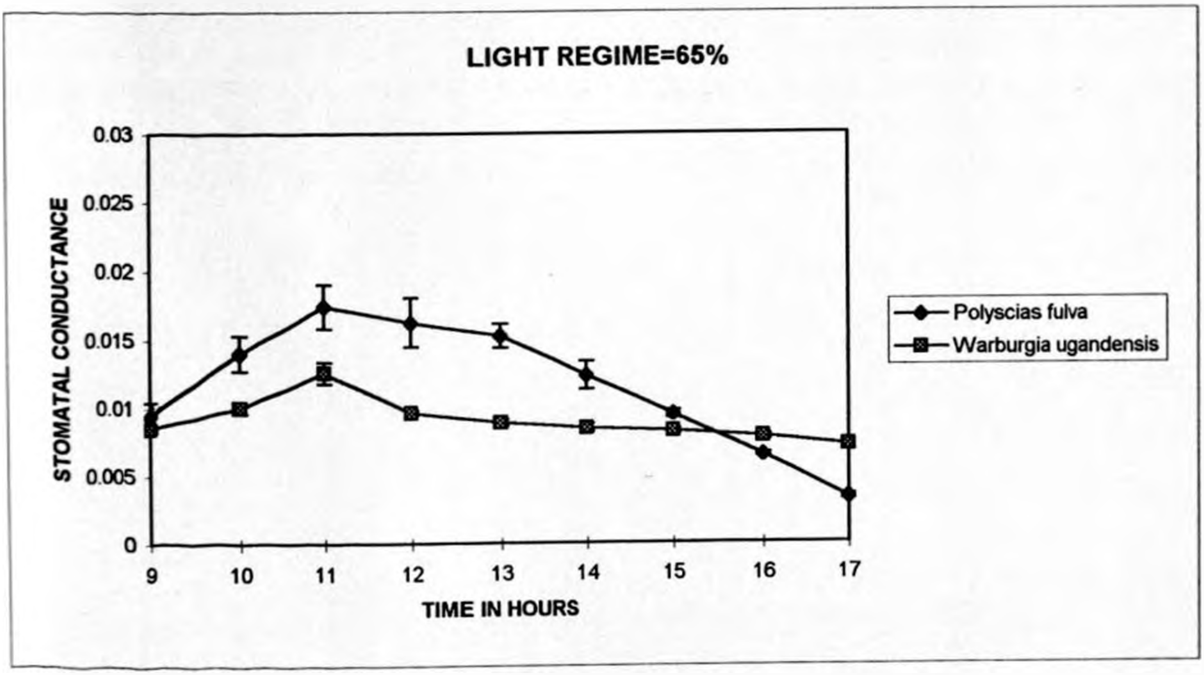
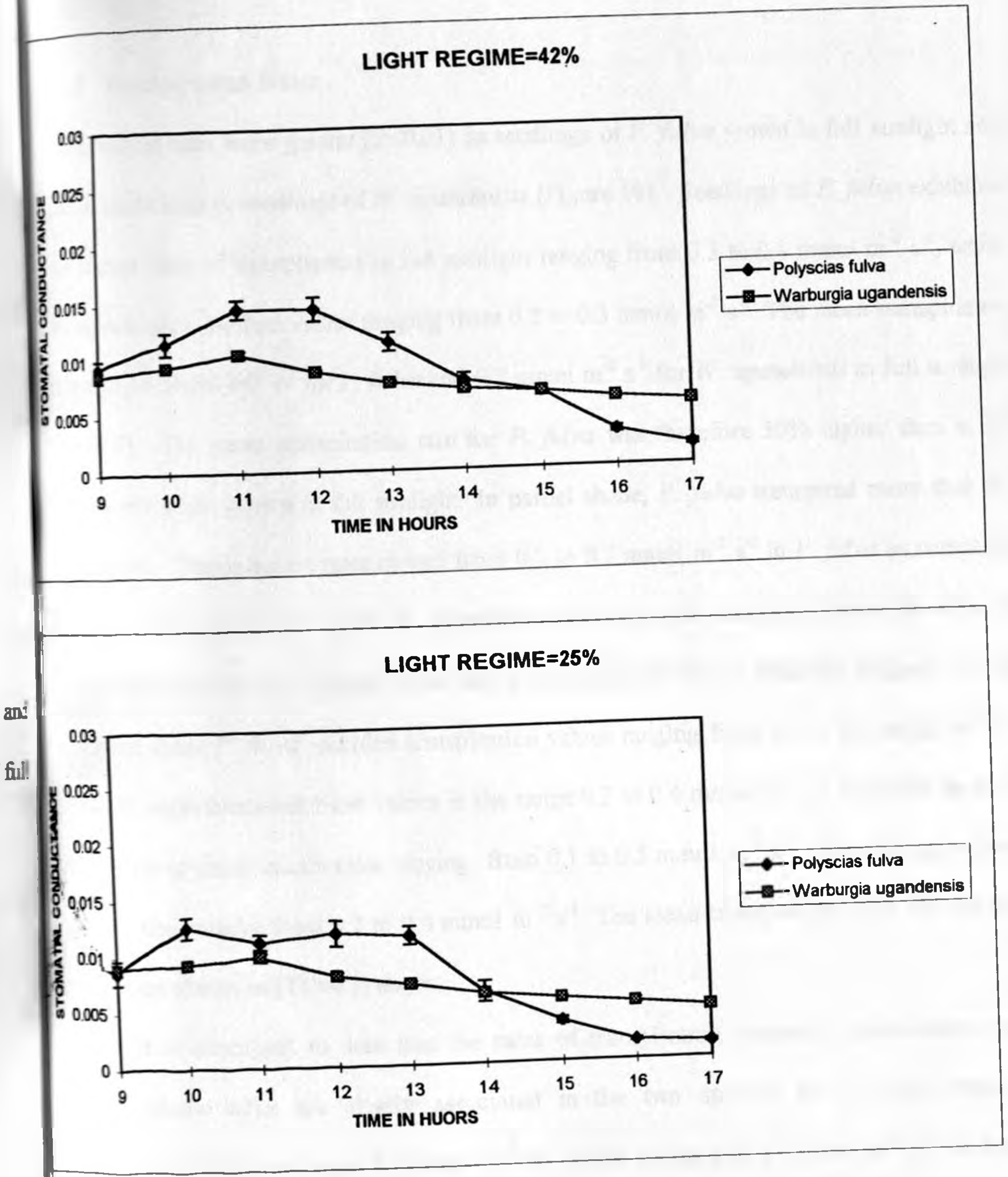

LIGHT REGIME=65%
STOMATAL CONDUCTANCE
0.03
0.025
0.02
0.015
0.01
0.005
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

Figure 9

Diurnal variations in stomatal conductances (mol m^{-2} s^{-1}) in exposed leaves of *P. fulva* an *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of ful sunlight). Vertical bars are the S.E. of the means.



3.1.5 Transpiration Rates

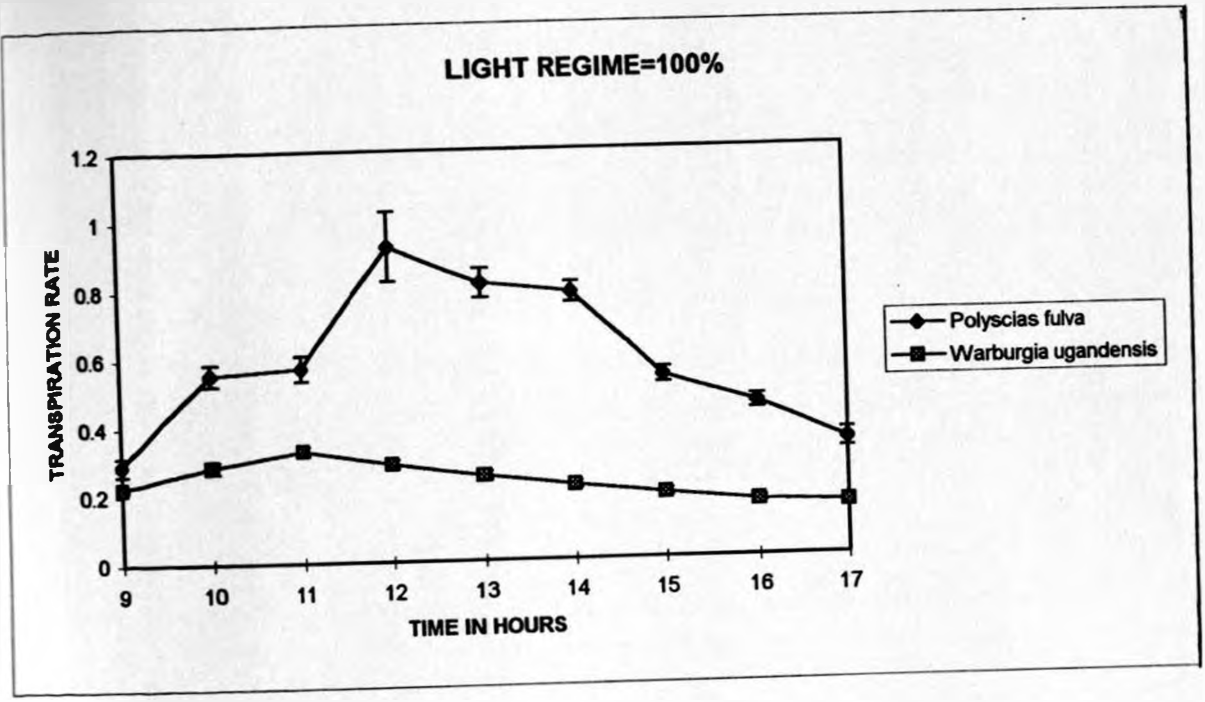
Transpiration rates were greater ($P<0.01$) in seedlings of *P. fulva* grown in full sunlight and partial shade than in seedlings of *W. ugandensis* (Figure 10). Seedlings of *P. fulva* exhibited the highest rates of transpiration in full sunlight ranging from 0.3 to 0.8 mmol m^{-2} s^{-1}, while *W. ugandensis* exhibited values ranging from 0.2 to 0.3 mmol m^{-2} s^{-1}. The mean transpiration rate was 0.6 mmol m^{-2} s^{-1} for *P. fulva* and 0.2 mmol m^{-2} s^{-1} for *W. ugandensis* in full sunlight (Table 3). The mean transpiration rate for *P. fulva* was therefore 50% higher than in *W. ugandensis* when grown in full sunlight. In partial shade, *P. fulva* transpired more than *W. ugandensis*. Transpiration rates ranged from 0.2 to 0.7 mmol m^{-2} s^{-1} in *P. fulva* as compared with 0.2 to 0.4 mmol m^{-2} s^{-1} for *W. ugandensis*. In dense and moderate shades the rates of transpiration in the two species were not significantly ($P>0.05$) different (Figure 11). In moderate shade *P. fulva* recorded transpiration values ranging from 0.1 to 0.6 mmol m^{-2} s^{-1}, while *W. ugandensis* exhibited values in the range 0.2 to 0.4 mmol m^{-2} s^{-1}. In dense shade *P. fulva* showed transpiration rates ranging from 0.1 to 0.5 mmol m^{-2} s^{-1}, while *W. ugandensis* gave values ranging from 0.2 to 0.4 mmol m^{-2} s^{-1}. The mean transpiration rates for the two species are shown in (Table 3) above.

It is important to note that the rates of transpiration, stomatal conductances and photosynthetic rates are closely associated in the two species. In *P. fulva* rates of transpiration decreased from 0.6 mmol m^{-2} s^{-1} in full sunlight to 0.3 mmol m^{-2} s^{-1} in dense shade, a pattern observed in stomatal conductances and rates of photosynthesis (Table 3). In *W. ugandensis* transpiration rates increased from 0.27 mmol m^{-2} s^{-1} in dense shade to 0.3 mmol m^{-2} s^{-1} in partial shade, and this reduced to 0.2 mmol m^{-2} s^{-1} in full sunlight, a similar trend was observed in rates of photosynthesis and stomatal conductances.

Knebitzsch *et al*. (1997) found that the rate of transpiration in *I. palembanica* in full sunlight was 0.2 mmol m^{-2} s^{-1} and this increased to 0.3 mmol m^{-2} s^{-1} in the shade. The study also observed that transpiration rate in *H. odorata* in full sunlight was 0.9 mmol m^{-2} s^{-1} and this reduced to 0.5 mmol m^{-2} s^{-1} in seedlings of the same species grown under shade. The results in the present study were similar to those observed in seedlings of *I. palembanica* and *H. odorata*. The rates of transpiration in *W. ugandensis* were the same with those of *I. palembanica* both in full sunlight and under shade. *P. fulva* appeared to behave like *H. odorata* both under shade and in full sunlight. *W. ugandensis* exhibited the lowest rates of transpiration in full sunlight. This was probably due to reduced stomatal conductances observed in this species. The species was probably unable to increase its water uptake capacity to match transpiration resulting in stomatal closure hence reduced transpiration rates at the expense of photosynthesis. *P. fulva* increased its rates of transpiration in high PPFD. This was probably due to increased stomatal conductances observed in this species. The increased stomatal conductances in *P. fulva* grown in high PPFD promoted high photosynthetic rates. Stomatal closure and photoinhibition resulted in reduced transpiration rates and photosynthesis in *W. ugandensis*.

Figure 10

Diurnal course in transpiration (mmol m^{-2} s^{-1}) in exposed leaves of *P. fulva* and *W. ugandensis* raised in full sunlight (100% sunlight) and partial shade (65% of full sunlight). Vertical bars are the S.E. of the means.


LIGHT REGIME=100%

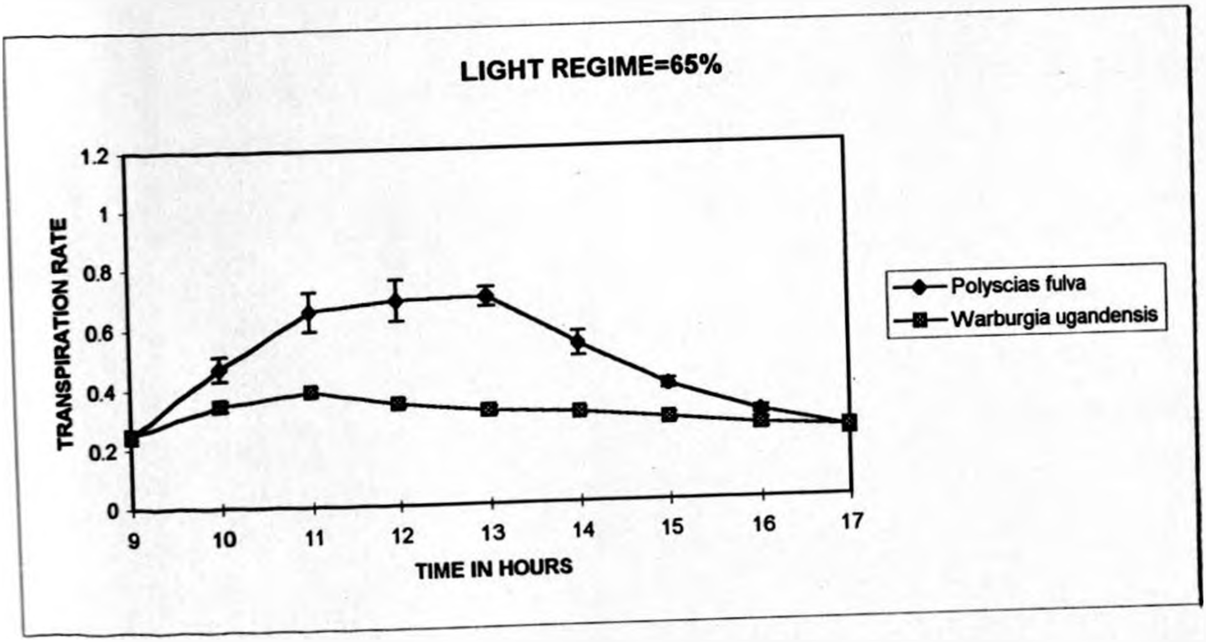
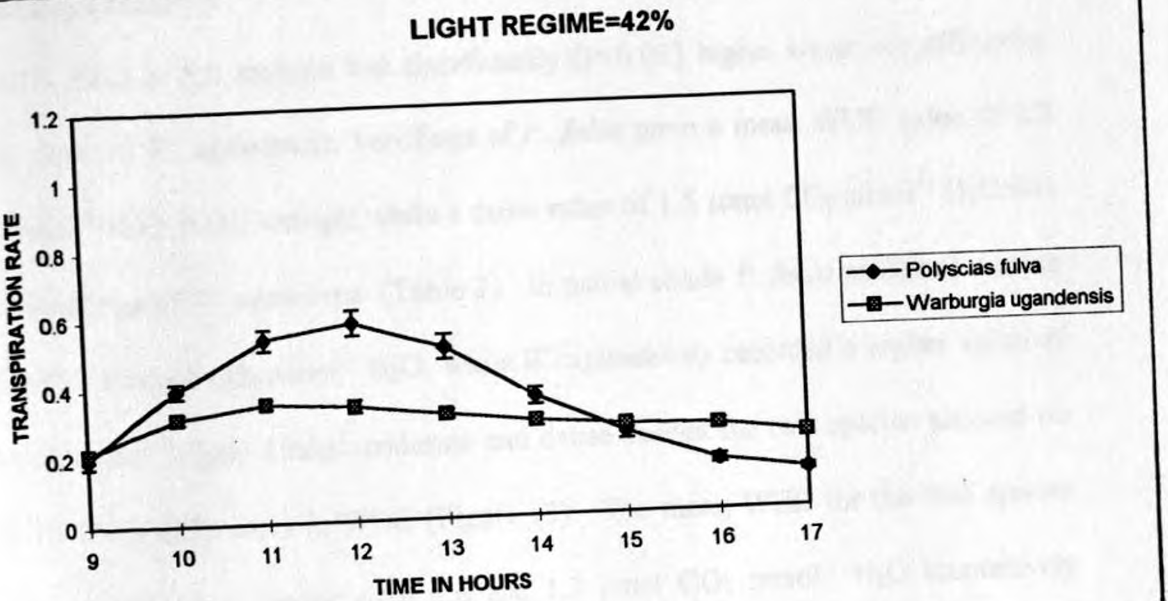
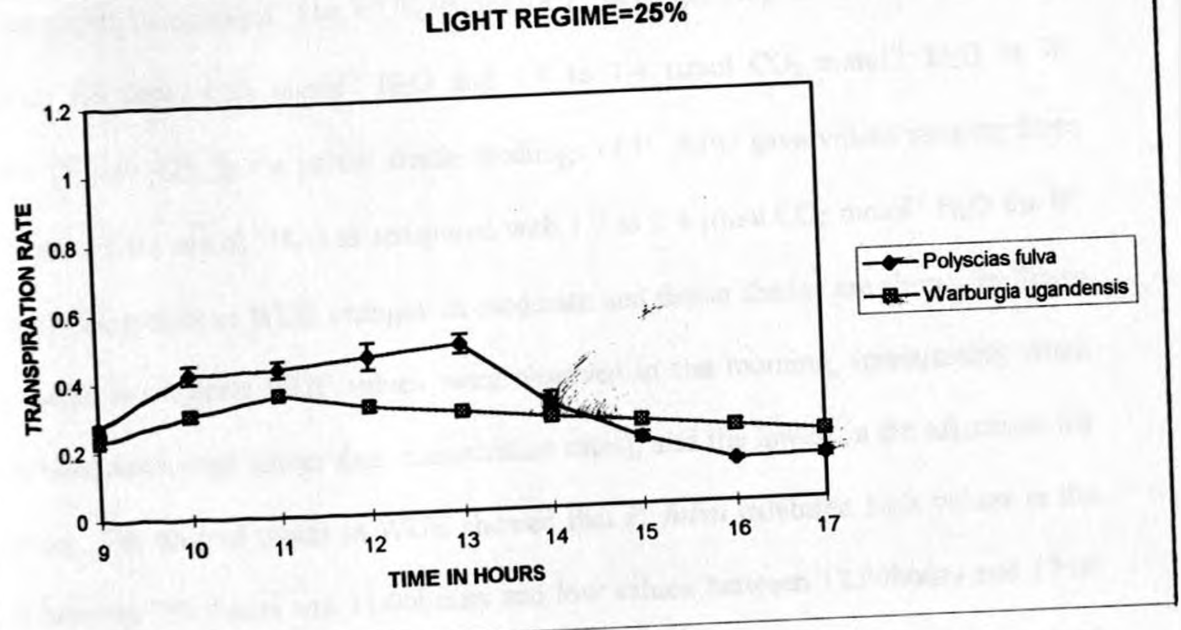

LIGHT REGIME=65%

Figure 11

Diurnal course in transpiration (mmol m^{-2} s^{-1}) in exposed leaves of *P. fulva* and *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of full sunlight). Vertical bars are the S.E. of the means.


LIGHT REGIME=42%
TRANSPIRATION RATE
1.2
1
0.8
0.6
0.4
0.2
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

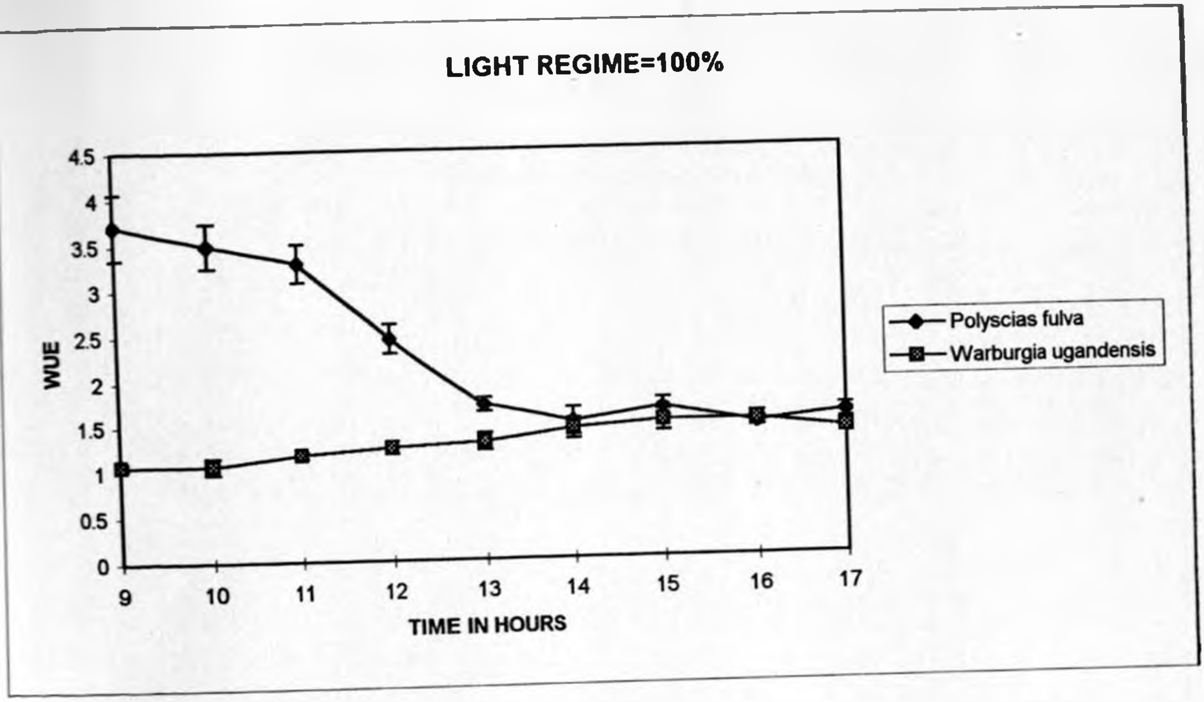

LIGHT REGIME=25%
TRANSPIRATION RATE
1.2
1
0.8
0.6
0.4
0.2
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

3.1.6 Water Use Efficiency

Seedlings of *P. fulva* in full sunlight had significantly ($P<0.01$) higher water use efficiency (WUE) than those of *W. ugandensis.* Seedlings of *P. fulva* gave a mean WUE value of 2.3 µmol CO_2 $mmol^{-1}$ H_2O in full sunlight while a mean value of 1.5 µmol CO_2 $mmol^{-1}$ H_2O was recorded in seedlings of *W. ugandensis* (Table 3). In partial shade *P. fulva* exhibited a mean WUE value of 1.8 µmol CO_2 $mmol^{-1}$ H_2O, while *W. ugandensis* recorded a higher value of 2.0 µmol CO_2 $mmol^{-1}$ H_2O. Under moderate and dense shades the two species showed no significant ($P>0.05$) differences in WUE (Figure 13). The mean WUE for the two species under moderate and dense shades were 1.6 and 1.3 µmol CO_2 $mmol^{-1}$ H_2O respectively (Table 3). The WUE values declined in both species as photosynthetic rates reduced and rates of transpiration increased. The WUE values for *P. fulva* growing in full sunlight ranged from 1.5 to 3.8 µmol CO_2 $mmol^{-1}$ H_2O and 1.0 to 1.4 µmol CO_2 $mmol^{-1}$ H_2O in *W. ugandensis* (Figure 12). In the partial shade seedlings of *P. fulva* gave values ranging from 1.4 to 2.8 µmol CO_2 $mmol^{-1}$ H_2O as compared with 1.7 to 2.4 µmol CO_2 $mmol^{-1}$ H_2O for *W. ugandensis*. The trends in WUE changes in moderate and dense shades are shown in figure 13. In general, the highest WUE values were observed in the morning, (presumably when photosynthetic rates were higher than transpiration rates), and the lowest in the afternoon for both species. The diurnal trends in WUE showed that *P. fulva* exhibited high values in the morning between 9:00hours and 11:00hours and low values between 12:00hours and 17:00 hours in full sunlight and partial shade. However, the WUE values increased slightly at 15:00 hours for *P. fulva* seedlings. This was probably due to increased stomatal conductance at this hour, leading to an increase in photosynthetic rate. The decline in WUE after 12:00 hours observed in *P. fulva* was presumably due to reduced rates of photosynthesis and increased transpiration rates (Figures 12 and 13) For *W. ugandensis* the WUE values were lower, throughout the day, than those of *P. fulva* under full sunlight. However, in partial shade WUE values for *W. ugandensis* were higher than those of *P. fulva* from 13:00 hours to 17:00 hours. This probably resulted from high stomatal conductances observed in *W. ugandensis* and hence increased photosynthesis and transpiration (Figure12). Although the two species showed no significant difference in WUE under moderate and dense shades, it is worth noting that *W. ugandensis* generally exhibited higher values than *P. fulva*. This means that WUE in *W. ugandensis* was enhanced by shade. Therefore, *W. ugandensis* lost less water while fixing a mole of CO_2 under shade, but the reverse applied for *P. fulva*. This may account for the differences observed in dry matter accumulation in the two species. Kriebitzsch *et al.* (1997) observed that WUE values in *I. palembanica* grown in full sunlight and under shade were 4.09 and 8.79 μmol CO_2 mmol^{-1} H_2O respectively. This pattern was similar to what was observed in *W. ugandensis* in full sunlight and partial shade. The study also found that *H. odorata* had higher WUE values in shade than in full sunlight. The behavior of *H.* odorata both under shade and in full sunlight is different from what was observed in *P. fulva* in the present study, despite the two species showing higher photosynthetic rates and rates of transpiration in full sunlight than under shade. *W. ugandensis* appeared to close its stomatal in full sunlight and hence low rates of photosynthesis, stomatal conductance, transpiration rates and hence reduced WUE. 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. The high WUE for *P. fulva* compared to *W. ugandensis* in full sunlight showed that the species lost less water while fixing a molecule of CO_2. Under shade, *W. ugandensis* raised its photosynthetic rates and hence higher WUE than in full sunlight.

Figure 12

Diurnal course in water use efficiency (μmol CO_2 $mmol^{-1}$ H_2O) in exposed leaves of *P. fulva* and *W. ugandensis* raised in full sunlight (100% sunlight) and partial shade (65% of full light). Vertical bars are the S.E. of the means.


LIGHT REGIME=100%
WUE
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

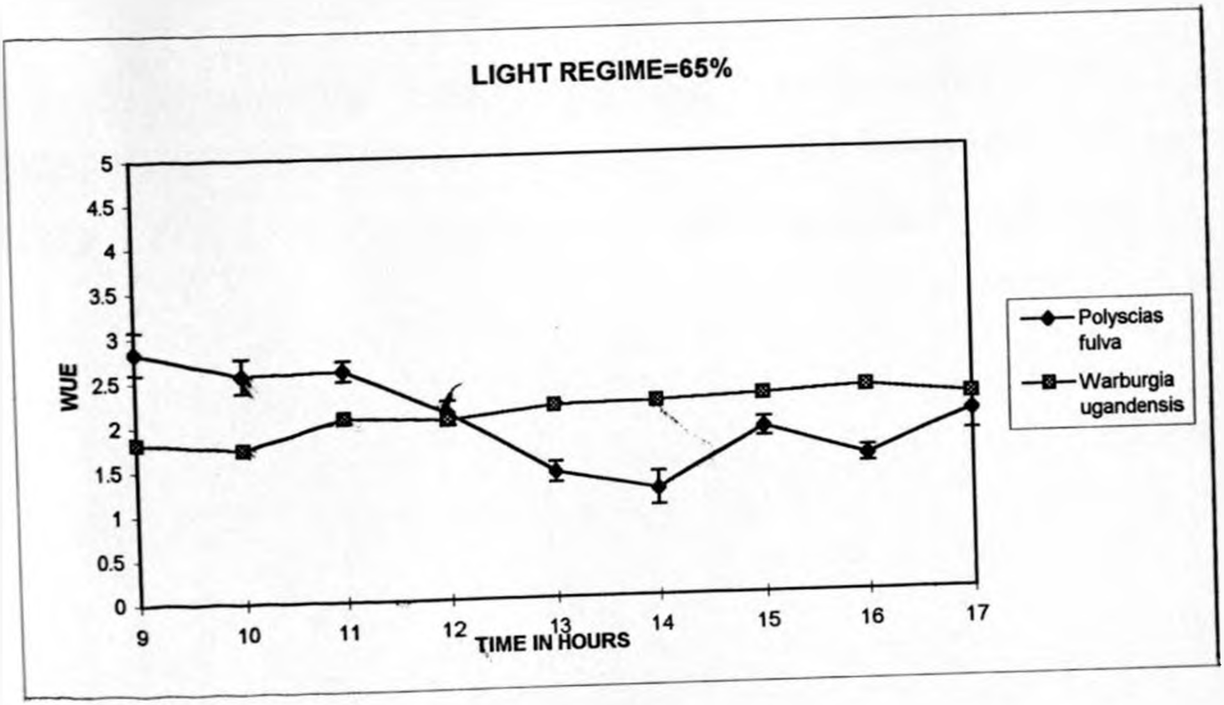
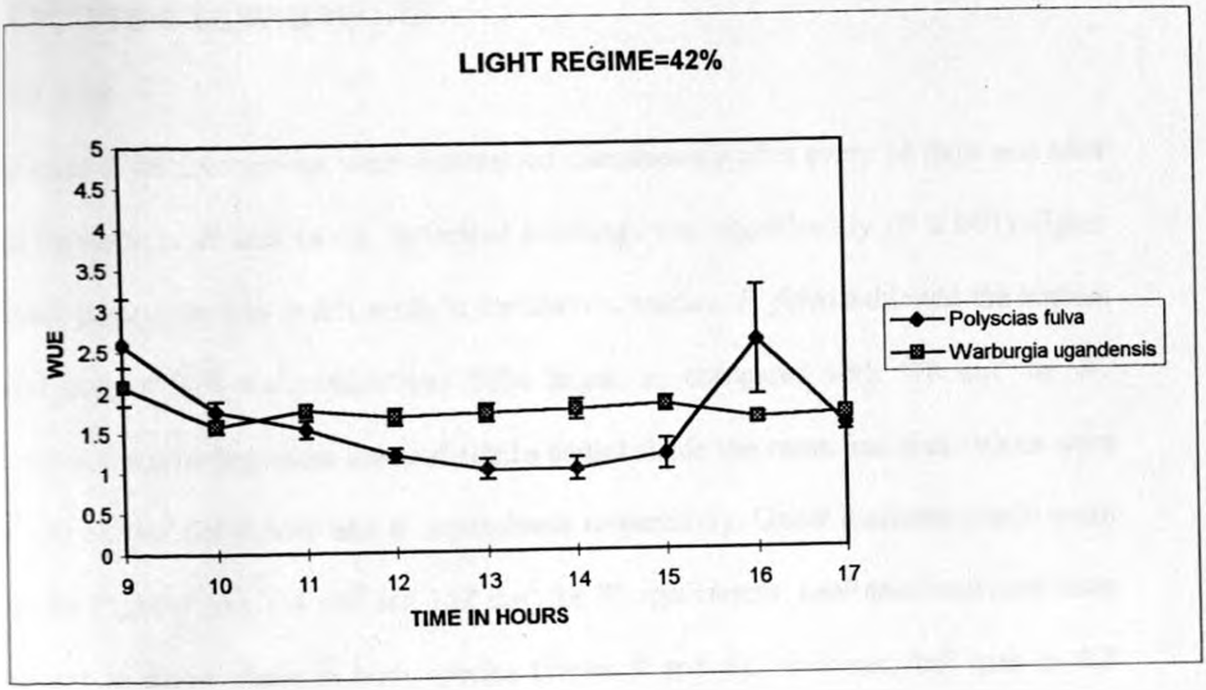
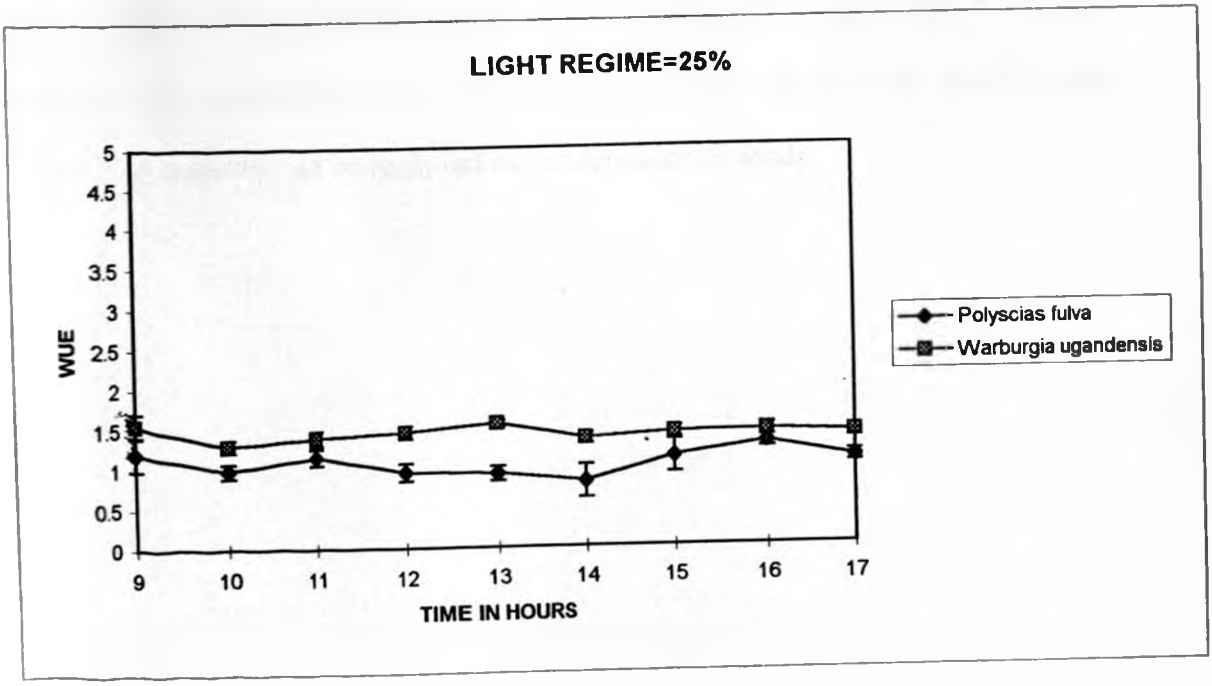

LIGHT REGIME=65%
WUE
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

Figure 13

Diurnal course in water use efficiency (µmol CO_2 $mmol^{-1}$ H_2O) in exposed leaves of *P. fulva* and *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of full sunlight). Vertical bars are S.E. of the means.


LIGHT REGIME=42%
WUE
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis


LIGHT REGIME=25%
WUE
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
9
10
11
12
13
14
15
16
17
TIME IN HOURS
Polyscias fulva
Warburgia ugandensis

3.2.0 GROWTH MEASUREMENTS

3.2.1 Leaf Area

The leaf areas of the two species were determined continuously after every 14 days and after the final harvests. Leaf area of the harvested seedlings was significantly ($P<0.001$) higher under shade treatments than in full sunlight for the two species. *P. fulva* exhibited the highest mean leaf area of 376 cm^2, which was 50% larger, as compared with 178 cm^2 for *W. ugandensis* when growing under dense shade.In partial shade the mean leaf area values were 253cm^2 and 117cm^2 for *P.fulva* and *W. ugandensis* respectively. Under moderate shade mean leaf area for *P. fulva* was 336 cm^2 and 152 cm^2 for *W. ugandensis*. Leaf area increased from full sunlight to dense shade in both species (tables 4 and 5). However, leaf area in full sunlight was significantly ($P<0.0001$) higher in *P. fulva* than in *W. ugandensis.* It appeared that the two species responded to shade by increasing the leaf area, but with varying degree of plasticity. This response can be regarded as an adaptation to shade.

Table 4. Mean values of growth measurements. Dry weight (DW in g), leaf area (LA in cm^2), specific leaf area (SLA in cm^2 g^{-1}), shoot/root ratio (S/R in gg^{-1}), number of surviving leaves (N) and height (H in mm) of *P. fulva* seedlings grown at four different light regimes. Mean values and standard deviations (S_x) are calculated from measurements on 30 seedlings. Values in dense and moderate shades differ significantly from those of full light and partial shade treatments (P=0.05).

LIGHT REGIMES

Growth parameter	Full Sunlight	Partial shade	Moderate shade	Dense Shade
DW	8.92	6.96	4.80	4.03
S_x	± 1.53	±1.07	±0.90	±0.72
N	28	31	35	37
S_x	±1.55	±2.42	±3.37	±2.35
LA	238	252.49	335.60	376.0
S_x	±46.89	±47.61	±62.68	±47.72
SLA	71.16	104.24	155.36	198.06
S_x	±13.68	±7.29	±8.52	±0.28
S/R	0.97	1.21	1.58	1.84
S_x	±0.14	±0.18	±0.30	±0.28
H	19.72	23.36	30.31	38.03
S_x	±3.09	±5.78	±2.89	±4.25

Table 5. Mean values of growth measurements. Dry weight (DW in g), Leaf Area (LA in cm^2), number of surviving leaves (W), specific leaf area (SLA in cm^2 g^{-1}), shoot/root ratio (S/R in gg^{-1}) and Height (H in mm) of seedlings of *W. ugandensis* grown at four different light regimes. Mean values and standard deviations (S_x) are calculated from measurements on 30 seedlings. Values in dense and moderate shade differ significantly from those of full sunlight and partial shade treatments. (P= 0.05)

LIGHT REGIMES

Growth parameter	Full sunlight	Partial shade	Moderate shade	Dense Shade
DW	0.62	2.43	1.72	1.46
S_x	± 0.34	± 1.17	±0.30	±0.48
N	21	25	26.28	28.94
S_x	± 7.63	±7.57	±2.89	±2.19
LA	33.13	117.16	151.49	177.80
S_x	±19.94	±53.23	±33.41	±30.40
SLA	105.39	123.87	187.86	220.70
S_x	±11.79	±11.68	±13.36	±31.44
S/R	2.73	3.45	5.41	6.42
S_x	±0.91	±0.85	±1.50	±1.39
H	35.64	49.11	74.89	89.42
S_x	±5.77	±8.75	±14.26	±10.09

Both species showed the highest rates in leaf expansion under shade treatments than in full sunlight (Figures 14 and 15). The highest growth in leaf area was attained when seedlings of both species were grown under dense shade. The rate of leaf expansion for *P. fulva* was 0.1 cm^2 /day, while for *W. ugandensis* it was 0.04 cm^2 /day in full sunlight. *P. fulva* exhibited the highest rate of leaf area expansion under dense shade. The rates were 0.5cm^2/day and 0.1cm^2/dayfor *P. fulva* and *W. ugandensis* respectively,under dense shade (table 6). The rate of leaf expansion was significantly ($P<0.001$) higher in *P. fulva* than *W. ugandensis* when grown under dense and moderate shades. The rate of leaf area expansion was not significantly ($P>0.05$) different for the two species in full sunlight and partial shade. The rates of leaf area expansion remained the same for W. ugandensis seedlings growing under partial, moderate and dense shade (table 6). In general, the highest growth in leaves of both species were observed in the first 28 days after unfolding with *P. fulva* exhibiting the highest values than *W. ugandensis* in full sunlight and in shade treatment (Figures 14 and 15). Although the two species showed a similar pattern in leaf area in response to shade *P. fulva* showed a higher degree of plasticity in leaf area than *W. ugandensis*. This was clearly depicted by the higher mean leaf area values recorded in *P. fulva* (table 4) and also higher rates of leaf expansion than *W. ugandensis* in the four light regimes.

Figure 14

Temporal changes in leaf area (cm^2) in seedlings of *P. fulva* and *W. ugandensis* grown in full light (100% sunlight) and in partial shade (65%of full sunlight). Vertical bars are S.E. of the means.

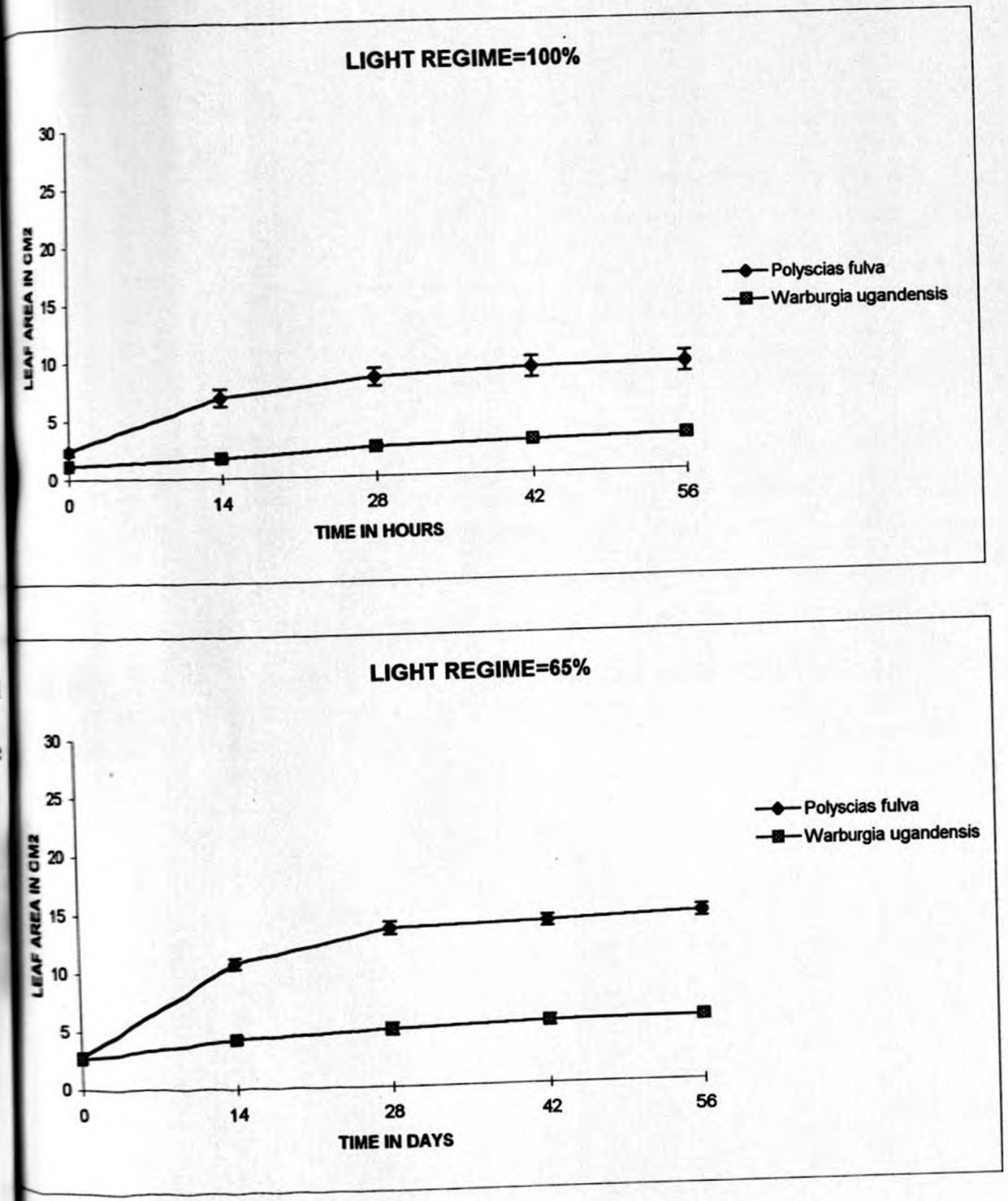
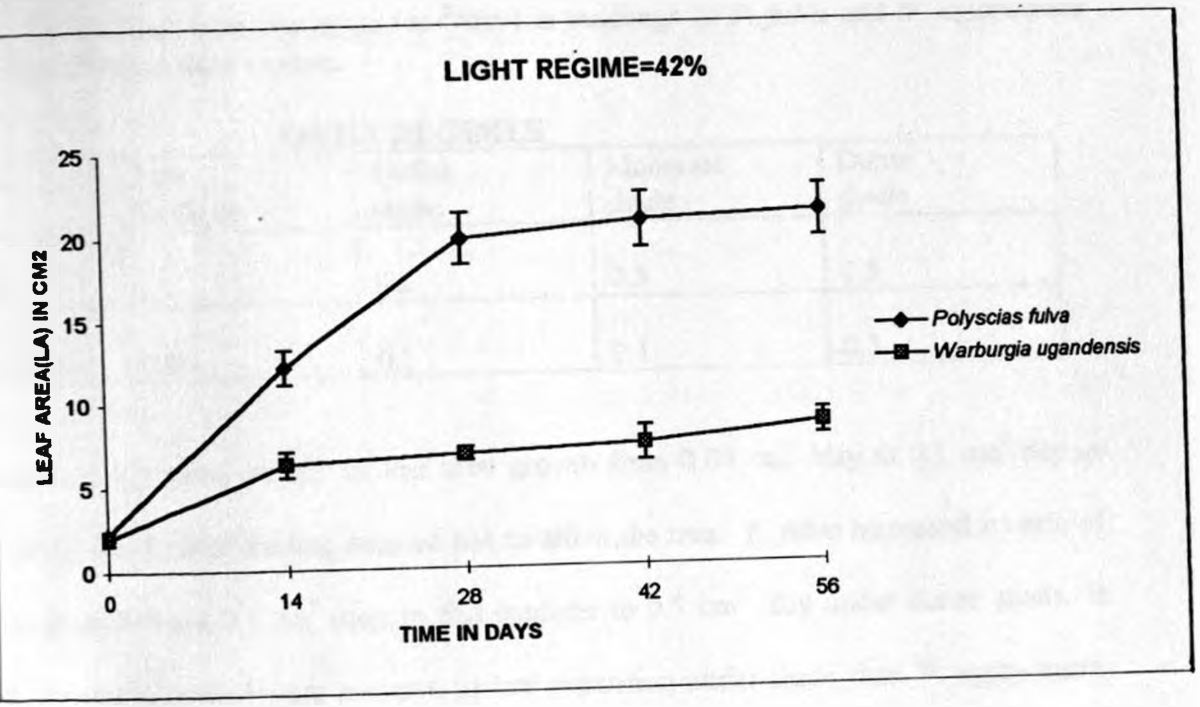


Figure 15

Temporal changes in leaf area (cm^2) in seedlings of *P. fulva* and *W. ugandensis* grown in moderate shade (42% of full sunlight) and in dense shade (25% of full light). Vertical bars are S.E. of the means.


LIGHT REGIME=42%
LEAF AREA(LA) IN CM2
0
5
10
15
20
25
0
14
28
42
56
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

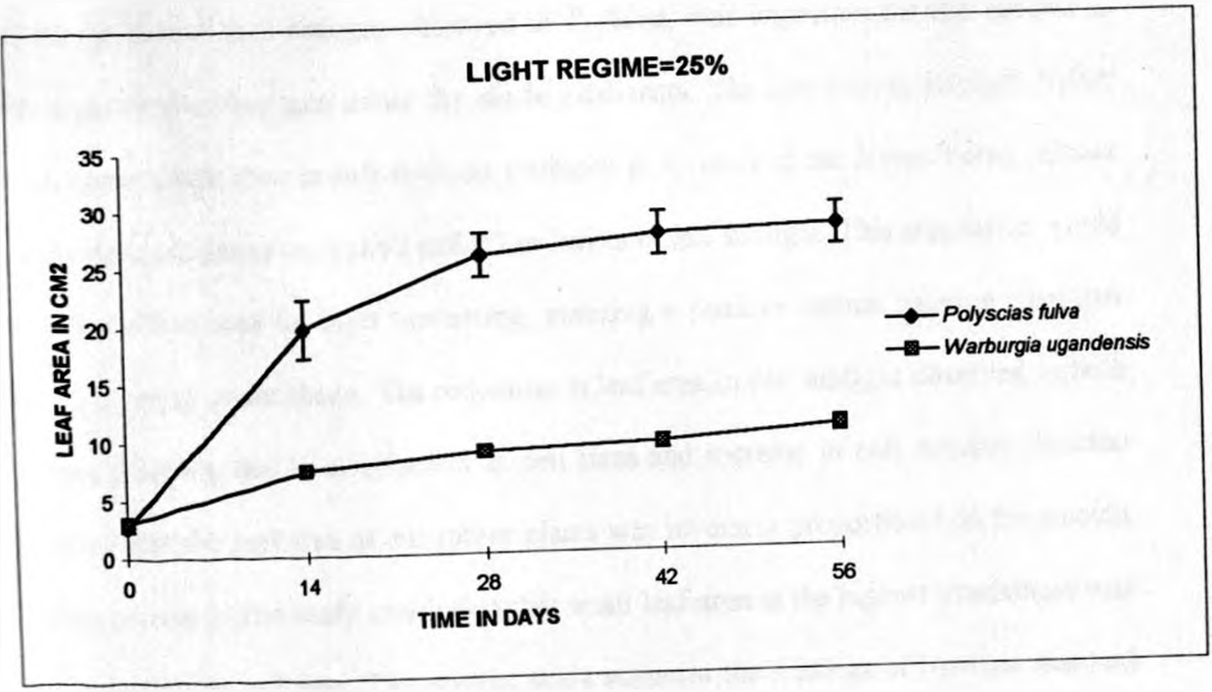

LIGHT REGIME=25%
LEAF AREA IN CM2
0
5
10
15
20
25
30
35
0
14
28
42
56
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

Table 6. Rates of leaf area expansion (cm^2/day) in seedlings of *P. fulva* and *W. ugandensis* grow in four different light regimes.

LIGHT REGIMES

Species	Full sunlight	Partial shade	Moderate shade	Dense shade
P. fulva	0.1	0.2	0.3	0.5
W. ugandensis	0.04	0.1	0.1	0.1

W. ugandensis increased its rate of leaf area growth from 0.04 cm^2 /day to 0.1 cm^2/day in partial shade and further shading seemed not to affect the rate. *P. fulva* increased its rate of leaf area growth from 0.1 cm^2 /day in full sunlight to 0.5 cm^2 /day under dense shade. It seemed *P.fulva* allocated more resource to leaf expansion under shade than *W. ugandensis*. This plasticity in leaf area changes observed in *P. fulva*, was important for the species to maintain a positive carbon gain under the shade treatments. The two species attained higher leaf areas under shade than in full sunlight probably as a result of the leaves being thinner and also having less dense mesophyll cells than leaves in full sunlight. This adaptation would increase the surface area for light harvesting, ensuring a positive carbon balance when the species are growing under shade. The reduction in leaf area in full sunlight observed in both species was probably due to a reduction in cell sizes and increase in cell number. Newton (1963) found that the leaf area of cucumber plants was inversely proportional to the amount of radiation received. The study concluded that small leaf area at the highest irradiances was due to a reduction in cell size. The current study supports the findings of Newton that leaf area varies with the amount of PPFD received. Kriebitzsch *et* al. (1997) found similar results in seedlings of *I. palembanica* and *H. odorata* that showed higher leaf areas when growing in shade than in full sunlight. Cocoa and coffee leaves that expanded in full sunlight were smaller and yellowish-green, while those growing in shade tended to be large and dark green in colour (Murrray and Nichol, 1966).

Oberbauer and Strain (1986) compared the leaf sizes in *Pentaclethra macroloba* in understorey, mid-canopy and canopy layers. The study found that leaf areas increased from the canopy level to the understorey and this was due to light. The findings support the results in the current study in that changes in leaf areas of the species resulting from a gradient of light parallel leaf area changes along the canopy gradient. It is therefore apparent that seedlings grown under artificial shades can provide a fair representation of leaf characteristics of seedlings and mature trees in the forest.

The two species had the highest leaf area changes during the first 28 days after unfolding and thereafter growth levels out (Figure 14 and 15). However, *P. fulva* demonstrated considerable capacity to vary leaf area in the four light regimes. This showed that leaf growth in the two species was determinate and the period of expansion limited. Leaf growth involves both cell division and cell enlargement and the cell number and final sizes reached are affected by external factors, (like light) internal and genetic factors (Longman and Jenik, 1987). It is therefore possible that in seedlings of *P. fulva* and *W. ugandensis* growing under shade cell enlargement was higher than in full sunlight and this could be the reason why the two species attained the greatest leaf areas under shade. The present study therefore supports the findings of other works (for example, Newton, 1963; Oberbauer and Strain, 1986, Murray and Nichol, 1966 and Kriebitzsch *et al*., 1997) that shade increases the leaf area of plant species. However, it is important to point out that the degree of plasticity in leaf area seems to be species specific as was observed in *P. fulva* and *W. ugandensis*.

3.2.2 Leaf Number and Leaf Loss

In both species the number of leaves increased with reducing PPFD, though at different rates. *P. fulva* had the highest number of surviving leaves than *W. ugandensis* in all the light regimes. In the four light regimes leaf number increased with time in seedlings of the two species (Figures 16 and 17). Leaf number was significantly ($P< 0.01$) higher in moderate and dense shades than in full sunlight and partial shade for seedlings of the two species (see Tables 4 and 5). The pattern of leaf formation was similar in the two species, in that each species increased its rate of leaf formation in response to increased shade. *P. fulva* exhibited a leaf formation rate of 1.4 leaves/day in full sunlight and this increased to 2.2 leaves/day under dense shade. For seedlings of *W. ugandensis* the rate of leaf formation was 1.1 leaves/day in full sunlight and 1.9 leaves/day under dense shade (Table 7). The rate of leaf formation was relatively faster for *P. fulva* seedlings than in seedling of *W. ugandensis* in the four treatments.

The higher leaf area observed in *P. fulva* in relation to *W. ugandensis* in all the treatments (Tables 4 and 5) was possibly as a result of the species having higher number of leaves with higher rates of expansion than the latter. The two species responded to reduced PPFD by increasing the number of leaves. This can be regarded as an adaptation to shade in the two species.

The greater leaf number under shade treatments enabled the species to increase their leaf area index and hence surface area for harvesting light. In *P. fulva*, leaf number and high rates of leaf expansion ensured higher leaf area than in *W. ugandensis* in the four treatments. It is therefore possible that leaf number played an important role in light harvesting capacities of the two species and thus rates of photosynthesis and dry matter accumulation.

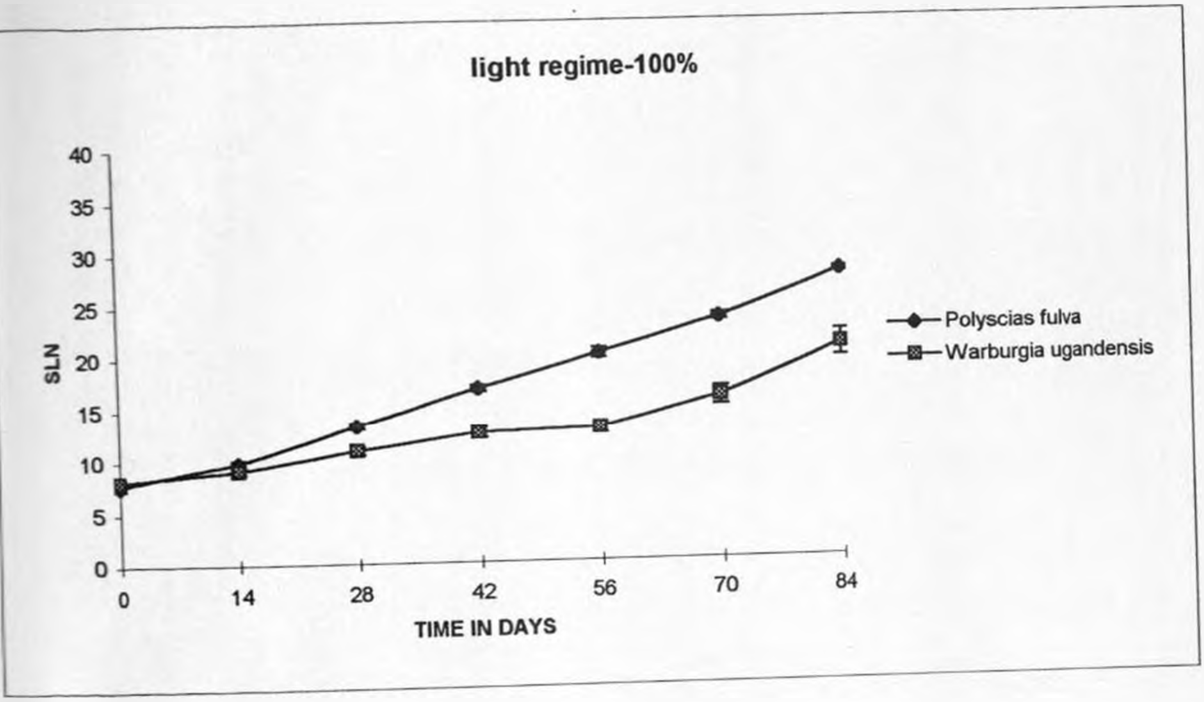
Table 7. Rates of leaf formation (in leaves/day) in seedlings of *P. fulva* and *W. ugandensis* grown under four different light regimes.

	LIGHT REGIMES			
SPECIES	Full sunlight	Partial shade	Moderate shade	Dense shade
P. fulva	1.4	1.7	2	2
W. ugandensis	1.1	1.4	1.6	1.9

Kriebitzsh *et al.* (1997) found that leaf numbers in *Intsia palembanica* and *Hopea odorata* were higher in shade than in full light. The result are similar with those of the current study in that both *P. fulva* and *W. ugandensis* showed higher leaf numbers under shade treatment than in full sunlight. However, differences in number of leaves do occur in tropical trees in response to light. For example, Kigomo (1990) observed that leaf number in *B. huillensis* was higher in full light than in shaded treatments. Kwesiga and Grace (1986) found similar results when working with *Khaya senegalensis* and *Terminalia invorensis*. These studies confirm the observation that tree species respond differently to environmental factors (Denslow, 1980).

Figure 16

Temporal changes in number of surviving leaves (SLN) in seedlings of *P. fulva* and *W. ugandensis* grown in full sunlight (100% sunlight) and partial shade (65% of full sunlight). Vertical bars are S.E. of the means.


light regime-100%
40
35
30
25
20
15
10
5
0
SLN
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

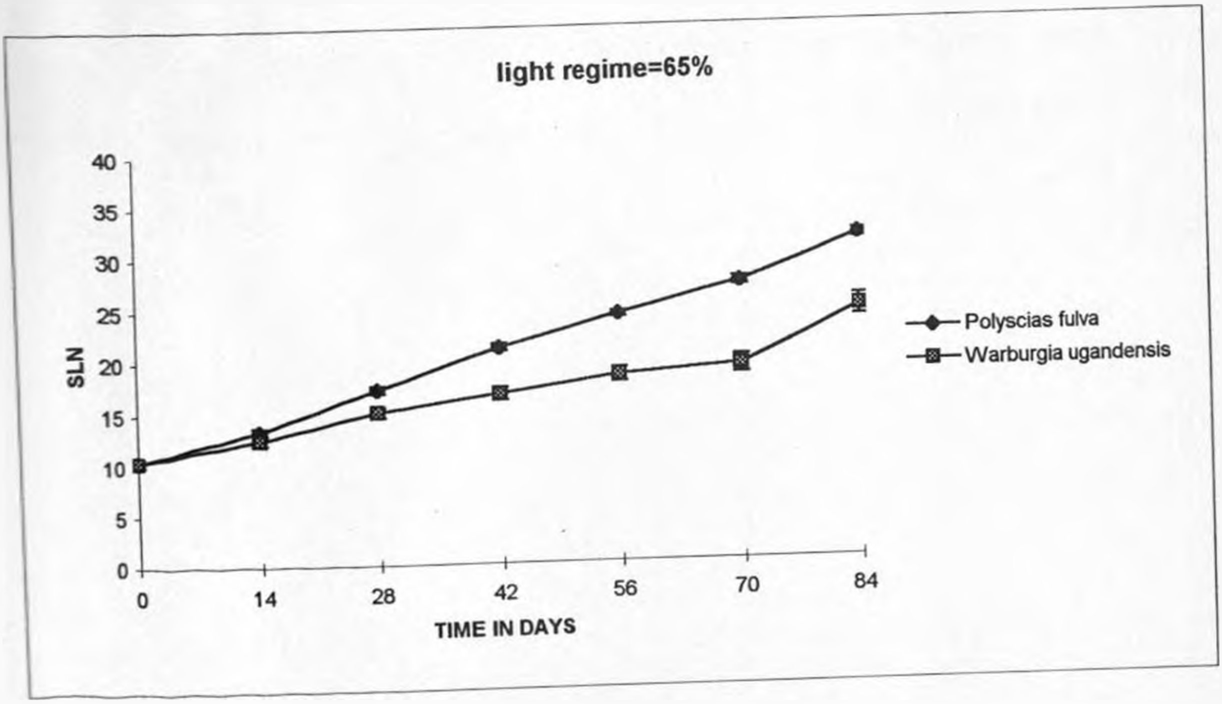
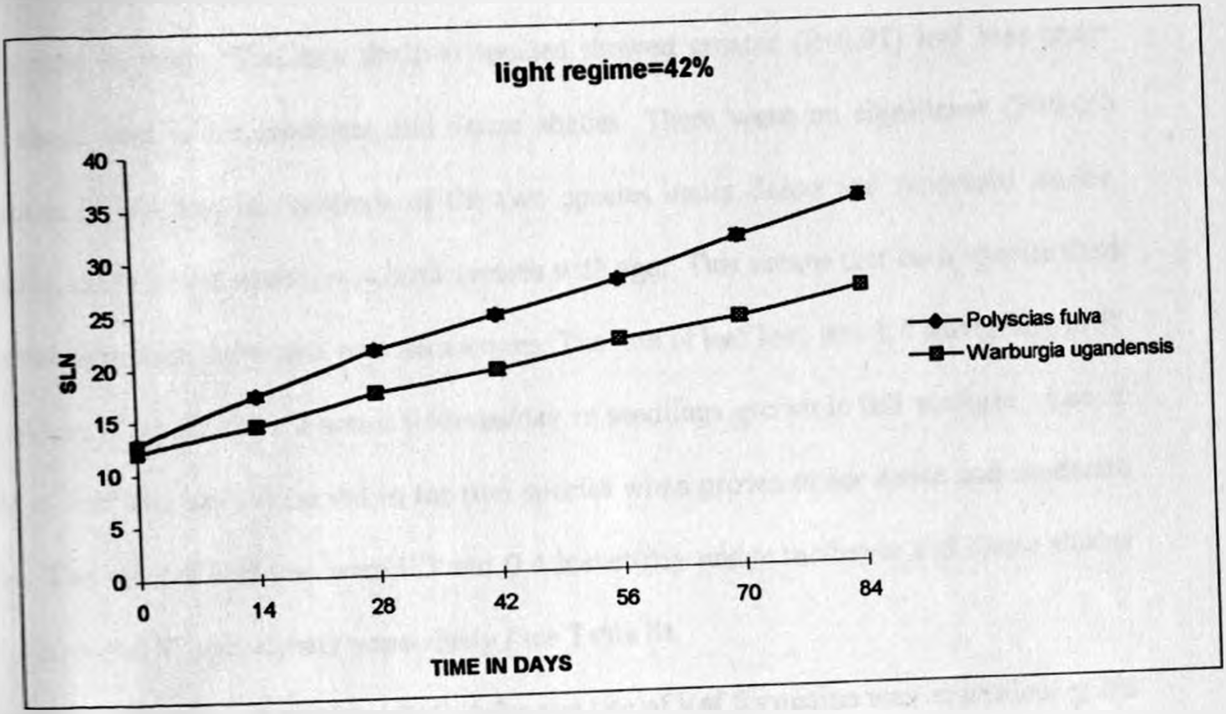
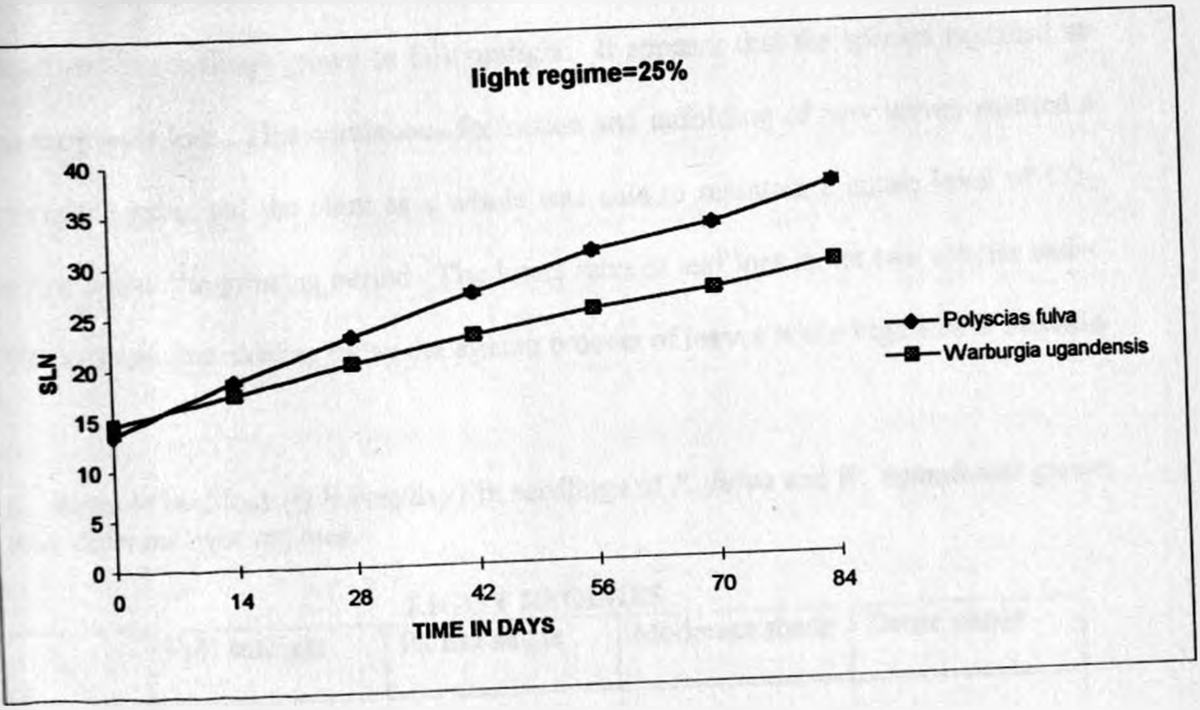

light regime=65%
40
35
30
25
20
15
10
5
0
SLN
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

Figure 17

Temporal changes in number of surviving leaves (SLN) in seedlings in seedlings of *P. fulva* and *W. ugandensis* grown in moderate shade (42% of full sunlight) and in dense shade (25% of full sunlight). Vertical bars are S.E. of the means.


light regime=42%
SLN
40
35
30
25
20
15
10
5
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis


light regime=25%
SLN
40
35
30
25
20
15
10
5
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

Leaf loss was significantly ($P<0.001$) higher in seedlings of both species when grown in full sunlight than in shade. Similarly the two species showed greater ($P<0.01$) leaf loss under partial shade than under moderate and dense shades. There were no significant ($P>0.05$) differences in leaf loss in seedlings of the two species under dense and moderate shades. Generally, more leaves were lost in both species with age. This means that each species shed old leaves to replace them with new active ones. The rate of leaf loss was 1.4 leaves/day in *P. fulva*, while *W. ugandensis* it was 0.9 leaves/day in seedlings grown in full sunlight. Lower values of leaf loss were observed in the two species when grown under dense and moderate shades. The rates of leaf loss were 0.3 and 0.4 leaves/day under moderate and dense shades for *P. fulva* and *W. ugandensis* respectively (see Table 8).

It is interesting to note that in *P. fulva* the rate of leaf formation was equivalent to the rate of leaf loss in seedlings grown in full sunlight. It appears that the species replaced its leaves as they were lost. This continuous formation and unfolding of new leaves ensured a constant carbon gain, and the plant as a whole was able to maintain a stable level of CO_2 fixation throughout the growing period. The lower rates of leaf loss in the two species under low PPFD indicate that shading delay the ageing process of leaves while high PPFD increase it.

Table 8. Rates of leaf loss (in leaves/day) in seedlings of *P. fulva* and *W. ugandensis* grown under four different light regimes.

	LIGHT REGIMES			
Species	Full sunlight	Partial shade	Moderate shade	Dense shade
P. fulva	1.4	0.9	0.3	0.4
W. ugandensis	0.9	0.6	0.4	0.4

[illegible]

[illegible] and D. respectively (see Table 8).

It is interesting to note that in B. [illegible] the rate of leaf formation was equivalent to the [illegible] in shade as grown in full sunlight. It appears that the species replaced its [illegible] as they were lost. This continuous formation and unfolding of new leaves ensured a [illegible] carbon gain, and the plant as a whole was able to maintain a stable level of CO_2 [illegible] throughout the growing period. The lower rates of leaf loss in [illegible] that shading [illegible]

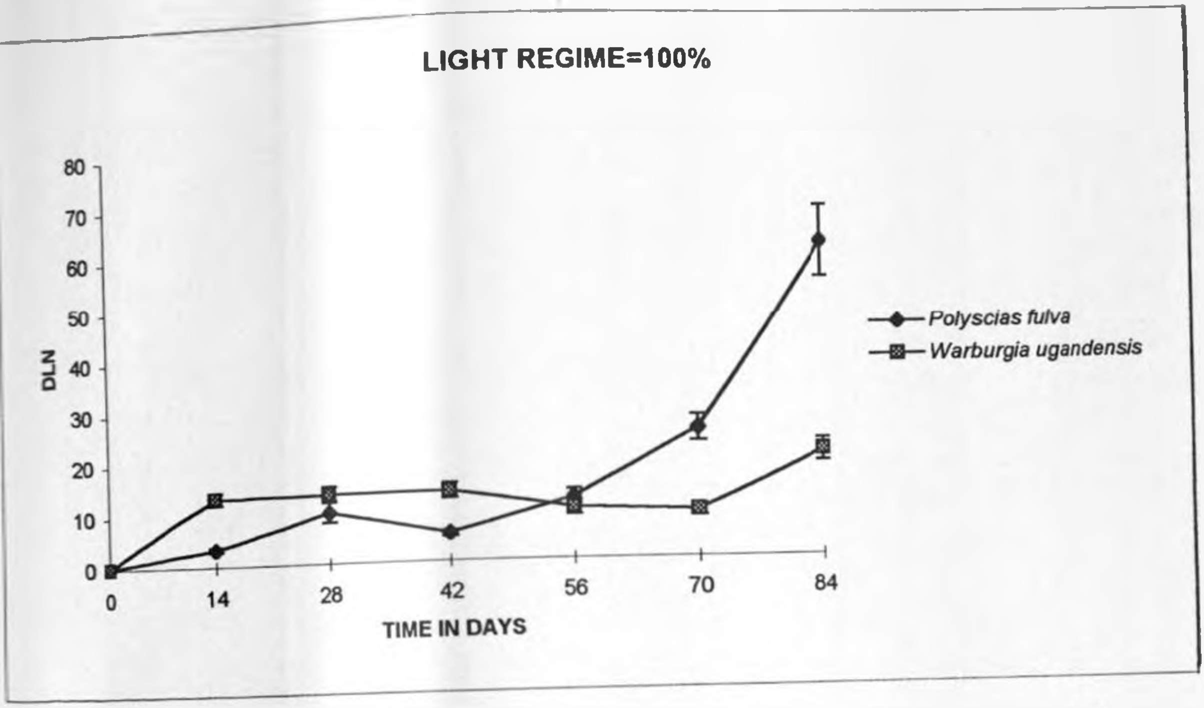
[illegible] Rates of leaf loss (in leaves/day) in [illegible] grown under different light regimes.

	Dense shade	Partial shade	Full sunlight	
	[illegible]	0.9		
	0.4	0.6	1.9	[illegible]mmer:

Figures 18 and 19 show that leaf shedding in both species increased with age of the seedlings with *P. fulva* recording higher values than *W. ugandensis* after 42 days of growth in all the treatments. In full sunlight *W. ugandensis* lost more leaves than *P. fulva* in the first 56 days of growth after which leaf shedding is higher in *P. fulva* (Figure 19). In partial shade both species shed the same number of leaves for the first 42 days of growth but later more leaves were lost in *P. fulva* than in *W. ugandensis*. It appears *W. ugandensis* responded to increased PPFD by shedding leaves, a pattern similar to that observed in *P. fulva*. It is therefore possible that under high PPFD the seedlings were subjected to a high heat load and increasing temperature (see Table 1) hence the need to increase leaf loss to cut down on transpiration. This is supported by the observation that transpiration was high in both species under partial shade and in full sunlight (Table 3). *W. ugandensis* responded to the high PPFD and temperature associated with full sunlight treatment by not only shedding its leaves but also reducing its stomatal conductances hence low rates of photosynthesis and dry matter accumulation. *P. fulva* on the other hand responded to high PPFD and temperature by shedding leaves like *W. ugandensis*, but it increased its stomatal conductances and also replaced the shed leaves with new active ones ensuring high photosynthetic rate and also more biomass accumulation as compared with *W. ugandensis*. The high rate of leaf loss in *P. fulva* can be important in the natural environment because it can provide good mulch and also make the soil under the tree quite fertile, this, together with the spreading, open crown make it a potentially excellent agroforestry species.

Figure 18

Leaf loss (Number of leaves lost) in seedlings of *P. fulva* and *W. ugandensis* raised in full sunlight (100% sunlight) and partial shade (65% of full sunlight). Vertical bars are S.E. of the means.


LIGHT REGIME=100%

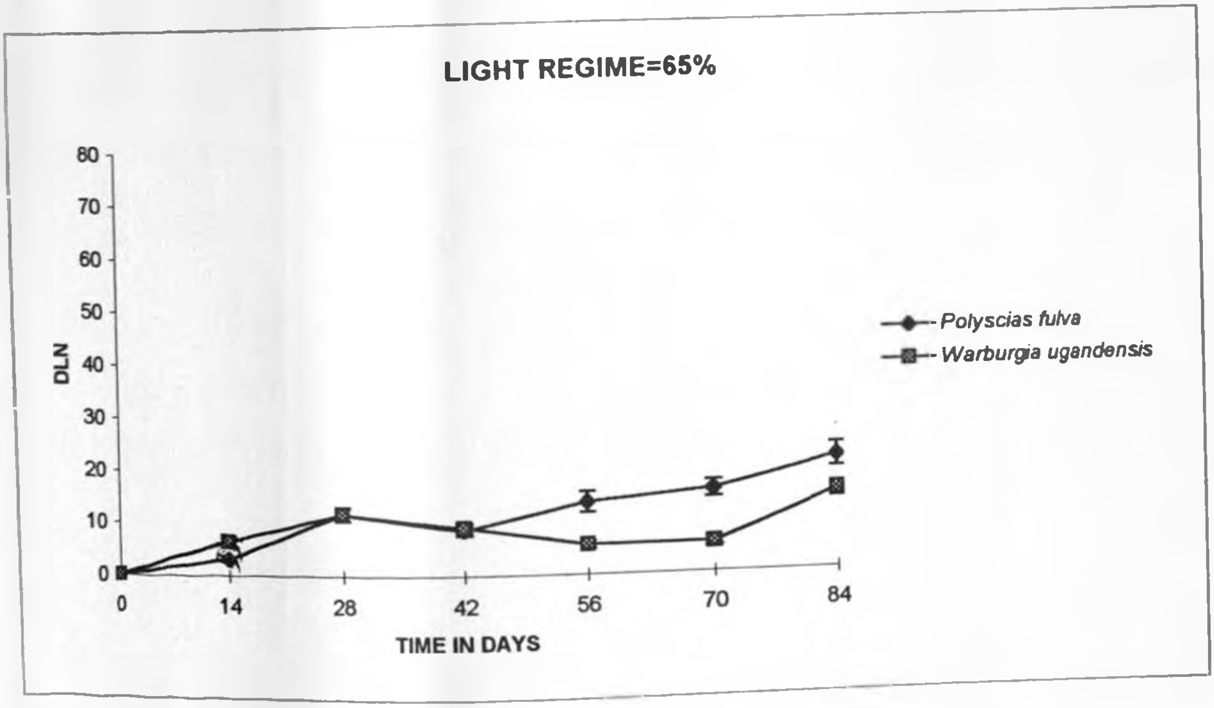
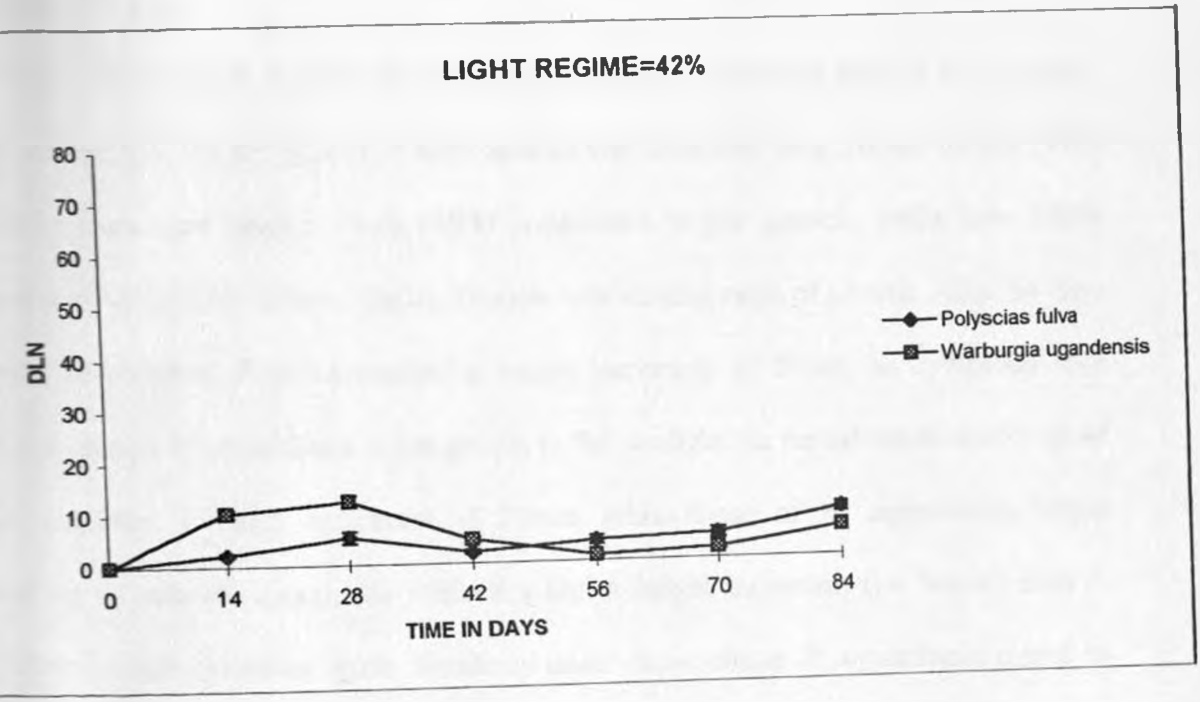
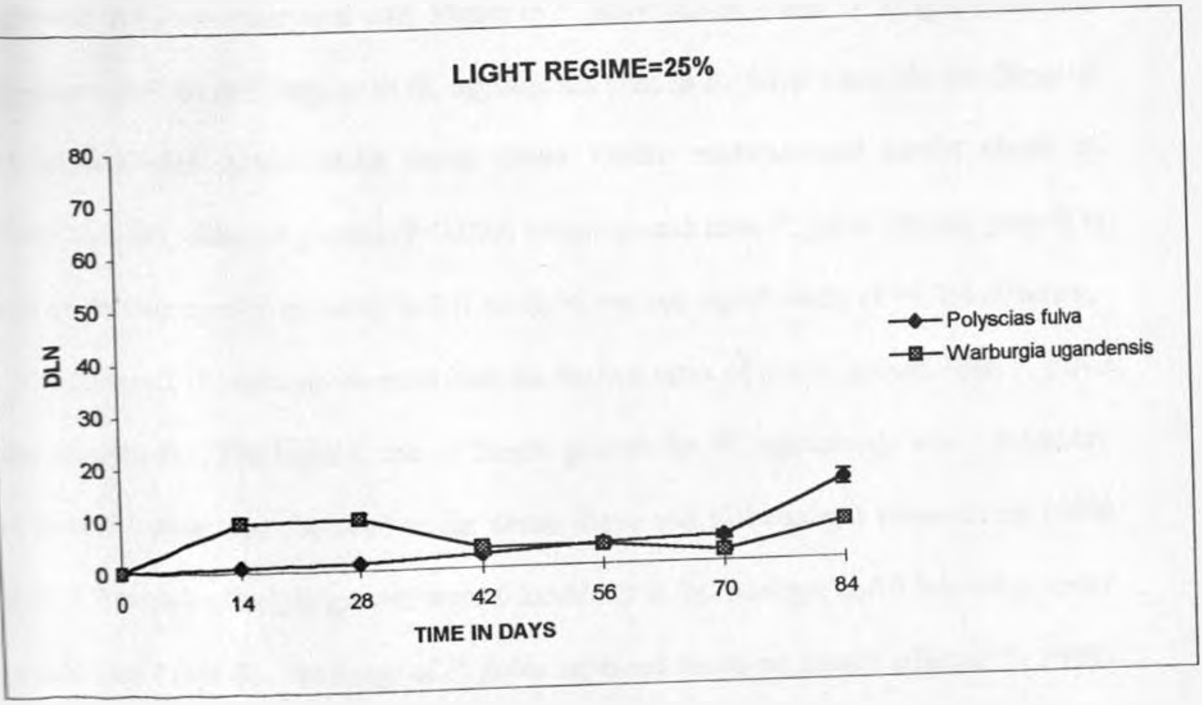

LIGHT REGIME=65%

Figure 19

Leaf loss (Number of leaves lost) in seedlings of *P. fulva* and *W. ugandensis* raised in moderate shade (42% of full sunlight) and dense shade (25% of full sunlight). Vertical bars are S.E. of the means.


LIGHT REGIME=42%
DLN
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis


LIGHT REGIME=25%
DLN
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

5.2.3 Height Growth

For the two species height growth was higher under shade treatments than in full sunlight (Figures 20 and 21). Height growth in both species was inversely proportional to the PPFD available in each light regime. High PPFD suppressed height growth, while low PPFD promoted stem elongation in both species, though with varying rates of growth. After 84 days of growth, seedlings of *P. fulva* attained a height increment of 20mm, as compared with 36mm in seedlings *W. ugandensis* when grown in full sunlight. In partial shade seedlings of *P. fulva* exhibited a height increment of 23mm, while those of *W. ugandensis* height increased by 47 mm. *W. ugandensis* attained a higher height increment (i.e 74mm) than *P. fulva* (30mm) under moderate shade. Similarly under dense shade *W. ugandensis* raised its height growth by 89mm compared with 38mm in *P. fulva* (tables 4 and 5). Height increment was significantly ($P<0.001$) higher in *W. ugandensis* than in *P. fulva* when the seedlings of the two species were grown under dense shade. Under moderate and partial shade *W. ugandensis* similarly showed greater ($P< 0.05$) height growth than *P. fulva*. Height growth in seedlings of the two species growing in full sunlight was not significantly ($P>0.05$) different.

Seedlings of *W. ugandensis* exhibited the highest rates of height growth than *P. fulva* in all the treatments. The highest rate of height growth for *W. ugandensis* was 1.1mm/day and the lowest 0.4mm/day observed under dense shade and full sunlight respectively (table 9). For *P. fulva* rates of height growth were 0.2mm/day in full sunlight and 0.5mm/day under dense shade (see Table 9). Seedlings of *P. fulva* appeared not to be greatly affected by PPFD gradient as was the case for *W. ugandensis*. Rate of height growth was therefore relatively faster in seedlings of *W. ugandensis,* as compared with those of *P. fulva* in all the treatments. Although the two species showed a similar pattern in response to light treatment in terms of eight growth the impact was varied, with *W. ugandensis* exhibiting higher rates of stem longation than *P. fulva*.

Table 9. Rates of stem elongation (in mm/day) in seedlings of *P. fulva* and *W. ugandensis* grown under four different light regimes.

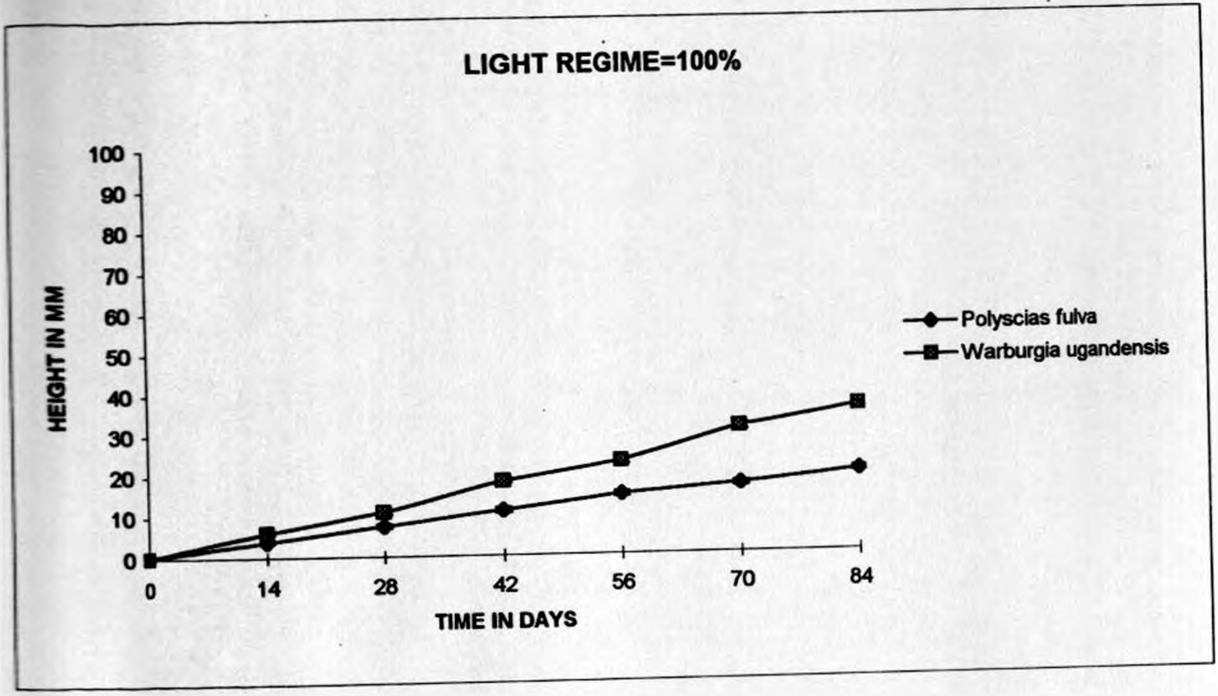
	LIGHT REGIMES			
Species	Full sunlight	Partial shade	Moderate shade	Dense shade
P. fulva	0.2	0.3	0.4	0.5
W. ugandensis	0.4	0.6	0.9	1.1

The poorest height growth was observed in full sunlight for the two species. This was probably due to dry matter allocation in favour of possibly leaves, branches or roots rather than the stem. In seedlings of *W. ugandensis* growing under shade increased height growth, was possibly as a result of increased allocation of resources to the stem from the leaves, branches and roots.

Various researchers have studied height growths of tropical trees. For example, Ross (1954) found that height growth in *Trema guianeensis* was 10m in 5 years approximately 6mm/day in a forest clearing in Nigeria. Swaine and Hall (1983) reported even higher values of 4m yr^{-1} for *Trema orientalis*. Kigomo (1990) found that in *Brachylaena huillensis* seedlings, height growth was 0.69 cm/month in dense shade. The results observed in the present study for *P. fulva* were similar to those of *B. huillensis* although the two species showed different responses to amount of light. The rates of growth in height observed in both *P. fulva* and *W. ugandensis* are low compared those found by Ross (1954) and also by Swaine and Hall (1983). Production of large seedlings of *P. fulva* will require more than 1 year and preferably 2 years if seedlings of 60 cm or taller are required. For *W. ugandensis* a period of less than two years will be required to produce seedlings of about 60 cm.

Figure 20

Temporal changes in height (mm) in seedlings of *P. fulva* and *W. ugandensis* grown in full light (100% sunlight) and partial shade (65% of full sunlight). Vertical bars are S.E. of the means.


LIGHT REGIME=100%
HEIGHT IN MM
100
90
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

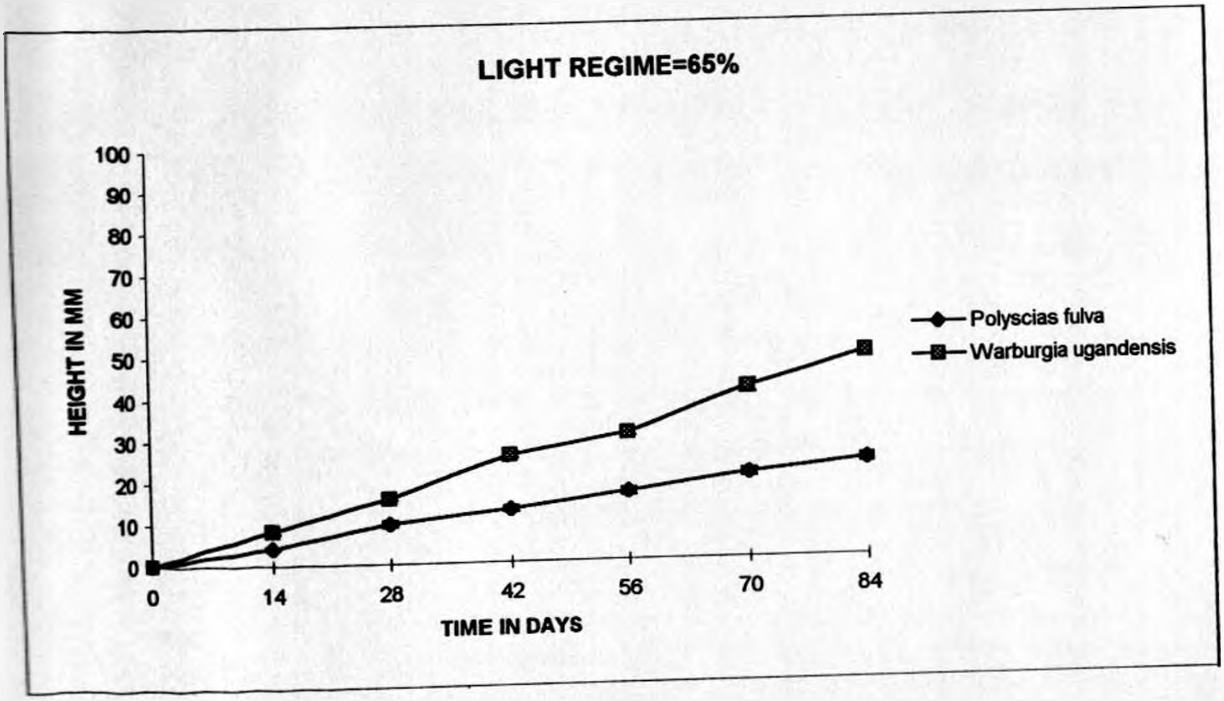
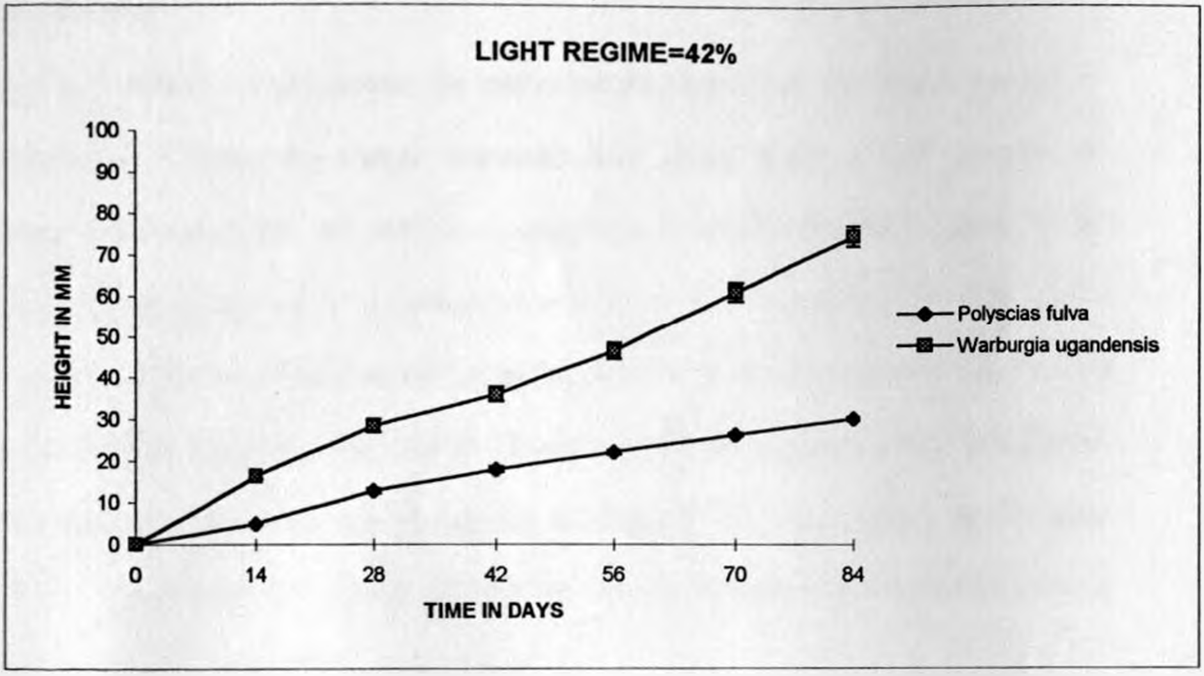
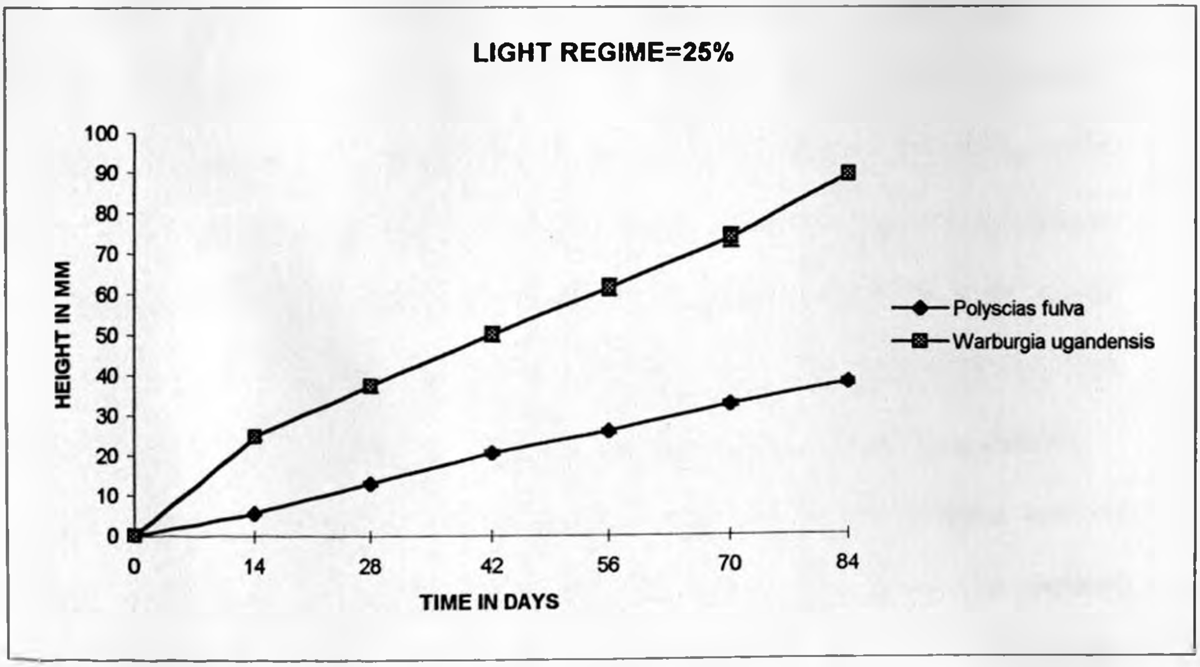

LIGHT REGIME=65%
HEIGHT IN MM
100
90
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

Figure 21

Temporal changes in height (mm) in seedlings of *P. fulva* and *W. ugandensis* grown in moderate shade light (42% of full sunlight) and dense shade (25% of full sunlight). Vertical bars are S.E. of the means.


LIGHT REGIME=42%
HEIGHT IN MM
100
90
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis


LIGHT REGIME=25%
HEIGHT IN MM
100
90
80
70
60
50
40
30
20
10
0
0
14
28
42
56
70
84
TIME IN DAYS
Polyscias fulva
Warburgia ugandensis

3.2.4 Dry Weight

Seedlings of *P. fulva* exhibited greater dry matter accumulation in all the treatments than *W. ugandensis*. For *P. fulva* dry weight increased from dense shade to full sunlight. *W. ugandensis* exhibited higher dry matter accumulation in shaded treatments than in full sunlight. The highest dry matter accumulation was observed in seedlings of *P. fulva* grown in full sunlight. The mean dry weight for seedlings of *P. fulva* grown in full sunlight was 8.9g and 4.0g under dense shade (Table 4). Seedlings of *P. fulva* grown in full sunlight had approximately 50% more dry matter than the seedlings of the same species grown under dense shade. Seedlings of *W. ugandensis* showed a mean dry weight of 0.6g when grown in full sunlight and 1.4g under dense shade (Table 5).

In general, high PPFD increased dry matter accumulation in *P. fulva* while shade enhanced dry matter production in *W. ugandensis*. Dry matter production was significantly ($P<0.01$) higher in seedlings of *P. fulva* in full sunlight and partial shade than seedlings of *W. ugandensis*. Under moderate and dense shade dry matter production was not significantly ($P>0.05$) different for the two species. The results therefore indicate that dry matter production in both species was light dependent with differences occurring in responses. High PPFD enhanced dry matter production in *P. fulva* while it was supressed in *W. ugandensis*.

Kigomo (1990) observed that seedlings of *B. huillensis* exhibited higher rates of growth in dry matter when grown in full sunlight than in shaded environments. The response of *B. huillensis* is similar to that of *P. fulva* in the present study. Kwesiga and Grace (1986) made similar observations in seedlings of *Khaya senegalensis* and *Terminalia ivorensis* in West Africa. Sasaki and Mori (1981) found in their study of dipterocarp seedlings that in some seedlings dry matter production was higher in full light than in shade while in others more dry weight was observed at 30-60% of full sunlight. Kriebitzsch *et al.* (1997) observed that seedlings of *Intsia palembanica* and *Hopea odorata* recorded more biomass in full light than under shade. Therefore, it is apparent that most species show enhanced dry matter accumulation when growing in increasing light intensities rather than in shade. However exceptions do occur for example in dipterocarp seedlings (Sasaki and Mori, 1981) and for *W. ugandensis* in the present study. It is therefore apparent that the response to light in terms of dry matter production is species specific. This supports the observation by several authors that tree species differ in their requirements for light and also respond differently to light variation (Richards, 1952; Bazzaz and Picket, 1980; Denslow 1980; Whitemore 1984 and Kigomo 1990).

3.2.4 Shoot/Root Ratio (S/R Ratio)

The two species showed the highest shoot/root ratio under moderate and dense shades. Shoot/root ratios were lowest in full sunlight for seedlings of the two species. The seedlings of *W. ugandensis* exhibited higher S/R ratios in all the light regimes than *P. fulva.* The mean S/R ratio for seedlings of *W. ugandensis* grown in full sunlight was 2.73 gg^{-1} as compared with 0.97 gg^{-1} for *P. fulva.* Under dense shade seedlings of *W. ugandensis* similarly showed a mean S/R ratio of 6.42 gg^{-1} which was comparatively higher than 1.82 gg^{-1} for *P. fulva* (Tables 4 and 5). Shoot/root ratios were significantly ($P<0.01$) higher for seedlings of the two species grown under moderate and dense shades than in full sunlight and partial shade. *P. fulva* exhibited little variation in S/R ratios in the four light levels, with values ranging from 0.97 to 1.84 gg^{-1}, while in *W. ugandensis* the values ranged from 2.73 to 6.42 gg^{-1} in the four the treatments. The S/R ratio for *W. ugandensis* was approximately 50% higher in the dense shade than in full sunlight. In general, the seedlings of the two species increased their S/R ratios in response to shade with values of *W. ugandensis* being higher than in *P. fulva*.

For the two species it appeared that, when growing under reduced light, allocation of resources was in favour of the shoots, but while growing in increasing light levels allocation of resource to the development of the root system became more important. Seedlings of *P. fulva* seemed to develop more root biomass when growing in full sunlight as compared with the seedlings of *W. ugandensis*. It is, therefore, possible that seedlings of *P. fulva* were able to improve their mineral and water uptake capacities when growing in full sunlight due to an elaborate root system. This resulted in enhanced photosynthesis rates and thus higher dry matter production in this species. Seedlings of *W. ugandensis* were possibly unable to increase their water uptake capacities in full sunlight due to poor root development. This species, therefore, responded to full sunlight by stomatal closure leading to low stomatal conductances, dry weight and photosynthetic rates.

Kigomo (1990) observed that seedlings of *B. huillensis* grown in high light intensities exhibited lower shoot/root ratios than under shade. Kriebitzsch *et al.* (1997) found that seedlings of *Instia palembanica* and *Hopea odorata* responded to reduced light intensities by increasing their S/R ratios. *H. odarata* showed a stronger increase in S/R ratio in response to full light than *I. palembanica*. Sasaki and Mori (1981) observed that in dipterocarp seedlings the shoot/root ratio dropped continuously with increasing PPFD. Kwesiga and Grace (1986) supported this while working with seedlings of *Khaya senegalensis* and *Terminalia ivorensis*. The results in the present study are, therefore, similar to those observed in seedlings of other tropical trees. For *P. fulva* full light was necessary to produce seedlings with high enough root relative to shoot to have a high chance of surviving the shock of being transplanted to our forests. For *W. ugandensis*, 40 – 65% of full light was necessary to produce seedlings that can withstand transplantation shock.

3.2.5 Specific Leaf Area

The two species had the greatest SLA under moderate and dense shades. *P. fulva* exhibited a mean SLA of 71.20 $cm^2\ g^{-1}$ in full sunlight, while 105.4 cm^2g^{-1} was observed for *W. ugandensis*. In partial shade, *P. fulva* recorded a mean SLA of 104.2 cm^2g^{-1} and 123.9 cm^2g^{-1} for *W. ugandensis*. Under moderate shade, *W. ugandensis* exhibited a mean SLA of 187.9 cm^2g^{-1}, as compared with 155.4 $cm^2\ g^{-1}$ in P. fulva. The highest SLA in both species was observed in seedlings growing under dense shade, with *W. ugandensis* recording 220.7cm^2g^{-1} and 198.1$cm^2\ g^{-1}$ in *P. fulva*. In both species SLA decreased with increasing PPFD. This response was, therefore, similar with that observed in leaf number, leaf area, height and shoot/root ratio. SLA was significantly ($P< 0.001$) higher in both species when growing under dense and moderate shades than in full sunlight and partial shade. Seedlings of the two species showed no significant ($P> 0.05$) difference in SLA when growing under full sunlight and partial shade. The high specific leaf area, leaf number and enhanced vertical growth observed in seedlings of the two species when growing under shade treatments can be interpreted as typical adaptations to shade.

Kwesiga *et al*. (1986) found that in seedlings of *Terminalia superba, Khaya senegalensis, Triplochiton scleroxylon* and *Terminilia ivorensis*, the specific leaf area was higher under shade than in high photon flux density. Sasaki and Mori (1981) and Kriebitzsch *et al.* (1997) while working with seedlings of tropical trees observed similar results. The results observed in *W. ugandensis* and *P. fulva* are therefore similar with findings in other tropical trees.

CHAPTER FOUR

4.0 CONCLUSIONS

The growth and photosynthetic parameters studied in both species indicate clear-cut responses to light intensities. As indicated by the significant differences in nearly all the parameters studied, the two species responded differently to the light treatments. The present study therefore supports the findings of other researchers working on tropical trees, who found that tree species differ in their requirements for light and also responded differently to a light gradient (for example, Richard, 1952; Denslow, 1980; Sasaki and Mori, 1981 Whitmore, 1984; Kwesiga and Grace, 1986; Kigomo, 1990 and Konuche, 1994). The hypothesis of this study that the two species showed similarresponse to different light regimes and that they display the greatest growth and photosynthetic rates under full sunlight conditions was therefore not supported. The results of this experiment indicated that individuals of the same species grown in contrasting light conditions exhibit morphological and physiological differences just as do individual leaves on a single plant that are differentially exposed to light (Boller and Nosberger, 1985; Theuri, 1995). The growth and photosynthetic measurements obtained in this study will, therefore, result in a better understanding of the control of productivity in our forests and also the strategies of individual species.

Seedlings of *P. fulva* showed the greatest growth under full sunlight conditions than in low light intensities, though even here the seedlings survive and grow. The enhancement of growth in *P. fulva* at high light levels is presumably as a consequence of high assimilation rates (Table 2). The capacity of seedlings of *P. fulva* to intercept and use high radiant energy for photosynthesis determined the availability of photosynthates for growth under full sunlight. *P. fulva* increased its photosynthetic rates as PPFD increased, consequently the growth of this species possibly follows the solar radiant energy curve. The assimilated carbon that was not lost by respiration increased the dry matter of the two species and was possibly used for growth and also accumulation of reserves. It is therefore possible that in both species the amount of photosynthates used in respiration and also the amount used for growth of the seedlings depended on the light regime. *P. fulva* accumulated more dry matter in full sunlight than in shade possibly due to increased rates of photosynthesis. This response resembles that of clones of herbaceous *Solanum dulcamara* when grown in sun and shade (Osmond, 1983). High photosynthetic rates in a given species occur as a result of increased resouce allocation to leaf structure (Chabot *et al.*, 1979). This is reflected in elaboration and differentiation of mesophyll tissue, which includes production of cell wall, cell and organelle membranes, and enzymes. The increased resource allocation is translated in such measures as SLA and SLW, mesophyll cell volume, electron-transport activity, and ribulose-1-5-bisphoshate carboxylase activity per unit leaf area. The higher photosynthetic rates in *P. fulva* as compared with *W. ugandensis* in increasing light intensity therefore involves, an increase in amounts of ribulose bisphosphate (Rubisco) carboxylase/oxygenase, increase in electron transport activity, reduced stomatal resistance and decreased concentration of chlorophyll as observed by Kwesiga and Grace (1986). The adaptability of the maximum rate of photosynthesis to PPFD during growth of seedlings of *P. fulva* appears to have been as result of a change in stomatal conductance accompanied by an adjustment of specific leaf area. The interpretation of this is that the leaves of *P. fulva* grown at high PPFD develop more mesophyll and so were thicker and had more photosynthetic machinery per area of leaf. The leaves of *P. fulva* were, therefore, able to utilise strong light due to greater capacity of their electron transport system and higher Rubisco activity and hence considerably higher photosynthetic yields.

Seedlings of *W. ugandensis* seemed to perform better under shade. This is supported by the higher dry weights and rates of photosynthesis under the shaded regimes compared to full light. The dry weight and also photosynthesis for *W. ugandensis* were reduced in full sunlight indicating that the species is most likely a shade tolerant species. The suppressed dry matter production and assimilation when seedlings of *W. ugandensis* were exposed to full sunlight was probably due to high heat load, increasing leaf temperatures and respiration. This perhaps resulting in an inability of the seedlings to take up enough water (due to increased S/R ratio) to match transpiration. The reduced capacity to take up water probably resulted in water stress and hence stomatal closure. Several authors have reviewed the impact of water stress on the photosynthetic process. There is general agreement that the most immediate effect is an increase in stomatal resistance (as observed in low stomatal conductances, Table 3) due to stomatal closure. This restricts the movement of CO_2 and H_20 and hence low rates of photosynthesis and transpiration. Stomatal closure may be due to decrease in leaf water status or a response to soil water depletion not associated with leaf water status (Bates and Hall, 1981). *W. ugandensis*, therefore, accumulated less dry matter due to low assimilation rates resulting from low stomatal conductances. However, increase in dry weight is not dependent on CO_2 uptake alone, the allocation of assimilates and specific growth pattern also play crucial roles (Larcher, 1995). Strong light seems to present the leaves of *W. ugandensis* with more photochemical energy than can be utilized for photosynthesis, overloading of the photosynthetic process results in lower 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 due to lower rates of respiration. For example, Loach (1967) found that shade tolerant and shade intolerant species has essentially equivalent rates of photosynthesis when grown in low light. One key to differential success in shade was a difference in dark respiration rate and therefore a lower light compensation point allowing them to maintain a positive carbon balance even at very low gross photosynthetic rates. The idea that the dark respiration rate is one key to survival in shade has been supported by several other authors for example, Logan, 1970; Willmot and Moore, 1973.

The results showed that dry matter production was influenced by light intensity and that seedlings grown under low light allocated more resources to shoot development (Tables 4 and 5). For *P. fulva* seedlings growing in increasing light intensities, allocation of resources to the development at root system became more important as indicated by the S/R ratios (table 4). High levels of light promoted root development in this species and therefore dry matter. This is the reason why the species recorded lower S/R ratio in full sunlight, as compared with the shade grown seedlings. Sasaki and Mori (1981) reported similar responses in nursery grown seedlings of *Vatica odorata* and also Kigomo (1990) in *B. huillensis*. The slow growth of seedlings of *P. fulva* under shade and fast growth in full sunlight showed that seedlings growth in the nursery, and therefore, possibly in nature is limited to some extent by light.

In the two species leaf number, height, leaf area shoot/root ratio and specific leaf area increased as seedlings approached lower light levels, these may be adaptive features to a certain range of light intensities. According to Ducrey (1994) plants require a high degree of plasticity in their photosynthesis and morphological parameters in order to adapt to shade. In P. fulva this plasticity is clearly manifested in morphological and photosynthetic parameters. Plants whose early development stages are typical of shade adapted species also require a high degree of plasticity if they are to prevail under strong radiation, a condition that is evidently not present in *W. ugandensis*. Studies indicate morphological adjustments to enhance light interception in shaded conditions (Grime, 1976; Loach, 1970; and Smith, 1982), these include broader thinner leaves with more chlorophyll per unit area. Blackman and Black (1959) agree that a reduction in light does increase the leaf area ratio and that for some species this can compensate for the decrease in the net assimilation rate. In the present study the leaves of both species in the shade were consistently larger and had a deeper green colour than the leaves of seedlings in full sunlight. Björkman (1981) observed that leaves which have grown at low photon flux density have an elevated specific leaf area, usually as a result of being thinner, and for thin reason alone they are likely to display different photosynthetic characteristics. In seedlings of both *P. fulva* and *W. ugandensis* the specific leaf area increased with increasing shade and this probably affected the photosynthetic rates of these species. The SLA is an indicator of leaf thickness and the degree of mesophyll development within a leaf blade (Jurik, 1986). It is possible that increased SLA in the two species implied important anatomical changes in mesophyll and palisade layers. Variations in light produce changes in leaf anatomical and biochemical structure (Nobel *et al.*, 1975; Chabot and Chabot, 1977 and Björkman, 1981) which determine net photosynthetic CO_2 fixation. For example, Nobel *et al* (1975) found that the palisade layer reduced from 2-3 cells to 1 cell in the shaded treatments and hence such leaves produced high values of SLA. The extent of mesophyll development largely determines the photosynthetic capacity of a leaf (Nobel *et al.*, 1975, Chabot and Chabot, 1977, Jurik and Chabot 1979), although intra-cellular effects of other factors such as nutrient supply also influence photosynthetic capacity. Thus, SLA can potentially be used as an indirect measure of the photosynthetic characteristics of a leaf, while also giving a direct measurement of allocations of biomass in a plant. Seedlings of *P. fulva* under high light intensity showed reduced SLA and high photosynthetic rates, this is probably due to reduced resistance to CO_2 diffusion. In plants of *Solidago Virgaurea* from exposed sites, high light intensity causes a thickening of the leaf that lowers resistance to CO_2 diffusion by increasing the pore space in the mesophyll layers Holmgren (1968). Chabot and Chabot (1977) found a high correlation between the rate of photosynthesis and the palisade/mesophyll thickness ratio. The palisade/mesophyll thickness ratio influence the rate of CO_2 diffusion to the chloroplasts which is very important at high light intensities. The changes in SLA early in leaf growth are presumably due to changes in relative rates of cell division and cell expansion (Steer, 1971).

In general, leaves in shady environments typically have higher SLA than leaves grown in sunny conditions, higher SLA represents a complement of leaf characteristics including decreased leaf thickness, decreased palisade cell development decreased RubP carboxylase, increased chlorophyll per unit, leaf mass, lower light saturation point and maximum rate of photosynthesis and decreased respiration rate (Boardman, 1977; Chabot and Chabot, 1977). Investigations have revealed that various environmental factors operate in determining SLA and photosynthetic capacity. Light primarily appears to influence anatomical development, with higher levels leading to thicker leaves with greater development of the mesophyll (Nobel *et al.*, 1975; Nobel, 1977; Chabot *et al.*, 1979; Björkman, 1981; Jurik *et al.*, 1982). This greater mesophyll development means lower SLA and often, higher photosynthesis per unit leaf area due to more photosynthesing cells per unit leaf area. Leaves apparently integrate the various light levels received over a day and adjust their anatomy in response to the total amount of light received (Nobel, 1976; Chabot *et al.*, 1979).

Investigations of spatial variation in SLA within forest canopies have found that SLA increases down through the canopy (Coyne and Van Cleve, 1977, Lewandowska and Jurvis, 1977; Schulze *et al.*, 1977; Van Elsacker and Impens, 1984). This trend in SLA apparently occurs in response to light, since other environmental factors have much smaller gradients through the canopy, as do factors within a tree such as nutrients supply and water supply. Del Rio and Berg (1979) found a positive linear relationship of SLA to log of light received at given point in the canopy. The current study showed a strong relationship between light and SLA (Tables 4 and 5). Some investigators have found a positive correlation between SLW and hence SLA and photosynthetic capacity per unit leaf area (For example, Pearce *et al.*, 1969; Dornhoff and Shibles, 1970, 1976). While others have found no correlation (Ku and Hunt 1973; Björkman, 1981). Since environmental and genetic factors may have effects on leaf anatomy and physiological characteristics that are not always translated into proportionate effects on photosynthesis, it is not surprising that a positive relationship between SLA and leaf photosynthetic capacity has not been consistently found, especially in comparisons among species. Species may have more or less dissimilar evolutionary histories that have resulted in particular combinations of leaf anatomy and intracellular photosynthetic capacity, so that different photosynthetic capacities may be achieved by leaves of the same SLA in different species, and vice versa. The species studied here show a fairly clear relationship between SLA and photosynthetic capacity per unit leaf area.

In both species shading enhanced the height growth while the full sunlight treatment depressed it (Figures17 and18). Reduction in height under full light treatment was associated with increased branching especially in seedlings of *W. ugandensis*. This suggested that in *W. ugandensis* under full sunlight conditions, there was greater allocation biomass from the stem to the branches and incase of *P. fulva* to the roots. Conversely, under shaded conditions, increased height growth was a result of increased allocation of biomass from leaves and possibly roots to the stem. Similar results were observed in seedlings of two tropical tree species, *Intsia palembanica* and *Hopea odorata* (Kriebitzsch *et al.*, 1997) and by Grime (1976). It is inconceivable that increase in height did not induce greater dry matter increase. The reduced weight under shade could be due to the fact that the leaf area of the shaded seedlings was greater and did not compensate for lower assimilation rate per unit area. In a closed canopy the increase in height, in *P. fulva,* would enable the species to reach the light, where, since it is relatively large plant, with leaves capable of overshadowing competitors, it is likely to be successful, once it has penetrated the canopy the consequent increase in intensity would inhibit further extension growth. The more rapid height growth in shaded areas compared to the open seems to be an adaptation to reduced light in the two species.

It is necessary to point out that the light regime is only one of several factors that influence growth and photosynthesis. Although an attempt has been made in the present experiment to hold other environmental factors constant, it is inevitable that nutrient supply to plants rooted in pots diminishes as the plant increase in size. Nitrogen supply is likely to be especially important, as it influence the photosynthetic rate and growth (Medina, 1984), but the supply of all nutrients seems to be very important in determining the distribution of tropical trees in the field (Grubb, 1977). Studies of the influence of light on photosynthesis and growth in the field are now required to ascertain whether the light treatment effects observed in the present experiment can be demonstrated in nature.

CHAPTER FIVE

5.0 General Conclusions and Recommendations

The present study was intended as a contribution on the autecology of two economically important tree species of Kenya that is *Warburgia ugandensis* and *Polyscias fulva*. The study was designed with light as the major variable. The shade material undoubtedly modified other factors like temperature, atmospheric humidity and soil moisture. However, these would vary similarly in the field. Light quality (spectral composition) under artificial shade is different from that found in the shaded understorey (Sasaki and Mori, 1981) and is known to affect many morphological features of seedlings, including stem elongation and shoot/root ratio (Sasaki and Mori, 1981). Therefore, caution is advised in assuming that growth and photosynthesis responses similar to those found for these species in the shaded enclosures would occur in the field. Species - specific field studies are a necessary complement to the results of this study. The findings of this study indicate that differences occurring in morphogenetic and photosynthetic parameters of species growing in forest gaps of various sizes and along a canopy gradient could primarily be due to light. It is apparent that seedlings grown under artificial shade can provide a fair representation of growth and physiological adjustments of seedlings in the forest.

The slow growth and low photosynthetic rates of seedlings of *P. fulva* under shade and the fast growth and 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 therefore possible that seedlings of this species growing on the forest floor exist through sophisticated physiological and morphological adaptations for growth at low light levels. This makes it possible for the seedlings to undertake efficient utilisation of a range of sunflecks. Growth and survival of *P. fulva* in the light levels below 100% may mean that although shade is crucial for the establishment and healthy growth of the species, other factors in the field especially competition for other resources could also be important. It will, therefore, be necessary to carry out more work aimed at finding out particularly the role of moisture and nutrients in determining the rate of seedling growth in the forest.

The two species generally showed differences in their light requirements. *P. fulva* was the most light demanding. It displayed the greatest growth under full sunlight conditions and is suitable for planting in clearings or open areas. It is not suitable for planting in small or medium size canopy gaps. *W. ugandensis* grows best under shaded conditions. Under full sunlight environment height growth, rates of photosynthesis and dry matter accumulation will be severely reduced *W. ugandensis* is therefore suitable for planting into medium and large canopy gaps such as those caused through selective felling.

CHAPTER SIX

6.0 REFERENCES.

ADDICOTT, F.T. (1982). Abscission. University of California Press, Berkeley. 45-70.

AOKI, M., YABUKI, K. & KOYAMA, H. (1975). Micrometeorology and assessment of primary production of a tropical rainforest in West Malaysia. *Journal of Agricultural Meteorology* **31**: 115-124.

ASHTON, P.S. (1978). Crown characteritics of tropical trees. In: Tropical Trees as living Systems. (Eds. P. B. Tomlinson and M. H. Zimmermann). Cambridge University Press, Cambridge. 591-615.

AUSPURGER, C.K. (1984a). Light requirements of neotropical trees seedlings: A comparative study of growth and survival. *Journal of Ecology* **72**: 777-795.

AUSPURGER, C. K. (1984b). Pathogen mortality of tropical tree seedlings: Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* **61**: 211-217.

AUSPURGER, C. K. (1984c). Seedling survival among tropical tree species: Interactions of dispersal distance, light gaps, and pathogens. *Ecology* **85**: 1705-1712.

BASS, S. (1992). Tree Plantation Review: Study No. 7: Social environment. Shell International Petroleum Campany/ WWF. 21-30.

BATES, L. M. & HALL, A. E. (1981). Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. *Oecologia* **50**: 62-65.

BATTISCOMBE, E. (1936). Trees and Shrubs of Kenya Colony. A Revision and Enlargement of a Descriptive Catalogue of some of the common trees and woody plants of Kenya colony. Printed and Published by the Goverment Printer.

BAZZAZ, F. A. (1984a). Dynamics of wet tropical forests and their species strategies. In: *Physiological Ecology of Plants of the Wet Tropics*. (Eds. Medina, E., Mooney, H. A. and Va'zquez-Yanes, C.) Dr. Junk Publishers, The Hague. 233-243.

BAZZAZ, F. A. & CARLSON, R. W. (1984). Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* **54**: 330-316.

BAZZAZ, F. A. & PICKETT, S. T. A. (1980). The physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics* **11**: 287-310.

BJORKMAN, O. (1981). Responses of different quantum flux densities. In: *Encyclopedia of Plant Physiology, vol. 1*. Physiological Plant Ecology, (Eds. O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegle eds.). Springer, Verlag, Berlin.

BJORKMAN, O. & LUDLOW, M. M. (1972). Characterization of the light climate on the floor of a Queensland rainforest. *Carnegie Institute Yearbook* **71**: 85-94.

BJÖRKMAN, O., LUDLOW, M. M. & MORROW, P. A. (1972). Photosynthetic performance of two rainforest species in their native habitat and analysis of the gas exchange. *Carnegie Institute Yearbook* **71**: 94-102.

BJÖRKMAN, O. & P. HOLMGREN (1963). Adaptability of photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiology of Plants* **16**: 889-914.

BLACKMAN, G. E. & BLACK, J. N. (1959). Physiological and ecological studies in the analysis of plant enviroment. Xi. A further assessment of the influence of shading on the growth of different species in the vegetative phase. *Annals of Botany* **23**: 51

BOARDMAN, N. K. (1977). Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* **28**: 355-377.

BOLLER, B. C. & NOSBERGER, J. (1985). Photosynthesis of white clover leaves as influenced by canopy, leaf age and temperature. *Annals of Botany* **56**:19-27.

BREWSTER, J. L. (1982). Growth, dry matter partition and radiation interception in an overwintered bulb onion (*Allium cepa* L.). *Annals of Botany* **49**: 609-617.

BROKAW, N. V. L. (1985a). Treefalls, regrowth, and community structure in the tropical forests. In: *The Ecology of Natural Disturbance and Patch Dynamics* (Eds. S. T. A. Pickett, and P. S. White). Academic Press, New Yolk. 53-69.

BROKAW, N V. L. (1985b). Gaps-phase regeneration in a tropical forest. *Ecology* **66**: 682-687.

BROKAW, N. V. K. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* **75**: 9-19.

BROUGHAM, R. W. (1960). The relationship between the critical leaf area, total chlorophyll content, and maximum growth rate of some pasture and crop plants. *Annals of Botany* **24**: 463-474.

BÜNNING, E. (1974). Longevity of individual leaves in a tropical rainforest under-storey. *Annals of Botany* **43**: 119-121.

CAEMMERER, S. VON & FARQUHAR, C. D. (1981). Some relationships between biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**: 376-387.

CARTER, G. S. (1934). Reports of the Cambridge expedition to British Guiana, 1933. Illumination in the rainforest at ground level. *Journal of Linn. Soc. (Zool)* **38**: 579-589.

CHABOT, B. F. & CHABOT, J. F. (1977). Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria* vesca. *Oecologia* **26**: 363-377.

CHABOT, B. F. JURIK, T. W. & CHABOT, J. F. (1979). Influence of instantaneous and integrated light flux density on leaf anatomy and photosynthesis. *American Journal of Botany* **66**: 940-945.

CHACHAN, P. (1963). In: Tropical Forest and its Environment. (Eds. K. A. Longman and J. Jeník). John Wiley and Sons, New Yolk.

CHACHAN, P. & DUVAL, J (1963). In: Tropical Forest and its Environment. (Eds. K. A. Longman and J. Jenik). John Wiley and Sons, New Yolk.

CHAPIN, F. S. (1980). The mineral nutrition of wild plants. *Annual Review of of Ecology and Systematics* **11**: 233-260.

CHAZDON, R. L. (1985) Leaf display and light interception of two understorey palms species. *American Journal of Botany* 72 : 1493-1502.

CHAZDON, R. L. (1986). Light variation and carbon gain in rainforest understorey palms. *Journal of Ecology* **74:** 995-1012.

CHAZDON, R. L. & FETCHER, N. (1984a). Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *Journal of Ecology* **72**: 553-564.

CHAZDON, R. L. & FETCHER, N. (1984b). Light environments of tropical forest. In: *Physiological Ecology of Plants of Wet Tropics.* (Eds. Medina, E., Mooney, H. A. and Vazquez-Yanes, C.). Dr. W. Junk Publishers, The Hugue.

CHAPIN, F. S. VITOUSEK, P. M. & VAN CLELLE, K. (1986). The nature of nutrient limitation in plant communities. *American Naturalist* **127**: 48-58.

CLARK, D. B. & CLARK, D. A. 1985. Seedling dynamic of a tropical tree: Imapacts of herbivory and meristem damage. *Ecology* **66**: 1884-1892.

CLARK, D. B. & CLARK, D. A. (1987b). Population Biology and microhabitat distribution of a neotropical rainforest emergent tree. *Biotropica* **19**: 236-244.

COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* **53**: 209-233.

COLEY, P. D., BRYANT, J. P. & CHAPIN, F. S. (1985). Resource availability and antiherbivore defence. *Science* **230**: 895-899.

COOMBE, D. E. (1957). The spectral composition of shade light in woodlands. *Journal of Ecology* **45**: 823-830.

COSTER, C. (1926). In: Tropical Forest and its Environment. (Eds. K. A. Longman and J. Jeník). John Wiley and Sons, New Yolk

COSTER, C. (1929). Anatomy and Physiology of selected species of the tropical rain forest. *Annals of Botany* **37**: 49-60.

COYNE, P. I. & VAN CLEVE, K. (1977). Fertilizer induced morphological and chemical responses of a quaking aspen stand in interior Alaska. *Forest Science* **23**:92-102.

DAMPTEY, H. B. (1964). Studies of Apical Dominance in woody plants. Msc. Thesis, University of Ghana.

DEL RIO, E. & BERG, A. (1979). Specific leaf area of Douglas fir reproduction as affected by light and needle age. *Forest Science* **25**: 183-186.

DENSLOW, J. S. (1980). Gap partioning among tropical rainforest trees. *Biotropica (suppl.)* **12**: 47-55.

DORNHOFF, G. M. & SHIBLES, R. (1970). Varietal differences in net photosynthesis of soyabean leaves. *Crop Science* **10**: 42-45.

DORNHOFF, G. M. & Shibles, R (1976). Leaf morphology and anatomy in relation to CO_2 exchange rate of soyabean leaf. *Crop Science* **16**: 377-381.

DUCREY, M. (1994). Influence of shade on photosynthetic gas exchange of seven tropical rainforest species from Guadeloupe (French West Indies). *Annals of Scientific Forestry* **15**: 393-399.

ELLIS, R. H. (1984). The meaning of viability In: *Seed Management Techniques for Genebanks.* (Eds. J. B. Dickie, S. Linington and J. R. Williams).

IBPGR, Rome. 146-181.

ESAU, K. (1977). Anatomy of Seed Plants (2nd. Edition). John Willey and Sons, New York. 124-230.

EVANS, G, C. (1956). An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks. *Journal of Ecology* **44:** 391-428.

EVANS, G. C. (1969). The spectral composition of light in the field.1. Its measurement and ecological importance. *Journal of Ecology* **56**: 109-125.

EVANS, G. S. (1972). The Quantitative Analysis of Plant Growth. Blackwell Scientific Publications, Oxford. 25-136.

EVANS, G. C. & HUGHES, A. P. (1961). Plant growth and the aerial environment.1. Effects of artificial shading on *Impatiens parviflora*. *New Phytologist* **60**: 150-180.

EVANS, G. C. AND HUGHES, A. P. (1962). Plant growth and the aerial environment. 3. On the computation of the unit leaf rate. *New Phytologist* **61**: 322-327.

FETCHER, N., OBERBAUER, S. F. & STRAIN, B. R. (1983). Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* **58**: 314-319.

FETCHER, N., OBERBAUER, S. F. & STRAIN, B. R. (1984). Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology* **29:** 145-155.

FETCHER, N., OBERBAUER, S. F., AND SRAIN, B. R. (1985). Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *International Journal of Biometeorology* **29**: 145-155.

FOOD & AGRICULTURE ORGANIZATION (FAO) (1988). An Interim report on the state of forest resources in the developing countries. Forest resources division, Forest Department FO: MISC/88/7. FAO Rome. 20-36.

GAUHL, E. (1979). Sun and shade ecotypes of *Solanum dulcamara* L.: Photosynthetic light-dependence characteristics in relation to mild water stress. *Oecologia* **39**: 61-70.

GIVINISH, T. J. (1982). On the adaptive significance of leaf weight in forest herbs. *American Naturist* **120:** 353-381.

GRACE, J., OKALI, D.U.U. & FASEHUN, F. E. (1982). Stomatal conductance of two tropical trees during the wet season in Nigeria. *Journal of Applied Ecology* **19**: 659-670.

GRIME, J. P. (1976). Shade avoidance and shade tolerance in flowering plants. In: Light as an ecological factor. (Eds. R. Bainbridge, G. C. Evans and O. Rackham). Backwel Scientific Publications, Oxford. 187-209.

GRUBB, P. J. (1977). Control of forest growth and distribution on wet tropical mountains with special reference of mineral nutrition. *A Review of Ecology and Systematics* **8:** 83-107.

HALLE, F., OLDMAN, R. A. A. & TOMLINSON, P. B. (1978). Tropical Trees and Forests. An Architectural Analysis. Springer, New York

HARIRI, M. & PRIOUL, J. L. (1978). Light-induced adaptive responses under greenhouse and controlled conditions in the fern *Pteris cretica* var. ouvardii.

Photosynthetic capacities. *Physiology of Plants* **42**: 97-102.

HARTSHORN, G. S. (1980). Neotropical forest dynamics. *Biotropica* **12**:23-30

HOLMGREN, P. (1968). Leaf factors affecting light-saturated photosynthesis in ecotypes of *Solidago virgaurea* from exposed and shaded habitats. *Physiology of Plants* **21**:676-698.

HUGHES, A. P. (1965). Plant growth and the aerial environment.7. The growth of *Impatients paviflora* in very low light intensities. *New Phytologist* **62:** 367-388.

HUGHES, A. P. & EVANS, G. C. (1962). Plant growth and the aerial environment.4. Effects of daylength on Impartients paviflora. *New Phytologist* **62**: 367-388.

HUXLEY, P. A. (1969). The effect of fluctuating light intensity on growth. *Journal of Applied Ecology* **6**: 273-276.

IDSO, S. B. & D. G. BAKER (1968). The naturally varying energy environment and its effects upon net photosynthesis. *Ecology* **49**: 311-316.

INOVE, M. T. (1976). Growth behaviour of *Cedrela odorata* L. and *Cedrera fissilis* Vell. (Meliaceae) in the young stage of development as a function of environmental factors. *Diss. Hamburg*: 99.

JANSEN, P. H. & WILSON D. E. (1974). The cost of being dormant in the tropics. *Biotropica* **6**: 260-262.

JURIK, T.W. (1986). Temporal and spatial patterns of specific leaf weight in successional Northern hardwood tree species. *American Journal of Botany* **73** (8): 1083-1092.

JURIK, T. W. & CHABOT, J. F. (1979). Ontogeny of photosynthetic performance in *Fragaria virginiana*. *Plant Physiology* **63**: 542-547.

JURIK, T. W., CHABOT, J. F. & CHABOT, B. F (1982). Effects of light and nutrients on leaf size CO_2 exchange and anatomy in wild strawberry (*Fragaria virginiana*). *Plant Physiology* **70**: 1044-1048

JURIK, T. W., & PLEASANTS, J. M. (1990). The effects light on the prairie compass plant. *Functional Ecology* **4**: 661- 665.

KIGOMO, B. N. (1990). Influence of shade on the growth of seedlings of *Brachylaena huillensis* in forest and nursery conditions. *East Africa Agricultural* and Forestry Journal. **56(2)** : 27-36.

KIRA, T. (1978). Community architecture and organic matter dynamics in tropical lowland rainforest of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: *Tropical Trees as Living Systems* (Eds. Tomlinson, P. B. and Zimmerman, M. H.). Cambridge University Press, Cambridge. 561-590.

KIRA, T., SHINOZAKI, K. & HOSUMI, K. (1969). Structure of forest canopies as related to primaryproductivity. *Plant and Cell Physiology* **10**: 129-142.

KOKWARO, J. O. (1976). Medicinal Plants of East Africa. East Africa Literature Bureau. 60-67.

KONUCHE P.K.A (1994). The influence of light environment on indigenous tree seedlings in Kenya A P.hd thesis submitted to the University of Edinburgh.

KRIEBITZSCH, W. U., HAROLD, M. & CHRISTIANE, T. (1997). Photosynthesis and growth of seedlings of two tree species from south east Asia at different light regimes. *Plant Research and Development* **46**: 99-107.

KU, S. B. & HUNT L. A. (1973). Effects of temperature on the morphology and photosynthetic activity of newly matured leaves of alfalfa. Canadian *Journal of Botany* **51**: 1907-1916

KWESIGA, F. R. (1985). Aspects of the Growth and Physiology of Tropical Tree Seedlings in shade. PhD thesis, University of Edinburgh.

KWESIGA, F. R. & GRACE, J. (1986). The role of the red/far-red ratio in the response of tropical tree seedlings to shade. *Annals of Botany* **56**: 283-290.

LADIPO, D., GRACE, J., SANDFORD, A.P.& LEAKEY, R.R.B. (1984) Clonal variation in photosynthetic and respiration rates and diffusion resistances in the tropical hardwood *Triplochiton scleroxylon* K. Schum. *Photosynthetica* **18**: 20-27.

LARCHER, W. (1995). Physiological Plant Ecology (third edition). Springer, Berlin. 32-46.

LANGENHEIM, J. H., OSMOND, C. B. & FERRAR, P. J. (1984). Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest tree species. *Oecologia* **63:** 215-224.

LEBRUN, J. & GILBERT, G. (1954). In: Tropical Forest and its Environment. (Eds. K. A., Longman and J., Jenik). John Wiley and Sons, New Yolk.

LEBRON, M. L. (1979). An autecological study of *Palicourea riparia* Bentham. as related to rainforest disturbance in Puerto Rico. *Oecologia* **42**: 31-46.

LEE, D .W. (1987). The spectral distribution of radiation in two neotropical rainforests. *Biotropica* **19**: 161-166.

LEWANDOWSKA, M. & JARVIS, P. G. (1977). Changes in chlorophyll and carotenoid content, specific leaf area and dry weight fraction in Sitka spruce in response to shading and season. *New Phytologist* **79**: 247-256.

LIEBERMAN, D., LIEBERMAN, M., HARTSHORN, G., & PERALTA, R. (1986). Growth rates aqnd age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology* **1**: 97-109.

LOACH, K. (1967). Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytologist* **66**: 607-621.

LOACH, K. (1970). Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. *New Phytologist* **69**: 273-286.

LOGAN, K. T. (1970). Adaptation of the photosynthetic apparatus of sun and shade grown yellow birch (*Betula allaghaniensis* Britt.). *Canadian Journal of Botany* **48**:1681-1688.

LONG, S. P. & HÄLLGREM, J. E. (1985). Measurement of CO_2 assimilation by plants in the field and the laboratory .In: *Techniques in Bioproductivity and Photosynthesis.* (Eds. J. Coombs, D.O. Hall, S.P. Long and J. M. O. Scurlock). Oxford. 62-94.

LONGMAN, K. A. & JENIK, J. (1974). Tropical Forests and its Environment. Longman, New York. 91-99.

LONGMAN, K. A. & JENIK, J. (1987). Tropical forest and its Environment. (2nd edition) John Wiley and Sons, New Yolk. 120-150.

LOOMIS, R. S., W. A. WILLIAMS & W. G. DUNCAN (1967). Community architecture and the productivity of terrestrial plant communities. In: *Harvesting the Sun.* (Eds. San Pietro A.; A. F. Green and T. J. Anny). Academic

Press, New York. 291-308.

MABBERLEY, D. J. (1983). Tropical Rain Forest Ecology. Blackie. Oxford. 28-237.

MACHARIA, J. N. M. (1981). Bioproductivity in Relation to Photosynthesis in four Grassland Ecosystems in Kenya. Msc. Thesis, University of Nairobi.

MEDINA, E. (1984). Nutrient balance and physiological processes at leaf level. In: *Physiological Ecology and Plants of the Wet Tropics.* (Eds. E. Medina, H.A. Mooney and C. Vazsquez-Yanes). Junk. The Hague.

MCGREGOR, W.D. (1934). Silviculture of the Mixed Deciduous Forest of Nigeria. Clarendon Press, Oxford.

MORI, T. (1980). Physiological studies of some dipterocarp species of the Penisular. *Malaysian Forest Department Research Pamphlet* **78:** 20-24.

MOONEY, H.A. & GULMON, S.L. (1982). Constraints on leaf structure and function in reference to herbivory. *Bioscience* **32**:198-206.

MOONEY, H.A., C. FIELD; C. VAZQUEZ-YANES & C. CHU. (1983). Environmental controls on stomatal conductance in a shrub of the humid tropics. *Proceedings of the National Academy of Science* **80**: 1295-1297.

MORGAN, D.C. & SMITH, H. (1981). Non-photosnthetic responses to light quality. *Encyclopedia of Plant Physiology* **12A**: 108-134.

MURRAY, D. B. & NICHOLS, J. M. (1966). Report on plant physiology. Cocao Research, Trinidad, Annual Report 1965: 30-34.

MYERS, N. (1983). A wealth of wild species. Westview Boulder, London. 28-47.

NATIONAL ACADEMY OF SCIENCES (NAS) (1979). Tropical Legumes: resource for the future. *BOSTID Publication* **25**, National Academy of Sciences Washigton, DC. 213-220.

NEWTON, T. (1963). Reproductive strategies in herbaceous plant communities during succession. *Ecology* **59**: 228-234.

NICHOLSON, M. L. (1960). Light requirements of seedlings of five species of dipterocarpaceae. *Malaysian Forester* **23**: 344-356.

NICHOLSON, D. L. (1965). A plot of *Albizzia falcata* (L.) Backer. *Malaysian Forester* **28**: 240-242.

NOBEL, P. S. (1976). Photosynthetic rates of sun versus shade leaves of *Hyptis emoryi* Torr. *Plant Physilogy* **58**: 218-223.

NOBEL, P. S. (1977). Internal leaf area and cellular CO_2 resistance: Photosynthesis implications of variations with growth conditions and plants spesies. *Physiology of Plants* **40**: 137-144.

NOBEL, P.S., ZARAGOZA, L.J. & SMITH, W.K. (1975). Relation between mesophyll surface area, photosynthetic rate, and illumination level during development for leaves of *Plectranthus parviflorus* Henckel. *Plant Physiology* **55**: 1067-1070.

OBERBAUER S. F. & STRAIN, B. R. (1984). Photosynthesis and successional status of Costa Rican rainforest tree. *Photosynthesis Research* **5**: 227-232.

OBERBAUER, S. F. & STRAIN, B, R. (1986). Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae). *American Journal of Botany* **73**: 409-416.

OLUSEGU, O. O. JULIAN, E. A., ANDREW, W. G., & MIKE, S. H. (1992). Growth of tree seedlings on tropical rainforest floor of Worter Queensland

Australia. *Journal of Ecology* 9: 1-18.

OSMOND, C. B. (1983). Interactions between irradiance, nitrogen nutrition and water stress in the sun-shade response of *Solanum dulcamara*. *Oecologia* **57**: 316-321.

PEARCY, R. W. (1983). The light environment and growth of C_3 and C_4 tree species in the understory of Hawaiian forest. *Oecologia* **58**: 19-25.

PEARCY, R. B., CARLSON, G.E., BARNES, D.K., HART, R.H. & HANSON, C.H. (1969). Specific leaf weight and photosynthesis in alfalfa. *Crop Science* **9**: 423-426.

PICKETT, S. T. A. (1983). Differential adaptation of tropical trees species to canopy gaps and its role in community dynamics. *Tropical Ecology* **24**: 68-84.

PINERO, D. & SARUKHAN, J. (1982). Reproductive behaviour and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *Journal of Ecology* **70**: 461-472.

RAVEN P. H. (1987). The scope of the plant conservation problem World-wide. In: *Botanical Gardens and the world conservation strategy*. 24-31.

RICHARDS, P. W. (1952). The Tropical Rain Forest (1st edition). Cambridge University Press. 394-410.

RICHARDS, P. W. (1983). The three-dimensional structure of tropical rain forest. In: Tropical Rain Forest Ecology and Management. Special publication number 2 of the British Ecological Society. (Eds. S. L. Sutton, T. C.Whitemore and A. C. Chadwich). Blackwell publishers, Oxford.

RIDDOCH, I., GRACE, J., FASEHUN, E., RIDDOCH, B. & LADIPO, D.O. (1991). Photosynthesis and successional status of seedlings in a tropical semi deciduous rain forest in Nigeria. *Journal of Ecology* **79**: 491-503.

ROSS, R. (1954). Ecological studies on the rain forest of Southern Nigeria. II. Secondary succession in the Shasha Forest Reserve. *Journal of Ecology* **42**: 259-282.

SASAKI, S. & MORI, T, (1981). Growth responses of Dipterocarp seedlings to light. *Malaysian Forester* **44**: 319-345.

SCHIMPER, S. & VON FABER, (1935). In: Tropical Forest and its Environment. (Eds. K. A. Longman and J. Jenik). John Wiley and Sons, New Yolk.

SCHULZ, J. P. (1960). Ecological studies on the rain forest in northern Suriname, north Holland, Amsterdam.

SCHULZ, E.D., FULCHS, M. & FUCHS, M.I. (1977). Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. III. The significance of the evergreen habit. *Oecologia* **58**: 218-248.

SHEELY, J.E. & COOK, D. (1977). Irradiance distribution and CO_2 flux in forage grass canopies. *Annals of Botany* **41**: 1007-1029.

SHEPHERD, K. R. (1986). Plantation Silviculture. Martinus Publishers, Martinus.

SHUKLA, R. P. & RAMAKRISHNAN, P. S. (1986). Architecture and growth srategies of tropical trees in relation to successional status. *Jounal of Ecology* **74**: 33-46.

SMITH, H. S. (1982) Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology* **33**:481-518.

STEER, B.T. (1971). The dynamics of leaf growth and photosynthetic capacity in Capsicum frutescens L. *Annals of Botany* **35**: 1003-1015.

STEINGRAEBER, D, A. & FISHER J. B. (1986). Indeterminate growth of leaves in *Guarea guidonia* (meliaceace): a twig analogue. *American Journal of Botany* **73**: 852-862.

SWAINE, M. D. & HALL, J. B. (1983). Early succession on cleared forest land in Ghana. *Journal of Ecology* **74**: 33-46.

SWAINE, M. D., HALL, J. B. & LIEBERMAN, D, (1984). Leaf dynamics in tropical forest trees. In: Tropical Rain Forest the Leeds Symposium. (Eds. Chadwick, A. C., Sutton S. L.). Leeds Philosophy and literature society. *Abstact* **68**: 321-322.

TAYLOR, C. J. (1960). Synecology and silviculture in Ghana. Nelson, Edinburgh.

THEURI, M. M. (1995). Photosynthesis and related processes of two mangrove species *Rhizophora mucronata* and *Ceriops tagal* at Gazi bay, Kenya. Msc. Thesis University of Nairobi.

TOMBOC, C. C. & BASADA, R. M. (1978). White laun (*Shorea contrata*) in the open and under second growth forest canopy. *Ecology* **63**: 463- 468.

UHL, C. K. CLARK, N., DEZZEO, & MAQUIRINO, P. (1988). Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**: 751-763.

UNESCO, (1978). Tropical forest Ecosystems. UNESCO/UNEP/FAO. UNESCO, Paris. 286.

VAN ELSACKER, P. & IMPENS, I. (1984). Photosynthetic performance of poplar leaves at different levels in the canopy. *Advances in Photosynthetic Research* **4**: 129-132.

VAZQUEZ-YANES, C. (1980). Light quality and seed germinatuion in *Cecropla obtusifolia* and *Piper auritum* from a tropical rain forest in Mexico. *New Phytologist* **38**: 33-35.

VAZQUEZ-YANES, C. & SMITH, H. (1982). Phytochrome control of seed germination in tropical rainforest pioneer trees and its ecological significance. *New Phytologist* **92**: 477-485.

VITOUSEK, P. M. & DENSLOW, J. S. (1986). Nitrogen and phosphorus availability in treefalll gaps of a lowland tropical rainforest. *Journal of Ecology* **74:** 1167-1178.

WAREING, P. F. & PHILLIPS, I. D. J. (1981). The control of growth and differentiation in plants (second edition). Pergamon Press, Oxford.

WHITEHEAD, D., OKALI, D.U.U. & FASEHUN, F.E. (1981). Stomatal response to enviromental variables in two tropical forest species during the dry season in Nigeria. *Journal of Applied Ecology* **18**: 571-578.

WHITEMORE, T. C. (1965). A study of light condition in forests in Ecuador with some suggestion for further studies in tropical forests. In: *Light as an Ecological Factor*. (Eds. R. Bainbridge, C. G. Evans and O. Rackham). Blackwell, Oxford. 235-237.

WHITEMORE, T. C. (1975). Tropical Rainforests of the Far East (first edition). Oxford University Press,Oxford. 352.

WHITEMORE, T. C. (1978). Gaps in the forest canopy. In: *Tropical Trees as Living Systems*. (Eds. P. B.Tomlinson, and M. H. Zimmermann) Cambridge

University Press, Cambridge. 639-655.

WHITEMORE, T. C. (1984). Tropical Rainforest of the Far East. (Eds. West, C., Briggs, G. E. and Kidd, F.). Clarendon Press, Oxford. *New Phytologist* **19:** 200

WILLIAMS, M. (1989). Deforestation: Past and Present. Progress in Human Geography. 176-208.

WILLMOT, A. & MOORE, P.D. (1973). Adaptation to light intensity in *Silene alba* and *Silene dioica*. *Oikos* **24**: 458-464.

YODA, K. (1974). Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Japanese Journal of Ecology* **24**: 247-254.

ZOBEL, B. J. VAN WYK, G. & STAHL, P. (1987). Growing Exotic Forests. Wiley Interscience, New Yolk.

ZAR, J. H. (1984). Biostatistical Analysis. Prentice Hall INC., Inglewood Cliffs, New Jersey.