Journal of Tropical Ecology (2001) 17:269–283. With 5 figures

Growth and photosynthesis of seedlings of four tree species from a dry tropical afromontane forest

MASRESHA FETENE[1] *and* YONAS FELEKE

Department of Biology, Faculty of Science, Addis Ababa University, P.O. Box 30193, Addis Ababa, Ethiopia

(Accepted 2nd September 2000)

ABSTRACT. Growth, photosynthesis and carbon allocation pattern were studied in four dry afromontane forest tree species (*Olea europea* subspecies *cuspidata*, *Podocarpus falcatus*, *Hagenia abyssinica* and *Juniperus procera*) under varied light regimes in a greenhouse. The objective of the study was to assess the potential of the species for growth under forest canopies and to identify their habitat preferences. The light regimes were created using shade cloth and they corresponded with deep forest understoreys (2% of the light in the open gap); moderate shade (10%), slight shade as is found in edges of forest gaps (20%) and 100% representing open gaps.

Seedling biomass was significantly influenced by light regimes for all species as were total leaf area and relative growth rate. *H. abyssinica* had the highest growth rate but the lowest survival rate in shade. There was a consistent trend for higher specific leaf area (SLA) and leaf area ratio (LAR) at lower growth light regimes in *O. europea* and *P. falcatus*. *O. europea* and *P. falcatus* had similar allocation patterns whereby between 20–40% of the total biomass was allocated to stem, 20–30% to roots and 50–60% to leaves. In *H. abyssinica* up to 80% was allocated to leaves and only a small percentage to stem and to roots.

Within species there were significant differences in the light saturated rate of photosynthesis (A_{max}) per unit area among the plants grown at the lowest light level and in the open. For plants grown in the open there were very little among species differences in A_{max} per unit area. However, there were significant differences in the A_{max} of the different species grown at the lowest light level. Chlorophyll fluorescence measurements indicated that open-grown *P. falcatus* and *O. europea* experienced moderate photoinhibition. From the growth and photosynthesis results *P. falcatus* and *O. europea* appeared to be non-pioneer, shade-tolerant species, while *J. procera* and to a larger extent *H. abyssinica* showed pioneer, light-demanding characteristics. The results are discussed in terms of the occurrence of the species in the mosaic climaxes of afromontane forests.

KEY WORDS: afromontane forests, forest regeneration, *Hagenia, Juniperus, Olea*, pioneers, *Podocarpus*

[1] Email: Fetene@avu.org

INTRODUCTION

Montane forests in tropical Africa are characterized by a mosaic vegetation which comprises patches dominated by only one species as well as mixed forests of several species (Friis 1986, 1991; Weinert 1985). This characteristic owes much to the modes of forest regeneration which relate to the levels of establishment and potential for recruitment of the major canopy tree species. The potential of germination, growth and survival of a species in the shade of a forest undercanopy determines its successional status in a forest community. Species that are capable of regenerating in the forest understorey, known as climax species, have a higher chance of reaching the forest canopy once a gap is created. In contrast, pioneer species have a low seedling abundance in the understorey of the undisturbed forest (Whitmore 1989) and therefore do not close gaps in such forests unless the gaps are large clearings.

In afromontane forests of Ethiopia in particular, and in the forests of eastern and northeastern African mountains in general, *Podocarpus falcatus* and *Olea europea* constitute as members of mixed forests whereas *Hagenia abyssinica* and *Juniperus procera* sometimes make monodominant forest stands (Bussman 1994, Friis 1986, 1991). Studies have indicated that some afromontane species require clearing of the canopy, e.g. by fire, for regeneration (Schmitt 1991). Regeneration and successional status of *J. procera* in dry tropical afromontane forests is controlled by fire (Bussman & Beck 1995, 1996) and *H. abyssinica* depends on clearing by fire for initiation of its regeneration cycles. These two afromontane species may therefore be classified as early successional species that require large clearings. Monodominant stands (uniform aged forest patches of a single tree species) arise from such large clearings. Smaller gaps in monodominant forests may take a long time to close because pioneers do not make seedling banks in their own forests. Also non-pioneer seedlings may not be present in the understorey of monodominant forests as this usually depends on several factors such as distance of parent trees, dispersal mechanisms and seed size. On the other hand members of mixed forests such as *P. falcatus* and *O. europea*, have been observed to grow both in the forest understorey and in forest gaps (Dalle 1999, Teketay 1996) as is typical for late successional species. Such differences in the capacity of species to establish in forest understoreys and in clearings may explain the existence of monodominant and mixed climaxes of tropical afromontane forests forming a mosaic. For a better understanding of the occurrence of monodominant stands caused by episodic events and mixed forests, more information is needed on the light requirements for seedling growth and survival of the dominant trees. In this study we present the first report on growth, carbon allocation patterns and on photosynthesis of four dry afromontane forest species grown at different irradiance levels. The following questions were addressed: (1) What are the growth and carbon allocation patterns of the individual species when grown at different irradiance levels; (2) how do species differ in their photosynthetic adaptation to shade; and (3) what determines interspecific variation in shade adaptation and what are the ecological implications.

MATERIAL AND METHODS

Species

Four species were selected for this study: *Olea europea* L. subsp. *cuspidata* (Wall. ex DC.) Ciffieri, *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb, *Hagenia abyssinica* (Bruce) Gemelin and *Juniperus procera* Hochst. ex Endl.. All four species are dominant canopy trees of dry afromontane forests (see Friis 1996). *H. abyssinica* and *J. procera* are also found constituting the subalpine zone of eastern and northeastern African mountains. *H. abyssinica* and *J. procera* are considered as pioneer species (Bussman 1994) whereas *O. europea* and *P. falcatus* have been described as shade tolerant (G. Dalle & M. Fetene, unpubl. data; Teketay 1996).

Growth conditions

Seeds were obtained from representative individuals in Menagesha Natural Forest, central Ethiopia, 30 km northwest of Addis Ababa at 8°56′–9°00′N and 38°32′–38°56′E. The altitude of the forest extends from 2400–2900 m. The forest has a mean annual rainfall of about 1250 mm and mean annual temperature that ranges between 15 and 24 °C. The seeds were germinated in Petri dishes on wet filter paper in the dark in an incubator set at 25 °C except for seeds of *H. abyssinica* which were germinated in light. Freshly germinated seeds were singly transplanted into a soil:sand:compost mixture (2:1:1) in polyethylene bags (30 cm diameter and 40 cm depth) and further grown under controlled light conditions in a greenhouse. Nutrient levels in the soil mixture (e.g. N = 0.85% and P = 140 ppm) were comparable to most forest soils (see Lundgren 1971). Temperature and humidity of the greenhouse were not controlled but were recorded with a thermohygrograph. The daily temperature and relative humidity of the greenhouse averaged 24 °C and 56%, respectively.

Eighteen plants from each species were randomly allocated in each of the four light levels described below. Due to high seedling mortality or even failure of germination, it was extremely difficult to get enough seedlings of *J. procera*. Therefore seedlings priorly grown in the open for 3 mo were included in the experiment. In this case only seedlings that had comparable height and leaf numbers were selected and distributed into the four treatments. Growth and other measurements were started only after they had acclimated to the shade environment for at least 3 mo.

The different light levels were produced with shade cloth whereas the top of the greenhouse bench was used as the open treatment. In this study, due to experimental difficulties associated with effectively simulating the far-red enrichment typical of forest undercanopies, only plant response to total photosynthetic photon flux density (PPFD) was evaluated. The light levels were monitored using a PAR sensor (Li-Cor, Nebraska) at different spots in each light regime and integrated for several days. Total daily PPFD averaged 19.8 in the open, 4.3, 2.2 and 0.42 mol PPFD m^{-2} per d in the other light treatments. Henceforth, these treatments are referred to as 100, 20, 10 and 2% of full daylight, respectively. These light regimes corresponded to canopy gap (100%), edge-of-canopy gap (20%), forest undercanopy with moderate shade (10%) and dark forest undercanopy (2%) (G. Dalle & M. Fetene, unpubl. data). The experiment was started in September 1997 and was continued through the dry season and was complete by June 1998 before the start of the rainy season except for *J. procera* which was continued until August 1998. Although the light levels slightly varied depending on weather conditions, the proportion in the different light treatments remained basically the same.

Pots were watered to field capacity at least once a day. Positions within a batch were frequently exchanged and care was taken to avoid any mutual shading effect especially in the full light plants.

Growth analysis

Plants of *O. europea*, *P. falcatus* and *J. procera* were harvested 9 mo after the start of the experiment. Plants of *H. abyssinica* of all light regimes were followed for 7 mo except for those plants grown at 2% light level which could only be followed for 4 mo. At harvest, plants were divided in leaves, stem and roots, oven-dried at 70 °C to constant weight and weighed. At each harvest a minimum of three seedlings per species and per treatment were used. Leaf area was determined using a portable leaf area meter (Delta-T Devices). Leaf area of *J. procera* was not included as it was difficult to determine the area of the small overlapping cylindrical leaves of this species due to huge measurement errors. From the primary data the following variables were obtained: specific leaf area (SLA; leaf area/total leaf mass in $m^2\ kg^{-1}$), leaf area ratio (LAR; leaf area/total plant mass in $m^2\ kg^{-1}$), net assimilation rate (NAR; the increase to mass per unit area and time in $mg\ m^2\ d^{-1}$). The mean relative growth rate (RGR) was calculated following Radford (1967) as $RGR = (\ln W_{2-} \ln W_1)/(t_1 – t_2)$, where W_1 and W_2 are seedling dry weights at the first (t_1) and second (t_2) measurements of the time interval $t_1 – t_2$. In this study the total plant biomasses of 3-mo-old and 9-mo-old seedlings were used for *J. procera* and 2-mo-old and 9-mo-old seedlings for the rest of the species.

Photosynthesis

Photosynthetic oxygen evolution and apparent quantum yield (Φ) were determined in a CO_2 -saturated atmosphere with a Hansatech Leaf Disc electrode (Hansatech Instruments Ltd., King's Lynn, Norfolk, UK) as described in Fetene *et al.* (1997). $NaHCO_3$ buffer (1M) made up to pH 9 with 1M $NaCO_3$ was used to supply CO_2. The electrode was calibrated using oxygen from a pressured steel cylinder. A fan-cooled quartz-halogen lamp housing (model LS-2 Hansatech) was used as a light source, and neutral filters were applied to obtain the desired light attenuation. Light levels were provided for a leaf sample starting with the lowest intensity from 0 to 1200 PPFD (μmol m^{-2} per s), with an induction period of 20 min. A temperature-controlled water bath was used to maintain the temperature of the water jacket of the chamber at 25 °C. The apparent quantum yield was determined from the slope of the linear portion of the curve obtained using light levels of 0–80 μmol PPFD m^{-2} s^{-1}. The maximal photosynthetic rate, A_{max}, defined as the highest measured value of photosynthetic rate, was simply read from each plot.

Chlorophyll fluorescence

Chlorophyll fluorescence of dark-adapted leaf samples (maintained in the dark at least 20 min prior to measurement) was determined using a portable chlorophyll fluorescence measuring system (Plant Efficiency Analyzer, Hansatech Instruments Ltd., King's Lynn, Norfolk, UK). For each species at each light level a minimum of three seedlings was used to determine maximal fluorescence (F_m), dark fluorescence (F_o), and the potential quantum yield (F_v/F_m) during the course of a day. Chlorophyll fluorescence of light-adapted leaves (leaves exposed to ambient light) was determined using a portable pulse-amplitude-modulated chlorophyll fluorimeter (Mini-Pam, H. Walz, Effeltrich, Germany) as described in Fetene *et al.* (1997). The quantum efficiency for photosynthetic electron transport (Φ_e) in the light was calculated following Genty *et al.* (1989) as Φ_e >RQ< $(F'_m - F)/ F'_m = \Delta F/ F'_m$; where F'_m is the maximum fluorescence yield of a light-adapted leaf exposed to a pulse of saturating light; and F is the steady-state fluorescence yield of a light-adapted leaf. Non-photochemical fluorescence quenching (NPQ), was calculated as $NPQ = (F_m/ F'_m) - 1$ (Bilger & Björkman 1991). Both quantum efficiency and NPQ were determined at a PPFD level of 600 ± 30 μmol m^{-2} s^{-1}. Chlorophyll concentration of leaves was determined after extraction with acetone following the method of Arnon (1949).

Statistics

Data were analysed by analysis of variance (ANOVA) according to the general linear model (GLM) procedure of SPSS (Version 8.0). The differences between treatment means were considered significant when $P \leqslant 0.05$. This probability level refers to all citations of significant differences in the text.

RESULTS

Survival and growth analysis

The total percentages of seedlings that survived and established in the four light regimes at the end of the growth period are shown in Figure 1. Seedlings of *H. abyssinica* did not survive more than 20 wk at the lowest light level. Only 15% of the seedlings at the 10% light level survived at the end of the growth period. In all species total seedling biomass was strongly influenced by the

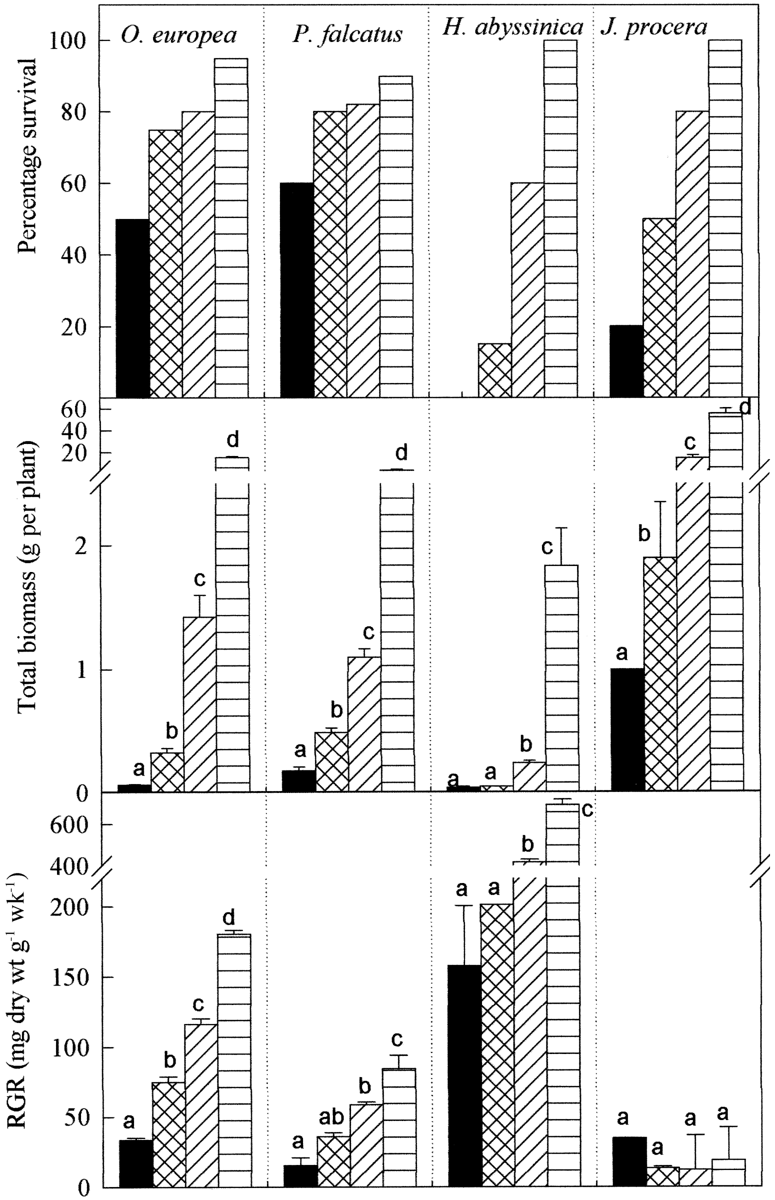

Figure 1. Percentage survival of seedlings, total seedling biomass and relative growth rate (RGR) of four dry afromontane tree species grown at four light regimes. Total seedling count at the end of the growth period was used to calculate percentage survival. Bars are + 1 SD. Bars that share the same lower case letter are not significantly different at $P < 0.05$. ■, 2%; ▩, 10%; ▨, 20%; ▤, 100%.

growth light level (Figure 1). There was a more than fourfold increase in biomass from one light level to the next in seedlings of *O. europea* and *P. falcatus*. Seedlings of shade-grown *H. abyssinica* did not differ markedly from one another. However, biomass of these seedlings was much smaller than that of seedlings grown in full light. Comparatively higher biomasses were recorded for *J. procera* which was due to a higher initial biomass (pre-treatment). RGR closely reflected total biomass accumulation (Figure 1).

Total leaf area differed by one order of magnitude between plants of the lowest light level and those in full light. While in *H. abyssinica* there was no difference between total leaf area in the two lowest light levels, *O. europea* and *P. falcatus* showed a stepwise increment in leaf area at each growth light level. A trend in the opposite direction was observed for SLA and LAR (Figure 2). The highest SLA and LAR were for plants grown at the lowest light levels. The differences in LAR and SLA of seedlings grown at various light levels were significant for both *O. europea* and *P. falcatus* but not for *H. abyssinica*.

Figure 3 shows biomass distribution in the four species between leaves, stems and roots. In 9-mo-old seedlings a remarkably small percentage of biomass was found with the roots, except for *J. procera* grown at full light. For all species but *J. procera* biomass fraction in the roots did not significantly respond to the light climate. *O. europea* and *P. falcatus* had similar distribution patterns whereby between 20–40% of the total biomass was allocated to stem, 20–30% to roots and 50–60% to leaves. In *H. abyssinica* up to 80% was allocated to leaves and only a small percentage to stem and to roots.

Photosynthesis acclimation

Intraspecific differences. In *O. europea*, *P. falcatus* and *H. abyssinica*, there were significant differences in A_{max} per unit area among the plants grown at the lowest light level and in the open (see Table 1 and Figure 4). In the three species, A_{max} per unit area was at least twice as much in open grown plants as in all shade grown plants. In *P. falcatus*, A_{max} per unit area of plants grown in the open was only moderately different from those plants grown in slight and moderate shade (20 and 10% of light intensity, respectively), while in *O. europea* shade plants had much lower A_{max} than full-light grown plants. However, when A_{max} is expressed per unit mass these differences disappear with the concurrent changes in leaf mass per unit area. Per unit mass, only plants of *H. abyssinica* and *J. procera* maintained consistent differences in A_{max} between deep shade and open grown plants. Very few differences were observed in the photosynthetic values at similar light intensities for *J. procera* plants grown in the three shade conditions which were much lower than the values for open grown plants. Nevertheless in this species there was light saturation of photosynthesis for plants grown in the deep shade (2%) (Figure 4).

Interspecific differences. There were little interspecies differences in A_{max} per unit area among *O. europea*, *P. falcatus* and *H. abyssinica* plants grown in the open. In the lowest light regime both *O. europea* and *P. falcatus* achieved A_{max} twice as high as in *H. abyssinica*. Again these differences disappeared when A_{max} is expressed per unit mass. Per unit mass the A_{max} of open grown plants of

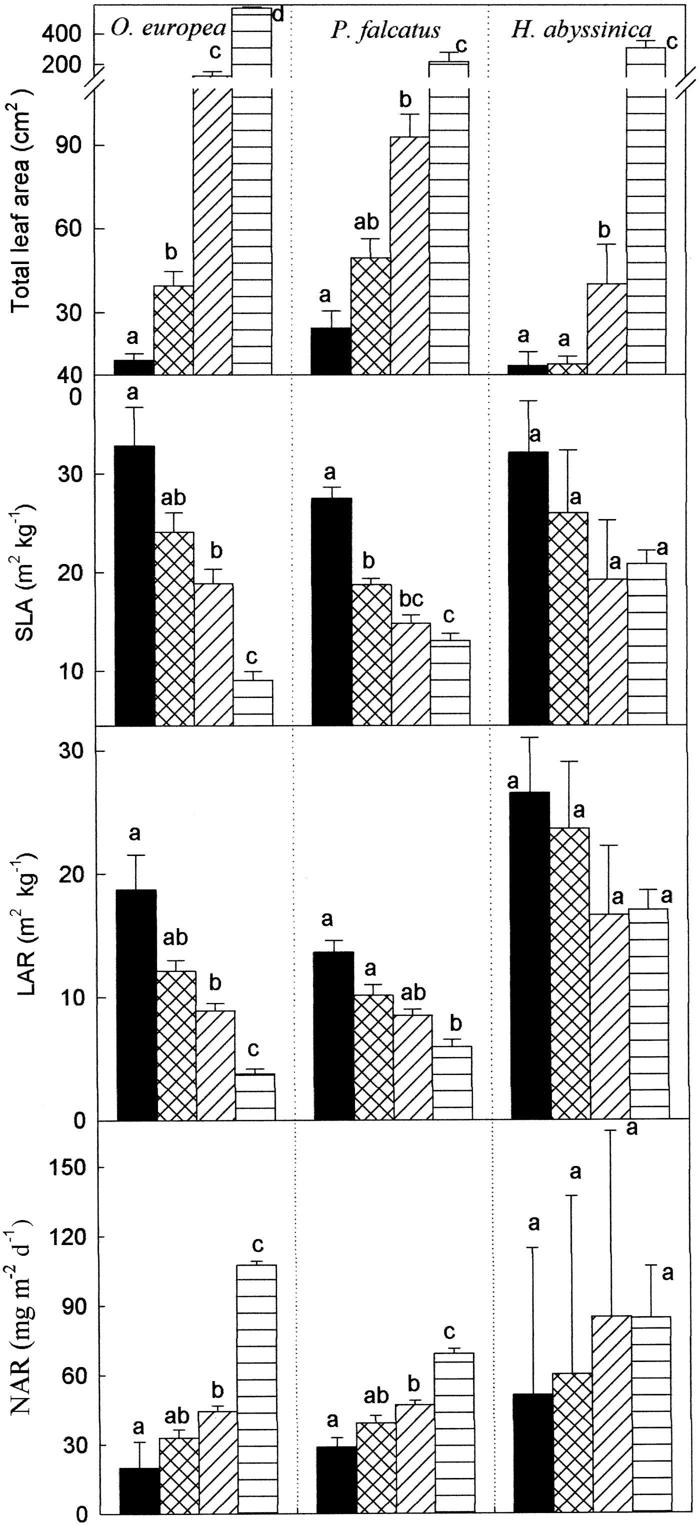

Figure 2. Total leaf area, specific leaf area (SLA), leaf area ratio (LAR) and net assimilation rate (NAR) of *O. europea*, *P. falcatus* and *H. abyssinica* grown at four light regimes. Bars are + 1 SD. Bars that share the same lower case letter are not significantly different at $P < 0.05$. ■, 2%; ▩, 10%; ▨, 20%; ▤, 100%.

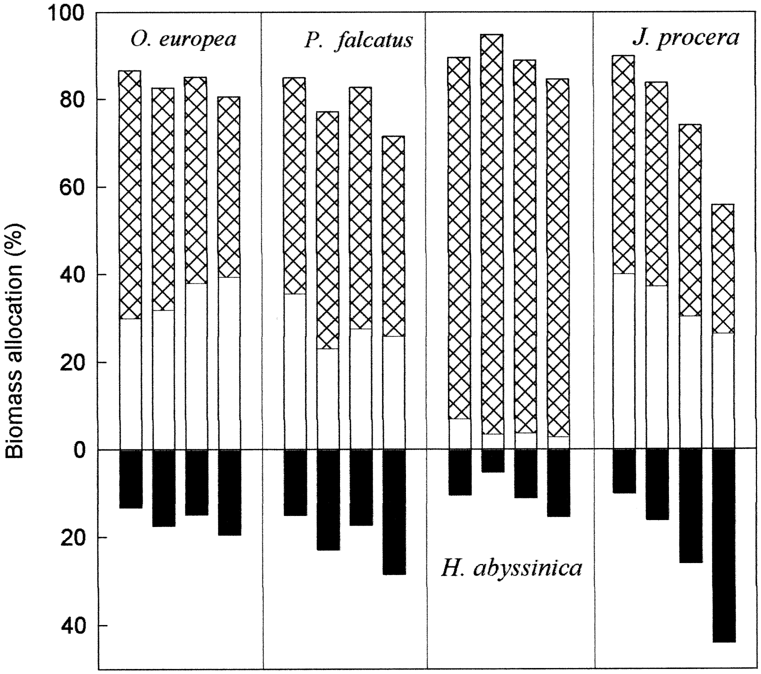

Figure 3. Per cent allocation of biomass to leaves (▨) (including petioles), stem (☐) and roots (■) in four dry afromontane species grown at four light regimes.

Table 1. Variation in light saturated photosynthesis (A_{max}), apparent quantum yield (Φ) and chlorophyll concentration of seedlings of 4-mo-old tree species grown under various light levels. Values in parentheses are SEMs.

	Treatment %	*Olea europea*	*Podocarpus falcatus*	*Hagenia abyssinica*	*Juniperus procera*
A_{max} (μmol m^{-2} s^{-1})	2	7.20 (0.36)^{aA}	7.00 (0.30)^{aA}	3.20 (0.12)^{aB}	—
	10	5.00 (0.36)^{aA}	14.50 (1.20)^{bB}	7.24 (2.06)^{bA}	—
	20	5.25 (0.32)^{aA}	11.60 (0.83)^{bB}	8.50 (1.73)^{bAB}	—
	100	19.40 (0.46)^{bA}	16.40 (2.40)^{bA}	18.04 (3.04)^{cA}	—
A_{max} (μmol g^{-1} s^{-1})	2	0.13 (0.006)^{aA}	0.19 (0.008)^{aB}	0.10 (0.003)^{aA}	0.15 (0.002)^{aAB}
	10	0.06 (0.004)^{bA}	0.27 (0.022)^{bB}	0.18 (0.049)^{aBC}	0.12 (0.004)^{aC}
	20	0.15 (0.003)^{aA}	0.17 (0.012)^{aA}	0.15 (0.030)^{aA}	0.10 (0.002)^{aB}
	100	0.07(0.004)^{bA}	0.21 (0.028)^{aB}	0.37 (0.062)^{bC}	0.32 (0.004)^{bC}
ϕ	2	0.030^{aA}	0.065^{aB}	0.038^{aA}	—
	25	0.050^{abA}	0.070^{aA}	0.075^{abA}	—
	50	0.050^{abA}	0.077^{aA}	0.075^{abA}	—
	100	0.060^{bA}	0.075^{aA}	0.080^{bA}	—
Chlorophyll (mg g^{-1} leaf wt)	2	0.666 (0.003)^{aA}	0.326 (0.001)^{aB}	—	—
	10	0.567 (0.005)^{aA}	0.277 (0.013)^{aB}	—	0.193 (0.002)^{aB}
	20	0.438 (0.009)^{abA}	0.234 (0.270)^{abAB}	0.069 (0.006)^{aC}	0.158 (0.009)^{aBC}
	100	0.143 (0.009)^{cA}	0.119 (0.027)^{bA}	0.096 (0.002)^{aA}	0.118 (0.002)^{aA}

For each parameter, means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at $P < 0.05$ as determined by Scheffé's test.

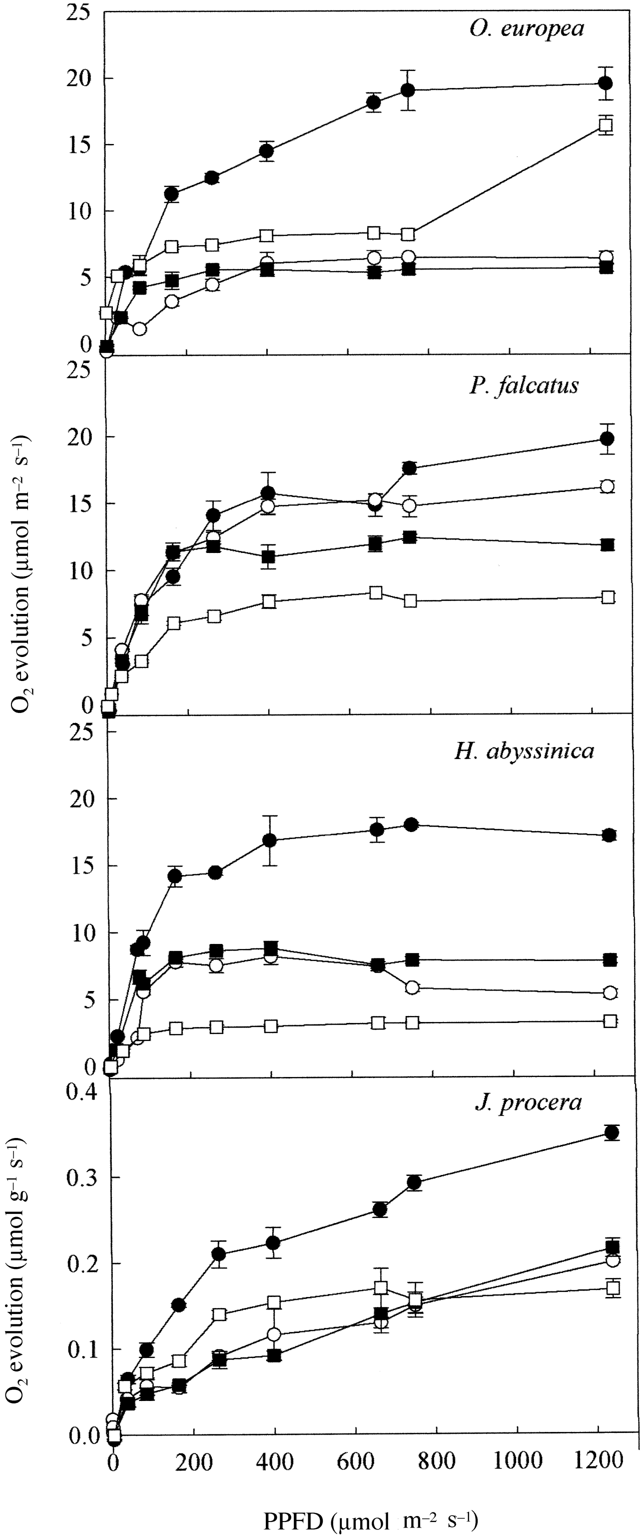

Figure 4. Light saturation curves of photosynthetic oxygen evolution of four dry afromontane tree species grown at 2 (□), 10 (■), 20 (○) and 100 (●) per cent of full light level in a greenhouse. Bars are ± 1 SD.

H. abyssinica and *J. procera* was two to three times higher than for *O. europea* and *P. falcatus*.

Apparent quantum yield (Φ) was twice as much in open grown plants as in deep shade grown in *O. europea* and *H. abyssinica*. There was little difference in Φ among the different treatments for *P. falcatus*. Among species significant differences in Φ were observed between low-light grown plants of *O. europea* and *H. abyssinica* on the one hand, and of *P. falcatus* on the other. However, there were no significant differences in Φ among open grown plants of the three species. Light intensity of saturation was *c.* 400 μmol m^{-2} s^{-1} for *H. abyssinica* and *P. falcatus* while *O. europea* and *J. procera* saturated at greater than *c.* 800 μmol m^{-2} per s^{-1} (Figure 4). In all species chlorophyll concentration of plants grown in the open was significantly lower than in shade grown plants. For the light regimes investigated, *O. europea* ranked first in chlorophyll concentration followed by *P. falcatus*, *J. procera* and *H. abyssinica* in that order.

Chlorophyll fluorescence

The potential quantum yield of photosynthesis (F_v/F_m) as determined by chlorophyll fluorescence of dark adapted leaves of the four species, the quantum efficiency (Φ_e) and NPQ of light adapted leaves are shown in Figure 5. F_v/F_m reflects the potential quantum efficiency of PSII and is used as a sensitive indicator of plant photosynthetic performance. Values around 0.83 have been found as average reference for the optimal performance of unstressed leaves of higher plants, whereas lower values indicate photoinhibition (Bjorkman & Demmig 1987). Φ_e is the relative measure of the efficiency of PSII photochemistry as determined by fluorescence, while NPQ is a measure of the efficiency of the photosystem to dissipate excess light as heat as a protective mechanism.

In the present study, irrespective of the species, all seedlings grown in shade had values of F_v/F_m close to 0.83. However in full-light grown seedlings of *P. falcatus* and *O. europea* F_v/F_m values averaged 0.76 and 0.78, respectively, which indicated that these plants had been under photoinhibitory light stress. Compared to other species very little difference was recorded among treatments in the quantum efficiency (Φ_e) of light adapted leaves of *P. falcatus* (Figure 5). This species had, however, the highest values of NPQ for both shade and open grown plants.

DISCUSSION

Striking differences were observed between the four studied species in their survival and growth under shade environments. *H. abyssinica* maintained, compared with other species, a higher relative growth rate irrespective of the light regimes. Nevertheless only few seedlings of *H. abyssinica* survived the lowest light regime more than 16 wk. *H. abyssinica* allocated 70–80% of the biomass to leaves and consequently had high LAR and RGR. This species has very small seeds. It is thus possible that in deep shade the seedlings may die following

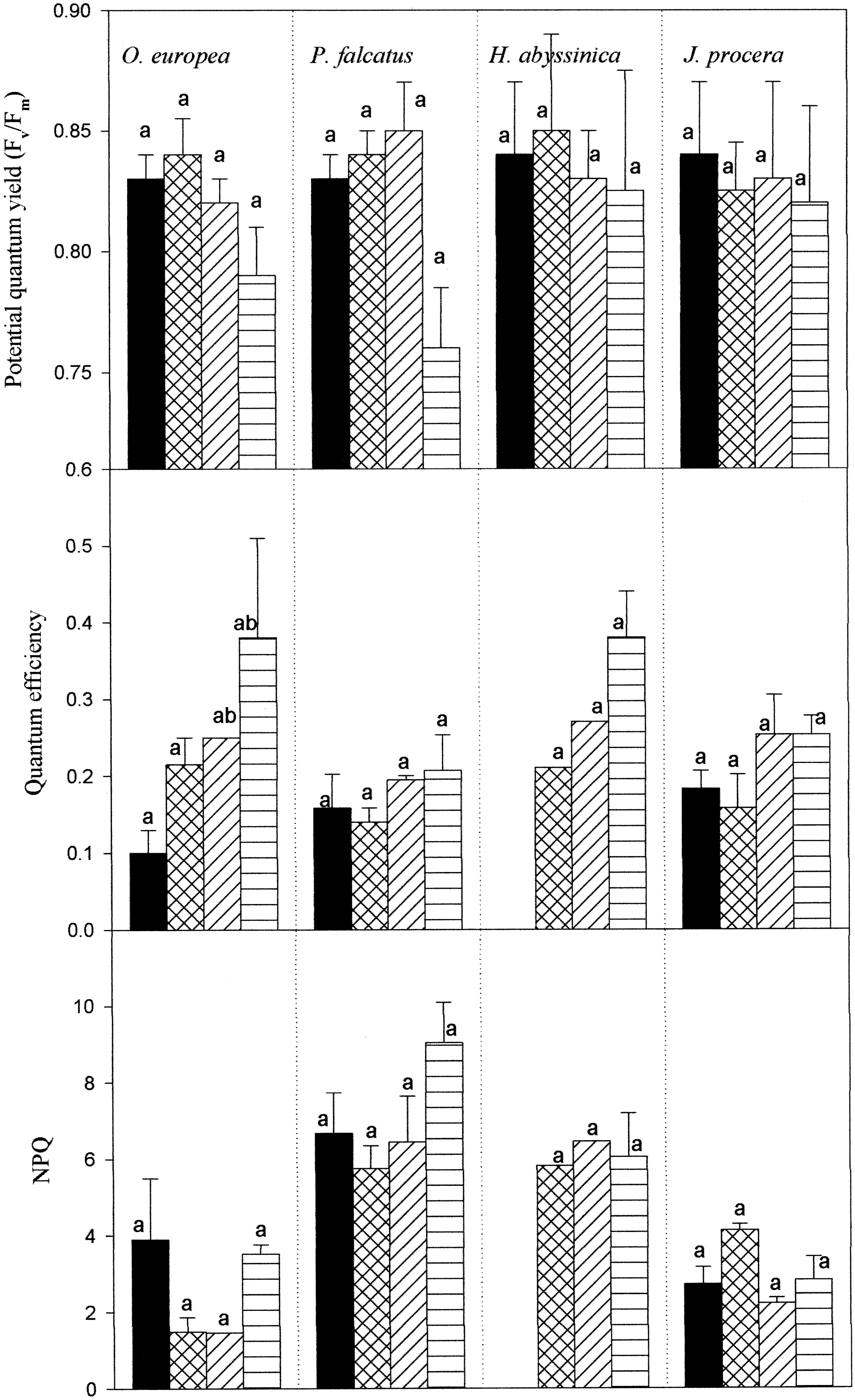

Figure 5. Potential quantum yield (F_v/F_m) of dark adapted leaves, quantum efficiency and non-photochemical quenching (NPQ) of four dry afromontane tree species grown at 2 (■), 10 (▩), 20 (▨) and 100 (▤) per cent of full light level. Quantum efficiency and NPQ were determined at a PPFD level of 600 ± 30 µmol m^{-2} per s^{-1}. Bars are ± 1 SD. Bars that share the same lower case letter are not significantly different at $P < 0.05$.

depletion of reserves as a consequence of high respiration following high LAR and RGR (Kitajima 1994). The poor survival of *H. abyssinica* in shade although it had a higher photosynthetic surface and higher growth rate supports the suggestion by Kitajima (1994) that how a seedling body is constructed (durable leaves, woody stem, well developed roots) may be more important for survival under low light than maximization of carbon gain and growth. Lange *et al.* (1997) reported that seedlings of *H. abyssinica* were never observed in the understorey of forests. The low potential of survival in shade of *H. abyssinica* might explain how this species could have been pushed up towards the more open subalpine zone of east African mountains.

P. falcatus and *O. europea* exhibited a reduced relative growth rate at low light regimes. In addition, there was a consistent trend for higher SLA and LAR in the shade. Similar patterns in shade acclimation were reported for other tropical tree species (Poorter 1999, Poorter *et al.* 1995). Formation of thin leaves with a high SLA leads to a high LAR and enhances light interception at low light intensity helping in maximization of carbon gain in the shade. The growth characteristics of the two species indicate that they are shade tolerant.

Trends in NAR among the treatments were closely reflected by the data on photosynthetic rate per unit area for *O. europea* and *P. falcatus* (Figure 2 and Table 1) which was not the case for *H. abyssinica*. At least for the two species whole plant level assimilation can be explained by leaf photosynthesis. The photosynthetic data showed that within species shade grown plants differed markedly from open grown plants except in *P. falcatus*. When grown in deep shade (2%) species significantly differed in their light-saturated rates of photosynthesis, apparent quantum yield and chlorophyll concentration. However, these differences disappeared in open grown plants. From these observations it can be said that, while they differed markedly in their capacity to grow under shade, all species studied had an equal capacity to photosynthesize at high photon flux density such as is found in forest gaps. This finding is in contrast with earlier findings that pioneers display greater photosynthetic acclimation to growth at high photon flux density (Bazzaz & Carlson 1982, Oberbauer *et al.* 1993), but is in agreement with Riddoch *et al.* (1991). In *H. abyssinica*, there were several-fold differences in light saturated rates of photosynthesis and apparent quantum yield across growth light regimes, indicating a high physiological plasticity. The results indicate that *H. abyssinica* shows in its photosynthetic characteristics similarity with early successional (pioneer) species. This characteristic is shared to a degree by *O. europea* and *J. procera*.

Plants of *P. falcatus* grown in 10 and 20% shade (which corresponded to slight and moderate shade) maintained a relatively high assimilation rate closer to plants grown in the open. Also the plants grown in 2% shade had a relatively higher light saturated photosynthetic rate and high apparent quantum yield. These results indicate that the species has a broad habitat tolerance. This is consistent with observations by Teketay (1996) and G. Dalle & M. Fetene (unpubl. data) who reported that *P. falcatus* is well represented in gaps while it also maintains a seedling bank in forest undercanopy. A shade tolerant species such as *P. falcatus* thus has a particular advantage when gaps are formed. Such species have already reached the seedling stage when others start from seeds.

There were little differences in the quantum efficiency (Φ_e) values among the different light treatments in *P. falcatus* which were comparatively low whereas similar but comparatively high NPQ values were recorded at all light levels. The low quantum efficiency especially of open grown plants may indicate that these plants are under some degree of light stress as also shown by the low F_v/F_m data. The three sets of data indicate that *P. falcatus* is also capable of growing in the open (albeit with a slightly reduced photosynthetic rate) by protecting its photosynthetic system with a high non-photochemical quenching. Thus, the survival and growth of *P. falcatus* both in shade and in the open may explain why this species is a dominant member of mixed afromontane forests.

Both Schmitt (1991) and Bussman & Beck (1996) suggested that fire stimulates the regeneration of both *J. procera* and *H. abyssinica*. This is in agreement with the results reported in the present study which indicate that photosynthetic characteristics of both species and growth characteristics of *H. abyssinica* are typical of early successional species. This may further explain why these two species make monodominant forest patches following large clearings that are caused by agents such as fire (Bussman & Beck 1996).

The present study has characterized the growth, carbon allocation and photosynthetic characteristics of the four afromontane species. The results indicate that the capacity to persist in shade with low RGR, high SLA, high LAR, high root-shoot ratio, high chlorophyll concentration, high quantum yield and high light saturated photosynthesis rate distinguish shade-tolerant plants from pioneers (light-demanders). *P. falcatus* and *O. europea* appeared to be non-pioneer, shade-tolerant species while *J. procera* and to a larger extent *H. abyssinica* showed pioneer, light-demanding characteristics. The results may partly explain the existence of mixed and monodominant forest climaxes in afromontane forests.

ACKNOWLEDGEMENTS

Financial assistance by Volkswagen-Stiftung, Germany is gratefully acknowledged. We thank Professor Erwin Beck for critically reading the manuscript and Professor Ulrich Lüttge for some of the chlorophyll fluorescence measurements. We are very grateful for the constructive comments of reviewers.

LITERATURE CITED

ARNON, D. I. 1949. Cooper enzymes in isolated chloroppoyphnoloxidases in *Beta vulgaris*. *Plant Physiology* 24:1–15.

BAZZAZ, F. A. & CARLSON, R. W. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54:313–316.

BILGER, W. & BJÖRKMAN, O. 1991. Temperature dependence of violaxanthin de-epoxidation and non-photochemical fluorescence quenching in intact leaves of *Gossypium hirsutum* L. and *Malva parviflora* L. *Planta* 91:541–551.

BJÖRKMAN, O. & DEMMIG, B. 1987. Photon yield of O^2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origin. *Planta* 170:489–504.

BUSSMANN, R. W. 1994. The forests of Mount Kenya (Kenya) – Vegetation, ecology, destruction and management of a tropical mountain forest ecosystem. Dissertation, Universität Bayreuth, Vol. 1–3.

BUSSMANN, R. W. & BECK, E. 1995. Regeneration and cyclic processes in the Ocotea forests (*Ocotea usambarensis* Engl.) of Mt. Kenya. *Verhandlungen der Gesellschaft für Ökologie* 24:35–38.

BUSSMANN, R. W. & BECK, E. 1996. Regeneration and succession processes in the Cedar-Forests (*Juniperion procerae*) of Mt. Kenya. *Ecotropica* 1:79–84.

DALLE, G. 1999. Tree seedlings and saplings in treefall gaps and forest undercanopies in Shashemene-Munessa Natural Forest. M.Sc. Thesis, Addis Ababa University.

FETENE, M., NAUKE, P., LÜTTGE, U. & BECK, E. 1997. Photosynthesis and photoinhibition in a tropical alpine giant rosette plant *Lobelia rhynchopetalum*. *New Phytologist* 137:453–461.

FRIIS, I. 1986. The forest vegetation of Ethiopia. *Symbolae Botanicae Upsaliensis XXVI* (2):31–47.

FRIIS, I. 1991. Forests and forest trees of NE tropical Africa. *Kew Bulletin Additional Series* 15:280 pp.

GENTY, B., BRIANTAIS, J. M. & BAKER, N. R. 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochemica et Biophysica Acta* 990:87–92.

KITAJIMA, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.

LANGE, S., BUSSMANN, R. W. & BECK, E. 1997. Stand structure and regeneration of the subalpine *Hagenia abyssinica* forests of Mt. Kenya. *Botanica Acta* 110:473–480.

LUNDGREN, B. 1971. *Soil studies in a montane forest in Ethiopia*. Royal College of Forestry, Department of Forest Ecology and Forest Soils, Research Notes No. 11, Stockholm. 35 pp.

OBERBAUER, S. F., CLARK, D. A., RICH, P. M. & VEGA, G. 1993. Light environment, gas exchange and annual growth of saplings of three species of rain forest trees in Costa Rica. *Journal of Tropical Ecology* 9:511–523.

POORTER, L. 1999. Growth responses of 15 rain-forest tree species to light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13:396–410.

POORTER, L., OBERBAUER, S. F. & CLARK, D. B. 1995. Leaf optical properties along a vertical gradient in a tropical rain forest canopy in Costa Rica. *American Journal of Botany* 82:1257–1263.

RADFORD, P. J. 1967. Growth analysis formulae. Their use and abuse. *Crop Science* 7:171–176.

RIDDOCH, I., LEHTO, T. & GRACE, J. 1991. Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytologist* 119:137–147.

SCHMITT, K. 1991. *The vegetation of the Aberdare National Park, Kenya*. Hochgebirgsforschung 7. Universitätsverlag Wagner, Innsbruck. 250 pp.

TEKETAY, D. 1996. *Seed ecology and regeneration in dry afromontane forests of Ethiopia*. Doctoral Thesis. Swedish University of Agricultural Sciences. Silvestria 4. Umea. 150 pp.

WEINERT, E. 1985. Die aktuelle Gebirgsvegetation am Horn von Afrika. *Flora* 176:231–243.

WHITMORE, T. C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70:536–538.