

# Analysis of the “shelter tree-effect” of natural and exotic forest canopies on the growth of young *Podocarpus falcatus* trees in southern Ethiopia

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**Abstract** Plantations of exotic trees on areas where tropical forest has been clear-felled have been reported to facilitate regrowth of indigenous tree species. This so-called nurse- or shelter tree effect was investigated in a montane semihumid site in southern Ethiopia where plantations of *Pinus patula* and *Eucalyptus saligna* grow in close vicinity to the natural *Podocarpus falcatus* mixed forest. Physiological performance of *P. falcatus* saplings growing in the exotic and the natural forests was investigated over the year. Compared with the natural forest, photosynthetic carbon gain and growth of the saplings were significantly enhanced under *Pinus patula* while likewise retarded under *Eucalyptus saligna*. Diverging effects of the differently dense shelter canopies on the saplings could be traced to differences in the sub-canopy microclimates and particularly to the intensities and temporal distribution of photosynthetic active radiation (PAR). Moisture also played an important role for photosynthetic carbon gain: while the morning patterns of CO<sub>2</sub> uptake were significantly correlated with the patterns of sunflecks, stomatal conductance was the determinant factor in the afternoon. Analysis of the photosynthetic efficiency of sunflecks revealed a lower quantum yield than the basic diffuse PAR intensity. Compared with a theoretically even distribution

of the daily PAR, CO<sub>2</sub> uptake under the real light climate was 70% under *Pinus* and in the natural forest, and 59% under *Eucalyptus*. Relating growth rates of *Podocarpus* saplings to photosynthesis the microclimate under *Pinus* was 2.5 times as effective as that in the natural forest and five times more effective than under *Eucalyptus*.

**Keywords** *Podocarpus falcatus* · Growth · Photosynthesis · Exotic plantations · Shelter tree effect · Ethiopia

## Introduction

The potential of exotic tree plantations as foster ecosystems for the regeneration of a forest of indigenous tree species is gaining worldwide attention by ecologists and foresters (Harrington and Ewel, Oberhauser 1997, Otsamo 1998; Ashton et al. 1998; Fimbel and Fimbel 1996, Selwyn and Ganesan 2009; Kasenene 2007; Keenan et al. 1997; Parrotta 1992, 1995; Lemenih 2006). Depending on the former vegetation, the climate and the exotic tree species used for afforestation or reforestation, positive or negative effects on soil hydrology (Huber et al. 2007, Little et al. 2009), soil physical and chemical properties (Binkley and Resh 1998), litter and nutrient turnover (Brasell and Sinclair 1983; Lisanevork and Michelsen 1993) and soil carbon stocks (Guo and Gifford 2002) prevail. Fast growing exotic species change dynamics of soil processes usually considerably (Little et al. 2009). Regeneration of indigenous forest under the shelter of a canopy of exotic trees, e.g. various species of pine and *Eucalyptus* has been studied in many regions, especially in Central America (Parrotta 1999; Cusack and Montagnini 2004; Hagggar et al. 1997; Healey and Robert 2003; Montagnini 2001) and

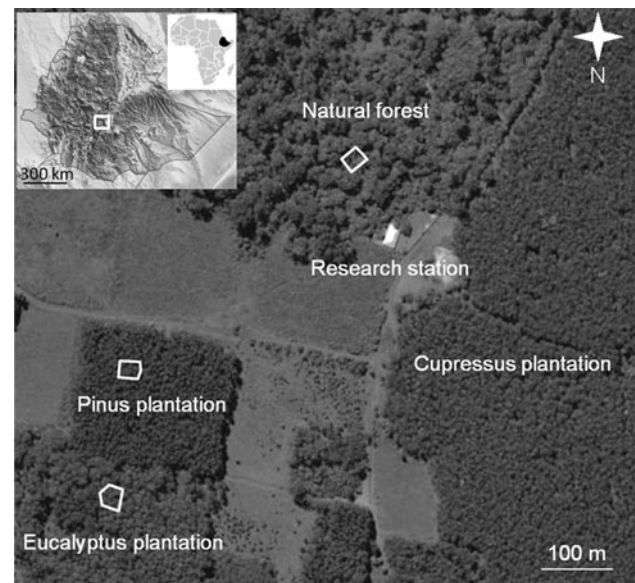
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Ethiopia (Lemenih et al. 2004, Lemenih 2006; Pohjonen and Pukkala 1990; Michelsen et al. 1993; Yirdaw and Luukkanen 2003; Senbeta et al. 2002). In Ethiopia studies concentrated on an afro-montane forest on the eastern escarpment of the Rift Valley. The so-called Munessa-Sheshamene Forest has a total area of 23,000 ha, of which about 30% has been converted to plantations of the exotic tree species *Cupressus lusitanica*, *Pinus patula*, *Eucalyptus globulus* and *E. saligna* (Feyera et al. 2002). Due to illegal logging and grazing of livestock, regeneration of the indigenous tree species, even in the natural forest, becomes a major problem (Teketay 1997; Tesfaye et al. 2010). Ethiopia's natural evergreen *Podocarpus* forests (Friis and Friis 1992) represent the typical vegetation between 1,800 and 2,800 m a.s.l. which consists of a mixture of evergreen and a few deciduous woody species (Chaffey 1980; Müller-Hohenstein and Abate 2004; Abate 2004). They are dominated by *Podocarpus falcatus* which grows up to 50 m high (Russ 1945). Except the very dense plantations of *Cupressus lusitanica*, natural regeneration of indigenous tree species, in particular of *Podocarpus falcatus* takes place to some extent in the plantations. This situation has been addressed in several papers on the ecophysiology of the dominating indigenous and exotic tree species (Feyera et al. 2002; Fetene and Beck 2004; Fetene and Feleke 2001; Lüttge et al. 2003; Fritzsche et al. 2006). Surprisingly, the *Pinus patula* and *Eucalyptus saligna* plantations harbour a denser though unevenly distributed population of *Podocarpus* saplings than the natural forest, if the areas are not too far from a seed producing *Podocarpus* tree (Tesfaye et al. 2010). Even more unexpected was the observation that the saplings apparently perform similarly or even better in the plantations than under the natural canopy (Tadele and Fetene in press). *Podocarpus falcatus* is known as a year round seeding tree (Tesfaye et al. 2010) whose seedlings and saplings are neither browsed by cattle and wildlife nor severely attacked by insects. A survival rate of 90% of the *Podocarpus* seedlings was recorded beneath the canopy of shelter trees, whereas in full light only 55% survived. However, after establishment of the seedlings, relative growth rates were highest under moderate light (Tesfaye 2008, Girma 2010). Finally, when it begins to overtop the canopy of the other trees the leaves of its crown must fully adapt to the intense tropical light intensities.

In the Munessa-Shashemene forest the natural forest and the plantations border each other (Fig. 1) and therefore the question arises as to why the *P. falcatus* saplings perform so well under the exotic trees. Soils (Ashagrie et al. 2005) and the climate are similar and therefore the hypothesis is put forward that differences in the subcanopy microclimate are responsible for the differences in growth. Major ecophysiological components of such microclimate are humidity and light (Chazdon and Fetcher 1984). Both



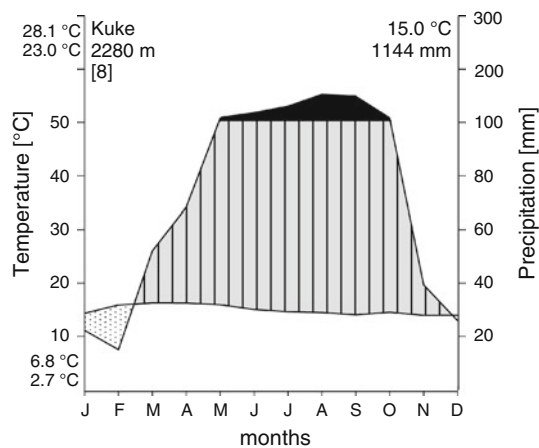
**Fig. 1** Map of Ethiopia and the study area showing the natural forests and the plantations (Google Maps 2007)

factors control carbon gain by affecting stomatal conductance and photosynthesis. Effects of the structure of the canopy on the intensities of diffuse radiation and the temporal patterns of sunflecks are obvious (Chazdon 1986; Pearcy 1990; Chazdon and Pearcy 1991; Leakey et al. 2004; Lemenih et al. 2004). Therefore, the hypothesis is put forward that varying patterns of irradiance and different contributions of sunflecks to the total understorey photosynthetic photon flux density (PAR) represent the main factor for the different performance of the *P. falcatus* saplings in the Munessa-Shashemene natural forest and exotic tree plantations. To examine this hypothesis, not only daily patterns of PAR and their effects on photosynthetic carbon dioxide uptake by the *P. falcatus* saplings were investigated, but also the effects of other environmental variables like temperature and humidity were included in the study. Data were recorded during dry and wet seasons over a period of 2 years and finally correlated with growth of the saplings.

## Materials and methods

### The research area

The area (7°26' N, 38°52' E) in the Munessa-Shashemene state forest, locally known as Kuke, is located 240 km south of the capital Addis Ababa on slightly sloping terrain at an altitude of 2,300 m. A research station is situated on a clearing in the centre of four different types of forest (Fig. 1), the natural montane *Podocarpus* forest (with trees about 40 m high) and monotonous plantations of *Cupressus lusitanica* (30 years old, 30 m high), *Pinus patula* (37 years old,



**Fig. 2** Walter-type climate diagram of the research area

35 m high) and *Eucalyptus saligna* (31 years old, but partly coppiced 7 years ago, 40 and 25 m high, respectively). Species composition and physiognomy of the forests have been described in detail by Müller-Hohenstein and Abate (2004). Except in the dense *Cupressus* plantation, *Podocarpus* seedlings and saplings were found in all forest types. Seeds from adult female trees in the natural forest are distributed by birds and monkeys (Negash 1995).

The climate has been recorded since 2001 (Fig. 2). The area receives an annual rainfall of about 1,150 mm at a mean annual temperature of 15°C. The pattern of rainfall has been referred to as bimodal (Freier et al. 2010; Fritzsche et al. 2006), with long rains from July to October and short rains from April to June. However, during the past 9 years the gap between the small and the long rains has disappeared and the climate in general has become more humid. Parent soil material consists of basic volcanites covered by deep and clayey Rhodic Nitisols (Freier et al. 2010). Soil properties, nutrient cycling and carbon stocks have been extensively studied (Solomon et al. 2002; Abate 2004; Lemenih et al. 2004; Ashagrie et al. 2005; Fritzsche et al. 2006) and similarity of the structure of soils in the natural forest and the plantations has been noticed. The original density of the planted *Pinus* and *Eucalyptus* trees was 466 stems/ha and 625 stems/ha, respectively. However, the plantations which are close to clearing or coppicing (*Eucalyptus*) have partly run wild and the tree layer as well as the understorey vegetation is not any longer homogeneous. Especially towards the edges and in bigger gaps, the densities of *P. falcatus* and some other indigenous broadleaf saplings were considerable.

#### Selection of plots and trees

In the natural forest a plot with five *P. falcatus* saplings on an area of 50 m<sup>2</sup> was selected. In the *Pinus* and *Eucalyptus*

plantations the corresponding data were 11 saplings on 80 m<sup>2</sup> and 7 saplings on 140 m<sup>2</sup>, respectively (Fig. 3). The saplings used for the measurements in the natural forest were between 1.6 and 4.7 m high (dbh between 1.6 and 4.9 cm). In the *Pinus* plantation, the saplings selected for measurements ( $n = 9$ ) reached heights between 1.9 and 3.5 m (dbh between 1.7 and 4.4 cm), whereas in the *Eucalyptus* plantation the variation in the size of the measured saplings ( $n = 5$ ) was greater, ranging from 1.8 to 7.0 m (dbh between 1.8 and 8.1 cm). Wooden scaffolds, between 10 and 12 m high were constructed for recording of subcanopy microclimate factors. The *Eucalyptus* canopy had two storeys, the lower from trees re-grown after coppicing (about 15 m high) and the upper from the older *Eucalyptus* trees. Due to the two storeys the light intensity reaching the forest floor was lower (highest LAI) than in the other two forest types.

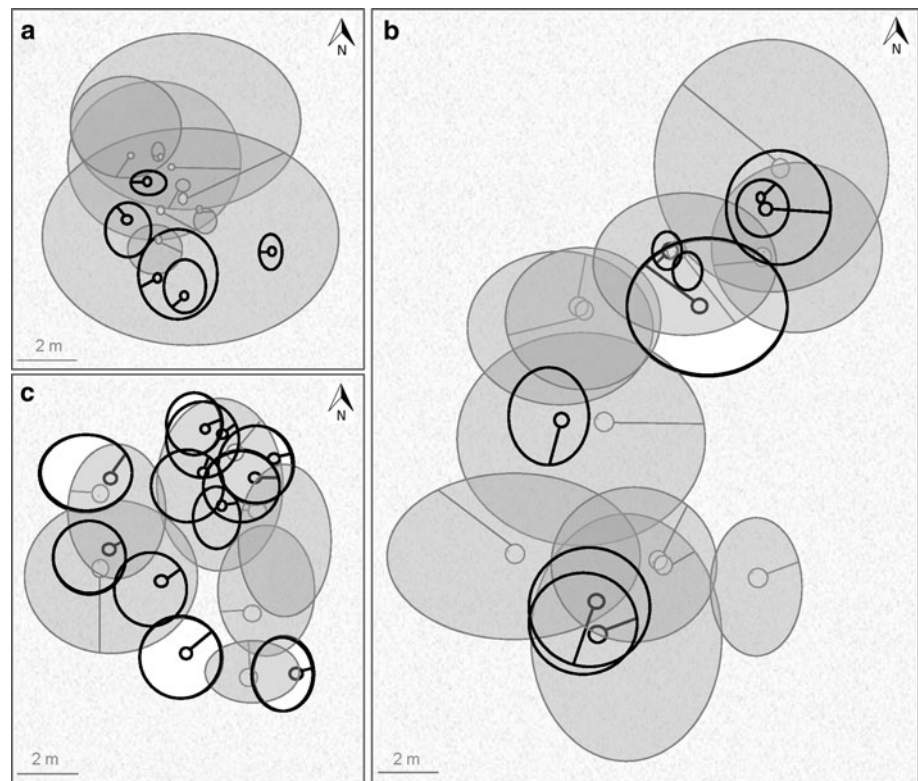
#### Canopy cover

Crown dimensions of all trees were measured with a canopy perpendicular and a measuring tape in the four cardinal directions (Fig. 3). Canopy cover was calculated as percentage of crown area projection related to ground area (Roehle 1986). Density of the canopy was estimated by the Leaf area index (LAI) that was determined with a LAI 2000 Plant Canopy Analyzer (Li-Cor Biosciences, Lincoln, Nebraska) 2 m above the ground. Measurements were conducted on cloudless days in the late afternoon to avoid errors from direct sunbeams (Lemenih et al. 2004). LAI was calculated as average of 25 individual measurements for each forest type on several days and referenced against the average of open sky measurements.

#### Microclimate measurements

Reference climate data (Metos climate station, Pessl Instruments, Weiz, Austria) were recorded in the wide clearing at the research station (reference climate station). The station was equipped with sensors for air temperature, relative humidity, solar radiation, wind speed, and precipitation. The sensors were installed at 2.0 m above the ground and the rain collector at 1.0 m. Subcanopy climate data were measured with sensors for relative humidity, air temperature, visible radiation, and photosynthetic active radiation (PAR) (Thies Clima, Adolf Thies GmbH & Co. KG, Göttingen, Germany). The sensors were mounted in various positions on the scaffolds. Throughfall was recorded 1.2 m above the ground with a tipping-bucket rain gauge combined with a HOBO Event Logger (Onset Computer Corporation, Bourne, MA, USA). Distance of the rain gauge from stem was 2 to 3 m. Electricity was provided from solar panels.

**Fig. 3** Topview of the investigated shelter trees and saplings in the different sites with vertical projections of the crowns of the *Podocarpus* saplings (black fringes) and of the shelter trees (grey). **a** Natural forest with *Podocarpus* shelter tree, *Podocarpus* saplings, other trees; **b** *Pinus* plantation with *Pinus patula* shelter trees, *Podocarpus* saplings; **c** *Eucalyptus* plantation with *Eucalyptus saligna* shelter trees, *Podocarpus* saplings



Climate data were measured every 10 min and hourly averages were recorded with a DL 15-data logger (Thies, Goettingen, Germany). Only 2 Thies microclimate stations were available. One of them was permanently installed in the natural forest, whereas the other was installed alternately for 3–4 months in one of the plantations.

#### Porometry

Daily courses of net CO<sub>2</sub> uptake, stomatal conductance, transpiration, and of environmental conditions were measured with a temperature- and humidity-controlled CO<sub>2</sub> porometer (Walz GFS-3000, Heinz Walz GmbH, Effeltrich, Germany). Smaller leaves, while still in nearly natural position on the twigs, were lined up to completely cover the area of the cuvette (4 cm<sup>2</sup>). The cuvette was mounted on a stand for constant positioning during the day. For light saturation curves artificial light was provided by the LED Light source 3040-L (Walz, Effeltrich, Germany). Measurements were taken from 8:30 in the morning until 18:00 in the evening, however only on days without strong rain and when the surfaces of the leaves were dry.

#### Simulation of sunflecks

Potential effects of sunflecks on the photosynthetic gain were simulated using the artificial PAR source on the top of the cuvette. Since the majority of the sun-flecks were in the

low light range, light pulses of 30 s with intervals of 60 s were superimposed on a continuous illumination of the leaves with 40 μmol m<sup>-2</sup> s<sup>-1</sup>. The intensities of the light pulses were set in the range between 200 and 400 μmol m<sup>-2</sup> s<sup>-1</sup>. CO<sub>2</sub> net uptake and stomatal conductance were recorded simultaneously. Measurements were performed during the morning hours when the leaves had already been exposed to the natural light climate for at least 2 h and the water supply to the plants was still sufficient to keep the stomates open.

#### The δ<sup>13</sup>C isotope ratio

Leaf samples for δ<sup>13</sup>C analysis were collected in July 2006 from three *Podocarpus* saplings and from three shelter trees of each site. The dried plant material was ground with a ball mill (Retsch GmbH, Haan, Germany) and the δ<sup>13</sup>C isotope ratio was determined in the laboratory of the Soil Science Department of the Bayreuth Centre for Ecology and Environmental Research (IRMS, delta S, Finnigan MAT, Bremen, Germany).

#### Statistical analysis

Statistical analyses of the data were carried out with the software R (R Foundation for Statistical Computing, Vienna, Austria). Not only routine tests on normal distribution of the data were performed (Shapiro–Wilk Test), but



also factorial analysis of variance (ANOVA), post hoc separation of averages with Scheffé's test was applied and the significance of differences of means was investigated with Levene's test (*t* test). Differences of the data were considered significant when  $p < 0.05$ .

## Results and discussion

### Canopy density

The density of the three canopies differed considerably. The canopy in the natural forest was closed (99% coverage), whereas the crowns in the *Eucalyptus* and the *Pinus* plantations did not completely overlap (Fig. 3). Canopy closure in the *Pinus* and *Eucalyptus* site was similar with 68% for *Pinus* and 72% for *Eucalyptus*. Due to the two-tiered canopy LAI was highest ( $4.4 \pm 0.2$ ) in the *Eucalyptus* site. The canopy of the natural forest had the lowest LAI ( $3.2 \pm 0.1$ ) whereas that of the *Pinus* plantation was in between ( $3.8 \pm 0.3$ ). About 10 years ago canopy closure and LAI have been measured in the same exotic tree plantations and on a site of natural forest in the Kuke area with a canopy cover of 70% (Lemenih et al. 2004). In that work lower LAI values have been measured, namely  $1.78 \pm 0.72$  for the natural forest,  $1.65 \pm 0.25$  for the *Eucalyptus* and  $2.46 \pm 0.32$  for the *Pinus* plantation. While a dramatic change of the canopy parameters of the *Eucalyptus* plantation is conceivable with regard to coppicing and regrowth, the higher recent canopy densities of the other two forests indicate vigorous growth, presumably due to the more humid conditions during the last years (Fig. 2).

### Mitigating effects of the canopies on the microclimate

#### Temperature

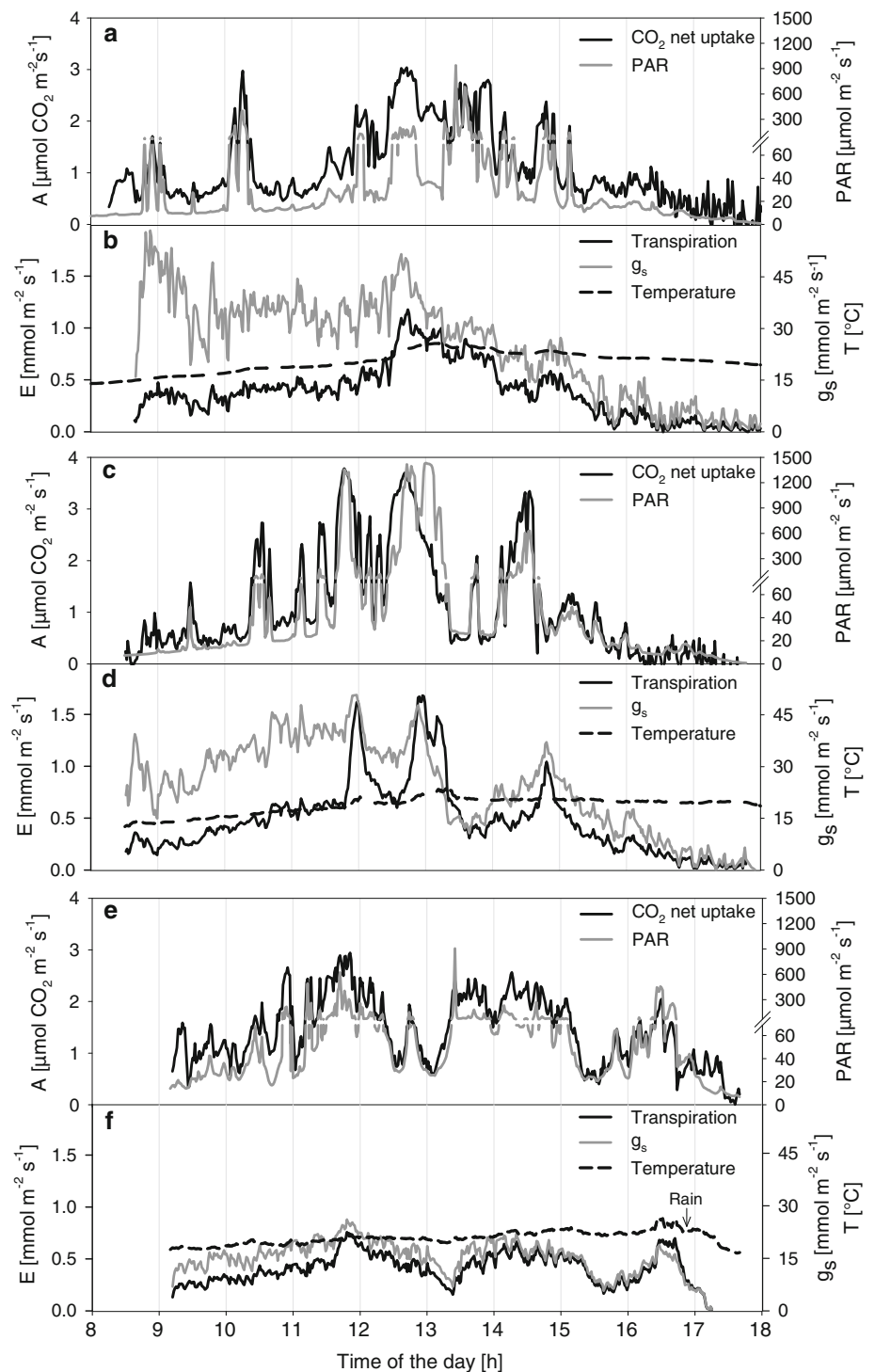
While the annual average of the air temperature at the reference climate station was  $15.0^{\circ}\text{C}$ , the monthly means ranged between  $13.0^{\circ}\text{C}$  in December and  $16.2^{\circ}\text{C}$  in March. The corresponding monthly means were  $11.4$  to  $15.0^{\circ}\text{C}$  in the natural forest,  $13.2$  to  $15.8^{\circ}\text{C}$  in the *Pinus* plantation, and  $14.4$  to  $16.1^{\circ}\text{C}$  in the *Eucalyptus* plantation. Thus, the natural forest was slightly cooler (statistically significant) and the *Eucalyptus* plantation slightly warmer (statistically not significant) than the open area. Extremes of air temperature (2 m above ground) ranged in the open field from  $2.7$  to  $28.1^{\circ}\text{C}$ , in the natural forest from  $4.4$  to  $26.0^{\circ}\text{C}$ , in the *Pinus* plantation from  $3.5$  to  $24.5^{\circ}\text{C}$  and in the *Eucalyptus* plantation from  $8.6$  to  $21.5^{\circ}\text{C}$  (only rainy season data available). Expectedly, the canopies dampened the extreme

temperatures. Minimum soil temperature in 10 cm depth was  $10.5^{\circ}\text{C}$ , maximum  $22.8^{\circ}\text{C}$ . The optimal temperature range for photosynthesis was from  $20$  to  $25^{\circ}\text{C}$ . As shown in Fig. 4 temperatures around and above  $20.0^{\circ}\text{C}$  were usually attained for several hours during the afternoon. Coincidence with high light intensities and stomatal conductance resulted then in maximum rates of photosynthetic  $\text{CO}_2$  net uptake. However, due to the usually small amplitude of the daily fluctuation of the air temperature, the effect of the temperature on the daily sum of carbon uptake did not exceed 5% as shown by ANOVA analysis.

#### Throughfall and VPD, stomatal conductance and overall water relations

Monthly throughfall was similar under the three canopies (Table 1). During the rainy season monthly means were 53 to 56% of the total precipitation, while maximal throughfall during the rare heavy rain events were 83, 69 and 73% for the natural forest, the *Pinus* and the *Eucalyptus* canopies, respectively. In the dry season, monthly throughfall in the natural forest and the *Pinus* plantation was 34 and 32%, respectively, of the total precipitation. However, due to the patchy canopy of the *Pinus* and the *Eucalyptus* plantation, throughfall was not homogeneous, as the gaps received a higher proportion of precipitation. Adding 70% of gross precipitation for the gap areas (Asdak et al. 1998) results in corrected monthly means of 60% for the *Pinus* and 59% for the *Eucalyptus* plantation. Throughfall as a variable of the microclimate depends on many factors, such as the structure and density of the canopy, intensity and distribution of the rainfall events, wind speed, VPD of the air and the proportion of surface stemflow (Crockford and Richardson 2000). In tropical and subtropical forests, interception ranges between 8.9 and 39% and stemflow between 0.1 and 13% (Crockford and Richardson 1990). The high proportion of interception plus surface stemflow of 46% of gross precipitation in the natural forest which is in full agreement with an earlier report (Ashagrie 2004) can be attributed to the mode of rainfall in the research area and to the heavy loads of epiphytes, mostly ferns and mosses on the stems and branches. Daily sums of rainfall rarely exceeded 20 mm and amounts above 40 mm were reached on less than 10 days per year (Fritzsche et al. 2006; Fig. 2). Water saturation of the canopy therefore is usually slow and the concomitant evaporative losses are high. This situation is exacerbated during spells of dry and hot days when canopy water storage capacity is high. Throughfall has not been measured previously in the *Pinus patula* and *Eucalyptus saligna* plantations. But the model of Schulze et al. (1978) for *Pinus patula* interception fits our data well. For a *Eucalyptus globulus* plantation in the same area considerably higher throughfall has been reported (82% for the

**Fig. 4** Daily courses of  $\text{CO}_2$  net uptake ( $A$ ), of stomatal conductance ( $g_s$ ) and transpiration ( $E$ ) by *Podocarpus* saplings, of PAR and air temperature on a sunny day (24 Nov 2006) in the natural forest (a, b); on a sunny day (12 Dec 2006) in the *Pinus* plantation (c, d); and on a cloudy day with some drizzle (20 March 2006) in the *Eucalyptus* plantation (e, f). Total sums of  $A_N$ : 36.4 (a), 34.7 (c) and 48.0 (e)  $\text{mmol m}^{-2} \text{ day}^{-1}$ ; total sums of PAR: 1.5 (a), 4.7 (c) and 2.5 (e)  $\text{mol m}^{-2} \text{ day}^{-1}$



rainy season and 68% for the dry season, Ashagrie 2004). However, those data were collected in an uncoppiced 30-year-old plantation and therefore are not comparable to the dense two-tiered canopy of the *Eucalyptus saligna* plantation investigated here. Due to the almost complete closure of the canopy in the natural forest, throughfall is considered more homogeneous and on average less precipitation ( $\sim 55\%$ ) reaches the bottom of the natural forest

than in the exotic plantations (68–70%).<sup>1</sup> However, the annual courses of soil matric potentials in the top and the subsoil were similar in the natural forest and the above

<sup>1</sup> Because of the repeated transfer of the second microclimate station between the *Pinus* and the *Eucalyptus* plantation and some problems with the sensor data for an extended series of days without precipitation, representing the dry season, are not available for the microclimate under the shelter of *Eucalyptus* trees.

**Table 1** Climate factors determined by the reference station outside the forest, and of the subcanopy space in the natural forest, the *Pinus* plantation and the *Eucalyptus* plantation

	Reference station	Natural forest	<i>Pinus</i> plantation	<i>Eucalyptus</i> plantation
Solar radiation ( $\text{mol m}^{-2} \text{ day}^{-1}$ )				
Rainy season	$45.0 \pm 2.5^a$			
Dry season	$72.0 \pm 1.5^b$			
PAR ( $\text{mol m}^{-2} \text{ day}^{-1}$ ) <sup>A</sup>				
Rainy season	$20.5 \pm 1.1^a$	$1.4 \pm 0.3^c$ ( $21.2 \pm 2.6$ )	$1.6 \pm 0.3^c$ ( $20.3 \pm 1.3$ )	$0.9 \pm 0.2^d$ ( $20.0 \pm 2.1$ )
Dry season	$33.0 \pm 0.7^b$	$1.6 \pm 0.3^c$ ( $30.7 \pm 1.9$ )	$2.0 \pm 0.3^c$ ( $34.4 \pm 0.9$ )	$0.9 \pm 0.2^d$ ( $32.2 \pm 1.0$ )
VPD (hPa)				
Rainy season	$1.3 \pm 0.4^a$	$1.4 \pm 0.3^a$ ( $1.7 \pm 0.6$ )	(no data)	$1.8 \pm 0.4^a$ ( $2.4 \pm 0.9$ )
Dry season	$4.2 \pm 0.5^b$	$4.0 \pm 0.4^b$ ( $4.2 \pm 0.5$ )	$4.0 \pm 0.7^b$ ( $4.7 \pm 0.6$ )	$3.8 \pm 0.1^b$ ( $4.4 \pm 0.9$ )
Precipitation ( $1 \text{ month}^{-1}$ ) and Troughfall (%)				
Rainy season	$148.6 \pm 22.7^a$	$53 \pm 7^c$ %	$56 \pm 4^c$ %	$54 \pm 8^c$ %
Dry season	$27.2 \pm 10.3^b$	$34 \pm 15^d$ %	$32 \pm 6^d$ %	(no data)

Numbers represent monthly means and standard errors. Data for VPD, precipitation and throughfall are calculated from 19 months (reference station), 15 months (natural forest), 5 months (*Pinus* plantation) and 6 months (*Eucalyptus* plantation) from both seasons, while mean values for solar radiation and PAR are calculated from 60 days for all sites (both seasons). Numbers in brackets show corresponding values of the reference station. Lowercase letters indicate significant differences between seasons and sites

<sup>A</sup> Monthly means of PAR of the reference station are calculated from solar radiation using a conversion factor of  $f = 0.46$  (according to Rao 1984)

mentioned *Eucalyptus globulus* plantation, ranging between almost 0 during the long rains and  $-55$  to  $-60$  kPa during the dry season. (Fritzsche et al. 2006). Compensation of the smaller water supply to the soil in the natural forest may be due to the higher water use efficiency of *Podocarpus falcatus* as compared with *Eucalyptus* (Fetene and Beck 2004).

Light intensity and stomatal conductance ( $g_s$ ) limit photosynthetic carbon uptake. Stomatal movement responds to signals from the roots, from light and from the atmospheric water vapour deficit (Comstock 2002). From June to October 2006, monthly means of VPD were very low reflecting the rainy season (Table 1). But even during the dry season (November to March) atmospheric VPD of the reference area was only moderate, and differences in the atmospheric humidity between the three forests were statistically not significant. Since stomatal conductance ( $g_s$ ) is calculated from transpiration and VPD, the relation between  $g_s$  and VPD is auto-correlated and therefore not relevant. Further on, measurement of a root signal was beyond the possibilities of the present work. That leaves the examination of a potential correlation between changes in light intensities and changes in stomatal conductance. Daily courses of stomatal conductance were compared with the simultaneously measured light intensities (Fig. 4). Generally only weak correlations were found, the strength of which differed between the three forest types: In the natural forest and the *Eucalyptus* plantation, light intensity had almost no effect on stomatal conductance of the

sapling leaves ( $r^2 = 0.19$ ;  $n = 17$ , and  $r^2 = 0.13$ ;  $n = 18$ , respectively) while in the *Pinus* plantation a small influence was indicated by correlation factors of  $r^2 = 0.28$  ( $n = 22$ , for compilation of all respective data see Table 5).

Due to varying daily fluctuations, mean values of stomatal conductance are not useful for long-term estimates of the water relations and for comparing the water use efficiencies (WUE) of the *Podocarpus* saplings at the three sites. Therefore, the carbon isotope signatures (Farquhar et al. 1989a, b; Adams and Grierson 2001; Flexas et al. 2008; Lüttge et al. 2011) which reflect mean leaf life WUE and the average ratio between leaf-internal to ambient  $\text{CO}_2$  concentrations ( $C_i/C_a$ ), were determined of young and mature leaves of the saplings and the shelter trees (Table 2). The  $\delta^{13}\text{C}$  values of young leaves from the three sites were virtually identical and also no effect of leaf maturation on the  $\delta^{13}\text{C}$  value could be detected with saplings from the natural forest and the *Eucalyptus* plantation. Such effect, although very small, was seen in *Podocarpus* saplings from the *Pinus* plantation which exhibited slightly lower  $\delta^{13}\text{C}$  ratios than the young ones ( $-28.6 \pm 0.2$  vs.  $-29.4 \pm 0.3$ ). The  $^{13}\text{C}$  signatures of the *Podocarpus* shelter trees were slightly lower than those of the saplings but young and mature leaves had identical  $\delta^{13}\text{C}$  ratios. Also with the other shelter trees leaf maturation had no effect on the  $\delta^{13}\text{C}$  ratios, but the generally higher discrimination of  $^{13}\text{C}$  suggests an overall higher stomatal (and mesophyll) conductance. Similar differences ( $\approx 2\%$ ) between the  $\delta^{13}\text{C}$

**Table 2** Carbon isotope discrimination of leaves of *Podocarpus* saplings and adult shelter trees

Trees	$\delta^{13}\text{C}$ values of young leaves ( $n = 9$ ) [‰]	$\delta^{13}\text{C}$ values of mature leaves ( $n = 9$ ) [‰]
<i>Podocarpus</i> saplings (natural forest)	$-29.5 \pm 0.2^a$	$-29.4 \pm 0.3^{af}$
<i>Podocarpus</i> saplings ( <i>Pinus</i> plantation)	$-29.4 \pm 0.3^{ae}$	$-28.6 \pm 0.2^{bf}$
<i>Podocarpus</i> saplings ( <i>Eucalyptus</i> plantation)	$-29.3 \pm 0.3^{ae}$	$-29.6 \pm 0.2^a$
<i>Podocarpus</i> shelter tree	$-28.8 \pm 0.1^{ce}$	$-28.7 \pm 0.1^{cf}$
<i>Pinus patula</i> shelter tree	$-31.0 \pm 0.2^d$	$-31.1 \pm 0.2^d$
<i>Eucalyptus saligna</i> shelter tree	$-29.3 \pm 0.6^c$	$-30.1 \pm 0.7^c$

Numbers represent means of leaves from three trees; each sample consisted of three sub-samples of young and mature leaves, respectively, means  $\pm$  SE. Lowercase letters indicate significant differences within the sites between young and old leaves and between the *Podocarpus falcatus* saplings and the *Podocarpus* nurse tree

signature of mature leaves from adult *Podocarpus* and *Eucalyptus* trees from the research area have also been reported by Freier et al. (2010).

Significance of the  $\delta^{13}\text{C}$  values for characterizing the water relations of canopies has been questioned (Broadmeadow et al. 1992; Griffith 1991) because several factors different from water availability can affect that ratio. Since investigations addressing the  $\delta^{13}\text{C}$  content of *Podocarpus falcatus* are scarce (Lüttge et al. 2003), a draft was made on data from other Gymnosperms. Mesophyll and stomatal conductance of *Prumnopitys ferruginea*, a close relative to *Podocarpus*, are very low and even lower are  $g_s$  and  $g_m$  of another Podocarpaceae, *Dacrydium cupressinum* (De Lucia et al. 2003). Slow diffusion (low  $g_s$  and  $g_m$ ) limits  $\text{CO}_2$ -assimilation and simultaneously decreases  $^{13}\text{C}$  discrimination (Broadmeadow et al. 1992). The comparatively low photosynthetic rates (see below) of *Podocarpus falcatus* leaves, irrespective of whether from a shelter tree or a sapling are in line with their low  $\delta^{13}\text{C}$  ratios (De Lucia et al. 2003). Thus, they are not necessarily indicating stomata closure because of water shortage. Comparing only the  $\delta^{13}\text{C}$  values of the shelter trees suggests a higher WUE of *Podocarpus falcatus* over the other two species. However, when WUE was estimated from the daily courses of  $\text{CO}_2$  net uptake and transpiration, the values were similar for all three species (*Podocarpus* 4.9; *Pinus* 4.8; *Eucalyptus* 4.9 mmol  $\text{CO}_2/\text{mol H}_2\text{O}$ ) and in the range expected for Gymnosperms (Larcher 2001). The differences of WUE as estimated using two different methods could result from the fact that the direct measurements were performed on selected days, whereas the  $\delta^{13}\text{C}$  ratio integrates over the entire life-span of the leaf. The isotope signature of the saplings could have additionally been affected by the high  $^{13}\text{C}$  content of the  $\text{CO}_2$  from soil respiration (Kodama et al. 2008). However, the  $\delta^{13}\text{C}$  ratio of soil-borne  $\text{CO}_2$  decreases exponentially with the vertical distance from the forest floor and Kao et al. (2000) showed that it is only significant below 2 m. Since the leaf samples of the saplings were collected in about 2 m height and higher up, the

contribution of soil-borne  $\text{CO}_2$  to the  $\delta^{13}\text{C}$  signature of the leaves can also be neglected. The statistically significant slightly lower  $\delta^{13}\text{C}$  value of the mature leaves of the saplings in the *Pinus* plantation may indeed indicate a WUE comparable to that of the *Podocarpus* shelter trees. Direct estimation from daily courses confirms that idea and shows a lower WUE of the saplings on the other two forest sites. Since WUE of all samples was in the range known for Gymnosperms (and *Eucalyptus*), water shortage should not be a factor that on a long term, e.g. for a whole season, limits photosynthetic carbon gain. However, it may temporarily restrict  $\text{CO}_2$  uptake, particularly so in the afternoons as shown in Fig. 4.

#### The subcanopy light relations

Daily accumulated global radiation ranged from 45 mol  $\text{m}^{-2} \text{d}^{-1}$  in the rainy season to 72 mol  $\text{m}^{-2} \text{d}^{-1}$  in the dry season, and applying the conversion factor 0.46 (Rao 1984) daily sums of PAR ranged between 20.5 and 33 mol  $\text{m}^{-2} \text{d}^{-1}$  (Table 1). Losses upon passage through the canopies were considerable as on average only 5.9% (natural forest), 6.9% (*Pinus* plantation) and 3.6% (*Eucalyptus* plantation) of the daily PAR reached the level of the *Podocarpus* saplings. Comparable values have been reported for a tropical lowland rain forest of Costa Rica (Chazdon and Fetcher 1984), a mixed coniferous–deciduous forest in New England (Canham et al. 1994) and for Californian redwood forests (Percy and Pfitsch 1994).

With regard to photosynthetic carbon gain, not only the average light intensities or the accumulated daily amounts of PAR are important but also the contribution of diffuse radiation and sunflecks to the daily light supply (Chazdon 1986; Chazdon and Percy 1986; Percy et al. 1994; Küppers et al. 1996). Because the records of the climate stations represent hourly means, they are useful for comparing the total light supply under the three canopies (Table 3). The highest daily subcanopy PAR sums were measured in the *Pinus* plantation and the lowest under the



**Table 3** The sub-canopy light climates of the three investigated forest areas and their effects on photosynthetic CO<sub>2</sub> net uptake

	Natural forest		<i>Pinus</i> plantation		<i>Eucalyptus</i> plantation	
Number of analysed daily courses	8	8	9	13	8	13
Weather condition	Cloudy	Sunny	Cloudy	Sunny	Cloudy	Sunny
Daily accumulated PAR (mmol m <sup>-2</sup> day <sup>-1</sup> )	1,399 ± 306 <sup>ab</sup>	1,630 ± 309 <sup>ab</sup>	1,563 ± 185 <sup>ab</sup>	2,044 ± 322 <sup>a</sup>	924 ± 248 <sup>b</sup>	1,080 ± 195 <sup>b</sup>
Daily numbers of sunflecks >40 μmol m <sup>-2</sup> s <sup>-1</sup>	31 ± 4 <sup>a</sup>	39 ± 4 <sup>a</sup>	40 ± 2 <sup>a</sup>	33 ± 3 <sup>a</sup>	35 ± 5 <sup>a</sup>	35 ± 4 <sup>a</sup>
Percent of daily accumulated PAR resulting from sunflecks >40 μmol m <sup>-2</sup> s <sup>-1</sup> (%)	55	67	71	72	40	51
Daily CO <sub>2</sub> net uptake (mmol m <sup>-2</sup> day <sup>-1</sup> )	28 ± 3 <sup>a</sup>	27 ± 4 <sup>a</sup>	33 ± 3 <sup>a</sup>	28 ± 2 <sup>a</sup>	23 ± 4 <sup>ab</sup>	18 ± 3 <sup>b</sup>
Percent of daily CO <sub>2</sub> net uptake resulting from sunflecks >40 μmol m <sup>-2</sup> s <sup>-1</sup> (%)	41	38	62	48	27	31

With regard to the typical weather situations two classes of the daily accumulated global radiation were defined: 19–59 mol m<sup>-2</sup> day<sup>-1</sup> for cloudy days with drizzle, typical for the wet season and 60–82 mol m<sup>-2</sup> day<sup>-1</sup> for sunny days of the dry season. Means ± SE. Lowercase letters indicate significant differences between seasons and sites

*Eucalyptus* canopy. PAR sums in the natural forest were close to those in the *Pinus* plantation. Comparison with LAI shows agreement in so far as radiation was lowest under the densest canopy of the *Eucalyptus* plantation. On the other hand, the highest daily light sums were found under the *Pinus* shelter, and not as expected from LAI in the natural forest. For a detailed assessment of the PAR relations under the three canopies 57 daily courses of PAR intensity were analysed, which were measured simultaneously with net carbon uptake ( $A_N$ ). Typical daily courses are shown in Fig. 4. Two weather situations were comprehended which could be representative of days in the rainy (e, f) and the dry season (a, b and c, d), respectively. These situations were defined on the basis of the incident global radiation measured by the reference station. Due to the technical limitations of porometry days with heavy rainfall could not be investigated. The basic diffuse PAR intensities of 15–40 μmol m<sup>-2</sup> s<sup>-1</sup> with an average of 23.8 ± 0.9 μmol m<sup>-2</sup> s<sup>-1</sup> were in the linear range of the light (PAR) response curves of photosynthetic CO<sub>2</sub> net uptake (Fig. 5) and well above the range of the light compensation points (1.4–3.9 μmol m<sup>-2</sup> s<sup>-1</sup>). Sunflecks were counted as individual events with PAR intensities >40 μmol m<sup>-2</sup> s<sup>-1</sup> (Chazdon 1986; Chazdon and Fetcher 1984; Pfitsch and Pearcy 1989; Weber et al. 1985; Valladares et al. 1997). Surprisingly, the average numbers of daily lightflecks were similar under the three canopies ranging between 31 and 40, but duration of the spells of direct irradiation was different. Longest-lasting sunflecks of high intensity were observed under the canopy of *Pinus* (Fig. 4c). The majority of the sunflecks exceeded the linear range of the light response curve (Fig. 5), but only a few exceeded saturation light intensity of photosynthesis. The shares of the sunflecks to the daily PAR sums were determined for the two weather situations (Table 3). Expectedly, the shares were higher on sunny days but the differences between the weather situations were only small.

The contribution of direct radiation to the daily accumulated PAR was highest under the *Pinus* canopy, the lowest under *Eucalyptus* while in the natural forest sunflecks contributed a little more than half of the daily PAR sum. Similar patterns of direct and diffuse radiation have been reported from a tropical premontane forest in Costa Rica (Chazdon and Fetcher 1984; Chazdon 1986; Küppers et al. 1995), in a tropical rainforest in India (Küppers et al. 1995), and in a tropical rainforest in Australia (Chazdon and Pearcy 1986).

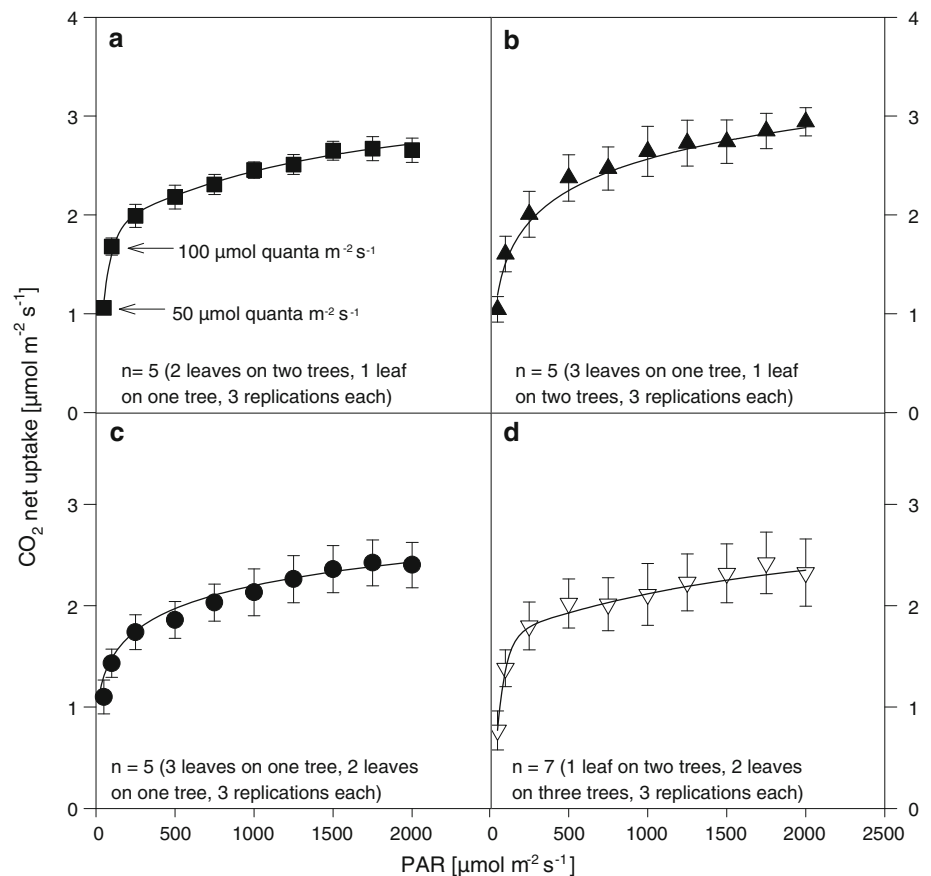
### Photosynthesis

Light response curves of CO<sub>2</sub> net uptake ( $A$ ) at ambient CO<sub>2</sub> concentration, constant temperature and air humidity were similar with leaves from the *Podocarpus* saplings in all three forest types, but the rates measured with saplings growing outside the shelter in the open area were 20% lower (Fig. 5) at low light intensities. A linear increase of  $A_N$  was observed up to 100 μmol PAR m<sup>-2</sup> s<sup>-1</sup> and light saturation was achieved between 1,500 and 2,000 μmol m<sup>-2</sup> s<sup>-1</sup>. However, the maximal rates of 2.5–2.7 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> of the shade-grown saplings were substantially lower than those of the *Podocarpus* shelter trees (4–4.5 μmol m<sup>-2</sup> s<sup>-1</sup>) which in contrast to the mentioned sapling are already adapted to high light intensities.

### Investigation of the effect of sunflecks on photosynthetic CO<sub>2</sub> uptake

The effect of the varying subcanopy light intensities on photosynthesis of the young *Podocarpus* trees was examined by simulating sunflecks with the artificial PAR source of the porometer at otherwise ambient conditions. Pre-illuminated leaves were used for that experiment. Photosynthetic CO<sub>2</sub> uptake responded with a delay of 8–10 s to the increase of the light intensity and returned to the

**Fig. 5** Light (PAR) response curves of photosynthetic CO<sub>2</sub> net uptake by *Podocarpus* saplings growing under the canopies of the natural forest (a), of *Pinus patula* (b), of *Eucalyptus saligna* (c) and without shelter in the open field (d). Data show mean values  $\pm$  SE of two to five saplings per site with three replications per leaf



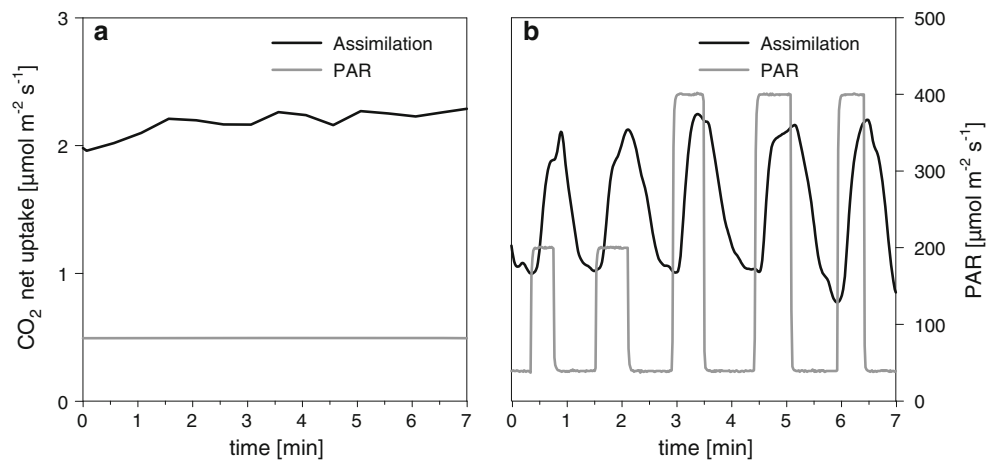
low-light level about 40 s after dying out of the light fleck (Fig. 6b). The fast response and a time lapse of only a few seconds until the maximum CO<sub>2</sub> uptake was achieved indicated that the leaves were in the photosynthetically active state (Percy 1990; Percy and Pfitsch 1994) when the simulation experiment was started. PAR intensities used for sunfleck simulation were 200 and 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, and because of these low intensities the post-illumination burst (Percy 1990) was only small. The response of CO<sub>2</sub> net uptake to the light fleck intensity matched the light response curve as  $A_N$  triggered by 400  $\mu\text{mol PAR m}^{-2} \text{s}^{-1}$  light flecks was only 1.18 times higher than that resulting from a light fleck of 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The corresponding relation from the light response curve of  $A_N$  (Fig. 5) is 1.11 and therefore in fair agreement with the measured value. In another set of experiments photosynthetic efficiency of intermittent light flecks was compared with the effect of an identical amount of PAR that was administered as constant diffuse illumination over the same time period (Fig. 6a). While the applied PAR intensities of the continuous illumination (83  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in Fig. 6a) and the basic radiation in the light fleck experiment (40  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were within the linear range of the light response, the lightfleck intensity (200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) extended into the non-linear range.

Therefore, efficiency of the lightfleck was lower than that of the basic diffuse PAR intensity. Likewise, if the daily sums of  $A_N$  were related to either the daily accumulated PAR in the actual sunfleck pattern or to the same amount of PAR virtually applied at constant intensity over the day, the actual light climate was less efficient than the theoretical (Table 4) which was calculated from the light response curves of  $A_N$ . Whereas about 70% of the theoretical CO<sub>2</sub> uptake was actually achieved under the canopies of the *Pinus* plantation and the natural forest, only 59% was measured under that of *Eucalyptus*.

#### Assessment of the daily courses of photosynthetic CO<sub>2</sub> net uptake

In Fig. 4 three daily courses of  $A_N$ , PAR, temperature,  $g_s$  and transpiration (E) are shown which are considered typical of the selected weather situations and forest types. Panels a to d represent dry weather conditions in the natural forest and the *Pinus* plantation, respectively, and panels e and f show the situation on an overcast day in the *Eucalyptus* plantation with some drizzle in the afternoon at the beginning of the rainy season. At the early dry season (panels a–d) the soils were still moist and thus water supply to the trees was sufficient resulting in a generally high

**Fig. 6** Analysis of the light fleck effect on photosynthetic  $\text{CO}_2$  uptake by two simulated light conditions, administering the same amounts of PAR over an identical time-span. **a** PAR provided as constant photon flux density of  $83 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; **b** PAR provided as intermittent light flecks of 30 s at an intensity of 200 or  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  on a basic intensity of  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The interval between the individual light flecks was 60 s



**Table 4** Photosynthetic efficiency of the actual sub-canopy light climate compared with a virtual constant illumination with the same amounts of PAR applied over the same time period

Forest/ plantation	Daily sum of PAR ( $\text{mol m}^{-2} \text{day}^{-1}$ )	Calculated average PAR intensity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Estimated daily $\text{CO}_2$ net uptake ( $\text{mmol m}^{-2} \text{day}^{-1}$ )	Measured daily $\text{CO}_2$ net uptake ( $\text{mmol m}^{-2} \text{day}^{-1}$ )	Apparent efficiency of the actual radiation (%)
Natural forest	1.5	50.5	38.3	27.7	72
<i>Pinus</i> plantation	1.8	58.9	42.1	30.0	71
<i>Eucalyptus</i> plantation	1.4	42.2	34.2	20.1	59

Estimated daily  $\text{CO}_2$  net uptake was calculated using the light response curves of A shown in Fig. 4

stomatal conductance. By contrast, soils were still rather dry at the beginning of the rainy season and water supply may have run short especially during the afternoons resulting in a lower stomatal conductance.

Given sufficient stomatal conductance ( $g_s > 10 \text{ mmol m}^{-2} \text{s}^{-1}$  and  $E$  up to  $1.5 \text{ mmol m}^{-2} \text{s}^{-1}$ ) photosynthetic  $\text{CO}_2$  net uptake responded very sensitively to any change in the light intensity especially during the morning hours. In the afternoon when stomatal conductivity was low sunflecks resulted only in small responses of  $A_N$  (e.g. panels a/b after 15 h and e/f between 15 and 16 h). The limiting effect of the stomatal conductance on  $A_N$  is also obvious from panels c/d during noon (12:30 h – 13:30 h) when light intensity is high but  $g_s$  low. The significance of light intensity and stomatal conductance for the rate of  $A_N$  can be estimated from their respective correlation coefficients (Table 5). Evaluation of 57 daily courses of  $A_N$ , PAR and  $g_s$  revealed the expected dominant effect of PAR over stomatal conductance, in particular during the morning hours when  $r^2$  was between 0.75 and 0.78. Stomatal conductance was of less influence, especially in the *Pinus* plantation, but its co-limiting effect on  $A_N$  is nevertheless remarkable, at least in the natural forest. In contrast to photosynthesis, the influence of light intensity on  $g_s$  is small and, if ever, in favour of photosynthetic  $\text{CO}_2$  uptake. As long as stomatal conductance was high, transpiration increased during the morning hours

(Fig. 4b, d, f), whereas it followed stomatal conductance closely in the course of the afternoon when the relative humidity of the air was low.

Fifty-nine daily courses of PAR and  $\text{CO}_2$  net uptake were analysed for the assessment of the physiological significance of the radiation intensity and distribution below the canopies of the three forest types (Table 3). Daily subcanopy PAR sums less than  $1 \text{ mol m}^{-2} \text{day}^{-1}$  have been reported for dense neotropical forests (Chazdon and Fletcher 1984; Chazdon 1986). Thus, the observed mean values between 1 and  $2 \text{ mol m}^{-2} \text{day}^{-1}$  as well as LAI indices between 3.2 (natural forest) and 4.4 (*Eucalyptus* plantation) indicate relatively porous canopies of the investigated Ethiopian forests. The light climate to which the *Podocarpus* saplings were subjected in the *Eucalyptus* plantation was less favourable, exceeding  $1 \text{ mol PAR m}^{-2} \text{day}^{-1}$  only slightly and on sunny days. Twice as much PAR was available under the *Pinus* canopy. Although the average numbers of sunflecks were in a similar range of 30 to 40 per day in all three forest types and not necessarily higher on sunny than on cloudy days, the average daily sums of PAR are consistently higher on sunny days. Due to differences in the structure and density of the canopies, the duration and intensities of the sunflecks and thus their contributions to the daily accumulated PAR were different. Long-lasting light flecks of high intensity were recorded

**Table 5** Correlation between photosynthetic active radiation and CO<sub>2</sub> net uptake (PAR/A), between stomatal conductance and CO<sub>2</sub> net uptake (g<sub>s</sub>/A), and between photosynthetic active radiation and stomatal conductance (PAR/g<sub>s</sub>) of the saplings in the three different sites

	<i>n</i>	PAR/A [ <i>r</i> <sup>2</sup> ]	g <sub>s</sub> /A [ <i>r</i> <sup>2</sup> ]	PAR/g <sub>s</sub> [ <i>r</i> <sup>2</sup> ]
<b>Natural forest</b>				
Whole day	17	<b>0.53</b>	<b>0.46</b>	<b>0.19</b>
Morning (8:30–13:00)	17	<b>0.57</b>	<b>0.24</b>	<b>0.10</b>
Afternoon (13:00–18:00)	17	<b>0.49</b>	<b>0.66</b>	<b>0.29</b>
Fig. 5a morning	1	0.75	0.24	0.18
Fig. 5a afternoon	1	0.56	0.83	0.44
<b>Pinus plantation</b>				
Whole day	22	<b>0.56</b>	<b>0.29</b>	<b>0.28</b>
Morning (8:30–13:00)	22	<b>0.61</b>	<b>0.33</b>	<b>0.27</b>
Afternoon (13:00–18:00)	22	<b>0.52</b>	<b>0.58</b>	<b>0.33</b>
Fig. 5c morning	1	0.78	0.46	0.16
Fig. 5c afternoon	1	0.57	0.76	0.60
<b>Eucalyptus plantation</b>				
Whole day	18	<b>0.56</b>	<b>0.38</b>	<b>0.13</b>
Morning (8:30–13:00)	18	<b>0.65</b>	<b>0.22</b>	<b>0.12</b>
Afternoon (13:00–18:00)	18	<b>0.46</b>	<b>0.51</b>	<b>0.15</b>
Fig. 5e morning	1	0.75	0.66	0.56
Fig. 5e afternoon	1	0.50	0.67	0.32

Numbers given are correlation factors (*r*<sup>2</sup>) between the datasets of 17, 22 and 18 daily courses in the natural forest, the *Pinus* and the *Eucalyptus* plantation, respectively, on the one hand (bold), and the three daily courses shown in Fig. 4 on the other

under the *Pinus* canopy (see also Fig. 4c) and to some extent also under the shelter of the natural forest (Fig. 4a). Therefore, the contributions to the total daily PAR sums were rather high (55–72%), whereas the share of the shorter and less intense sunflecks under the *Eucalyptus* canopy was significantly smaller (40–51%) and conversely, the contribution of the diffuse radiation was significantly higher. The differences in the photosynthetic efficiencies of the three subcanopy light climates become understandable on the background of the results of the experiment with artificial lightflecks. Only around 30% of the daily CO<sub>2</sub> uptake by the *Podocarpus* saplings in the *Eucalyptus* plantation resulted from sunflecks and 70% from the more effective low-energy diffusive radiation, whereas considerably higher shares of sunfleck-driven and with regard to yield less effective photosynthesis were recorded in the natural forest and in particular in the *Pinus* plantation.

Growth rates of *Podocarpus falcatus* saplings under the three types of canopies as related to photosynthesis

Stem extension growth of the young *Podocarpus* trees was monitored from April 2005 to March 2007 using plastic

dendrometers and tapeline (Table 6). Although the growth rates were not evenly distributed, patterns are clear: Highest relative growth rates were found with the *Podocarpus* saplings in the *Pinus* plantation while those under the natural and the *Eucalyptus* canopy grew at significantly lower rates. Growth rates during the dry and the rainy season did not differ significantly. To relate growth rates with daily sums of photosynthetic CO<sub>2</sub> uptake requires knowledge of the photosynthesizing leaf area. Collecting such data is easy when investigating seedlings (e.g. Fetene and Feleke 2001) but difficult when working with saplings. One sapling, 9-m high from the natural forest had a leaf area of 27 m<sup>2</sup> (4,680 g dry weight of leaves) and taking into account that the *Podocarpus* leaves are amphistomatous (Lüttge et al. 2003), twice as much photosynthesizing and transpiring surface could be assumed. Since harvest of the complete foliage is of course detrimental to the saplings and thus could not be applied, the vertical projections of the crowns were used as proxies for the photosynthesizing surfaces (Table 6). Although this approach cannot produce biomass data with regard to the use of photosynthates for growth, it is convenient for a comparison of the overall growth conditions under the three canopies. Highest photosynthetic production and also relative growth rates were measured under the canopy of *Pinus*. The ambient conditions there were about 2.7 times as effective as those under the canopy of the natural forest and about five times more effective than the subcanopy conditions in the *Eucalyptus* forest.

## Conclusion

The so-called nurse tree effect of two exotic tree species and of the indigenous trees in the natural forest on the growth of *Podocarpus falcatus* saplings could be traced down to a conversion of the high global radiation into a beneficial light climate while other variables of the climate were less affected. The presented results do not support the opinion of a detrimental effect of *Pinus* on the establishment and growth of *Podocarpus falcatus*. However, such conclusion could be drawn from the performance of *Podocarpus* saplings under the shelter of *Eucalyptus saligna*. In that case the two-tiered canopy of the shelter trees absorbed significantly more PAR than the other two canopies and thus per se gave rise to a lower photosynthetic production. However, not only photosynthesis was reduced under the shelter of *Eucalyptus*. The relative growth rate was additionally decreased, perhaps due to another allocation pattern of the photosynthates to the plant organs. In contrast to the situation in the *Pinus* plantation where the trees are usually felled after 30 to 40 years of growth, the *Eucalyptus* trees are regularly coppiced in 7- to 8-year

**Table 6** Relative growth rates (RGR), crown projection areas (CPA), ratio of RGR and CPA, mean daily sum of CO<sub>2</sub> net uptake, and the product of mean CO<sub>2</sub> net uptake and the ratio of RGR and CPA of *Podocarpus* saplings in the three different sites

	Natural forest	<i>Pinus</i> plantation	<i>Eucalyptus</i> plantation
RGR (rel. growth rate) [mm cm <sup>-1</sup> month <sup>-1</sup> ]	0.08 ± 0.02 <sup>a</sup>	0.28 ± 0.06 <sup>b</sup>	0.09 ± 0.02 <sup>a</sup>
CPA (Crown projection area) [m <sup>2</sup> ]	2.6 ± 1.1	3.7 ± 0.4	7.9 ± 2.1
RGR/CPA	0.029	0.081	0.011
Mean daily sum of CO <sub>2</sub> net uptake [mmol m <sup>-2</sup> day <sup>-1</sup> ]	27.8 ± 2.4 <sup>ab</sup>	30 ± 1.9 <sup>a</sup>	19.8 ± 2.4 <sup>b</sup>
Ratio RGR/CPA to mean CO <sub>2</sub> net uptake	10 × 10 <sup>-4</sup>	27 × 10 <sup>-4</sup>	5.5 × 10 <sup>-4</sup>

Numbers given for RGR and CPA are means and standard error of the saplings in the different sites (Natural forest:  $n = 5$ , *Pinus* plantation:  $n = 9$ , *Eucalyptus* plantation:  $n = 7$ ), numbers for the daily sum of CO<sub>2</sub> net uptake are means and standard error for 16, 22 and 21 daily courses in the natural forest, in the *Pinus* and in the *Eucalyptus* plantation, respectively. Lowercase letters indicate significant differences between the sites

intervals. When this happens the *Podocarpus* saplings shoot up (Feyera et al. 2002) making use of the improved radiation. Although data are not yet available the jerky growth modus of *Podocarpus* saplings in an *Eucalyptus* plantation may be not less effective than the more even growth under *Pinus* or in the natural forest.

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