LIGHT ENVIRONMENT AND PHOTOSYNTHESIS OF AN UNDERSTORE AND A PIONNER SPECIES FROM PREMONTANE RAINFOREST OF COSTA RICA

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ABSTRACT

Light environments of gap and understorey microsites were examined in a premontane wet forest area at the Reserva Biológica Alberto Ml. Brenes (RBAB), 40 km NW of San Ramón, Alajuela, Costa Rica. The light conditions varied both, in spatial and temporal patterns. Understorey sites were characterized by a low dimlight background (15-18 $\mu mol\ m^{-2}s^{-1}$), occasionally interrupted by short lightflecks of direct irradiance (<500 $\mu mol\ m^{-2}s^{-1}$). These lightflecks contributed the major part of total daily photon flux density (PFD) on clear days, whereas within a gap the PFD was mostly over 500 $\mu mol\ m^{-2}s^{-1}$ with peaks of up to 200 $\mu mol\ m^{-2}s^{-1}$. Two tree species typically occuring in these contrasting microsites were the pionner *Heliocarpus appendiculatus* (Turczaninow) and the understore species *Salacia petenensis* (Lundell). Steady - state measurements of leaf gas exchange demostrated a low light compensation point from *S. petenensis* linked with a low dark respiration and low light saturated rates. For *H. appendiculatus* high dark repiration and ligth saturated rates and a higher light compensation point were observed. Based on these steady - state photosynthesis rates and measured PFD at the individual sites, carbon gains calculated for every species. Leaf gas exchange measurements under fluctuating PFD showed a significant difference between both species, in light use efficiency (LUE) versus lightfleck - length as well as in the efficiency of carbon gain versus induction - state (IS) of the photosynthetic apparatus.

INTRODUCTION

Tropical forest show the highest complexity of species on earth. Up to now mechanisms that apply to this diversity are rarely understood. Besides relative stable and optimal environment conditions for plant growth over a geological time scale that allowed an undisturbed evolution, an enormous heterogeneity of forest structure creates various ecological niches (Whitmore 1993). One important factor for niche - richness are disturbances in the closed canopy - so called "gaps" -, caused by treefall, landslide, etc. Related to the size of a gap, the availability of essential resources changes significantly in comparison to understore site. This concerns mainly soil nutrient and light incidence (Denslow 1987). As the penetration of light on the forest floor below a non-disturbed canopy is typically aound 2 % of the received by the upper treetops(Chazdon 1986), light is an importan limiting factor for plant growth, stablishment of seedlings and the development of samplings.

An occurence of a gap is followed by colonization of pioneer tree species that "key in" new environmental conditions (Bazzaz & Pickett 1980). Main characteristics of this ecological group are high photosynthetic capacities combined with fast growth rates and a high turn - over of leaves and supporting tissue (Bazzaz & Carlson 1982, Ackerly 1993). In contrast, the understore contains species featuring low light compensation and saturation points with a high

quantum efficiency (Oberbauer & Strain 1984, Pearcy & Sims 1994). In addition, initial construction costs for leaves and branches are in comparison to pioneers more expensve, but due to longer longevity on a long - tern view more economic (Chabot & Hicks 1982). In understore sites, the major part of total daily photon flux can be contributed by short durations of direct sunlight, called lightflecks. Related to forest structure and climatic conditions the amount of lightflecks is 10-78 % of the daily irradiance (Chazdon 1986, Pearcy 1988). Very likely, survival of plantas under these conditions depends strongly on an efficient utilization of these lightflecks.

In this study we compared a typical pioneer and an understore tree species growing at the natural sites. Measurements of light environment and steady - state photosynthesis rates were combined to obtain approximate daily carbon gain. Furthermore, photosynthetic responses to fast changing light conditions were examined to work out possible acclimations to the natural light conditions.

STUDY AREA AND SPECIES

The study was conducted during december 1993 and march 1994 at the RBAB, located in Atlantic side of the Cordillera Tilarán, Costa Rica (10º13´N, 84º37´W; 875 m above sea level). Rainfall occurs relatively aseasonal with up to 4000 mm per annum, with a sligtly drier season from febreary to april. Mean monthly temperatures are 21ºC all over the year. The forest canopy reaches a height of 30-40 m, by is most parts not very dense. Different canopy - layers contain numerous small and medium -sized gaps and permit a well -developed understore flora (Wattenberg & Breckle 1995). The two species involved in this study are the pioneer tree Heliocarpus appendiculatus (Turczaninow) and the shade - tolerant tree Salacia petenensis (Lunndell). H. appendiculatus is abundant in gaps and large clearing, reaching final heights of up to 25 m, while S. petenensis is common in undisturbed forest sites with well developed trees below the upper canopy - layer and exceptional emergents of more than 25 m.

METHODS

Measurements of PFD were made, using light - sensors (LS) sensitive to photosynthetic active radiation (Hamamatsu G 1118), taking into account a slight underestimation of red light in the spectrum sensor (LI 190SB, Li-Cor Inc.). The connected data - logger (21X: Campbell Scientific, Inc.) recorded PFD at 1 s intervals and computed 10 s averages.

LS were placed horizontally at four positions within the canopy of every individual. Signals were logged over several days under defferent weather conditions, ranging from clear to very cloudy.

Recorded PFD were analyzed in terms of their daily frecuencies and their contribution to total diurnal irradiance.

Photosynthetic measurements were made with an open, differential gas exchange system (CQP 130i, Fa. Walz). To obtain steady - state light responses of net photosynthesis we used an artificial ligth (halogen lamp, 150 W), reducing irradiance with neutral density filters.

Diurnal PFD from the different forest habitats and data of the light - response curve were used as inputs to calculate total daily net carbon gain. Though simplified, this approach is sufficient precise to yiel quantitative estimates of daily carbon gains.

Induction of the photosynthetic apparatus was calculated from comparing the CO_2 assimilation at the end of the lightfleck versus the maximal assimilation under constat PFD (Chadzon & Pearcy 1986a). The computation is based on the following equation:

$$I = \frac{A_{end}}{A_{const}}$$

where I is the induction - state (%), A_{end} is the maximal CO_2 assimilation rate at the end of the lightfleck ($\mu mol\ m^{-2}s^{-1}$) and A_{const} ($\mu mol\ m^{-2}s^{-1}$) is the corresponding CO_2 assimilation decline was determined by applying lightflecks of 30 s at saturating PFD to fully induced leaves after an increasing duration of darkness, ranging from 1 min up to 20 min.

Light use efficiency (LUE) (%) of a fully induced leaves in saturating light is expressed by the relation between thw carbon gain obtained during a lightfleck, A_{lf} ($\mu mol\ m^{-2}s^{-1}$) versus the

predicted carbon gain. A_{pred} (μmol m^{-2}s^{-1}). as calculated from steady - state rates (Chazdon & Pearcy 1986b):

$$LUE = \frac{A_{lf}}{A_{pred}}$$

RESULTS

Light environment

Fig. 1 show daily PFD measured on a sunny day above the treetop (at 10 m) of *H. appendiculatus* grow in a large gap (~ 500 m^2). In contrast, Fig. 2 represents the PDF on the same day intercepted by a sensor mounted above a *S. petenensis* tree at 10 m height in the understore.

In comparison to a sensor mounted above the forest canopy, the gap site received 89 % (32 mol d^{-1}) whereas the understore location obtained approximately 14 % (6.4 % mol d^{-1}) of total daily radiation. The dimlight background in the understore (~ 40 μmol m^{-2}s^{-1}) was interrupted by short lightflecks varied in duration and intensity, due to the size of openings in upper canopy - layer and penumbrial effects.

A remarkable difference to the understore was the generally higher radiation (> 500 μmol m^{-2}s^{-1}) of the gap site. Furthermore, the occurence of lightflecks was mainly caused by variable clouds and not by openings in open canopies.
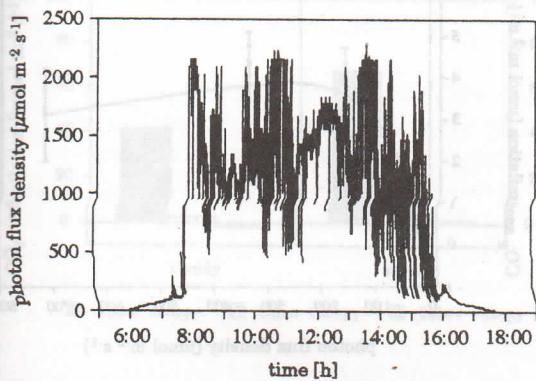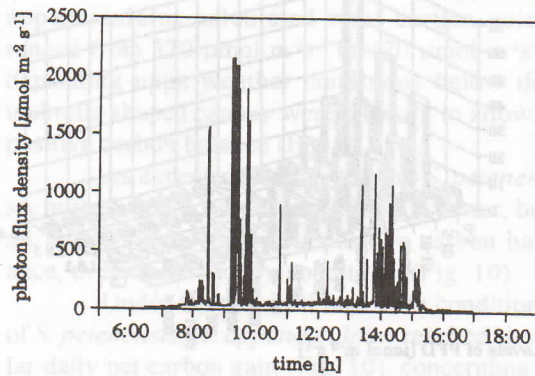

Fig. 2   Representative diurnal course of PFD for *S. petenensis* on a sunny day in a typical understore microsite.
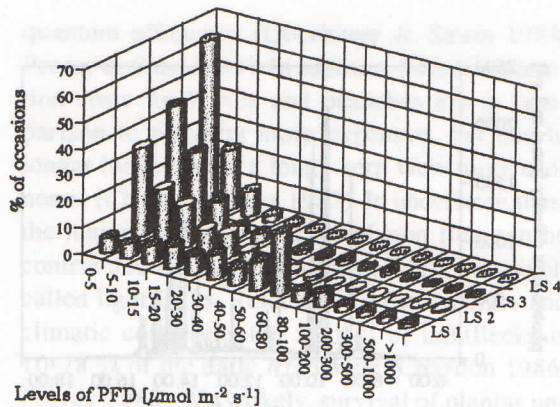
A more detailed analysis of the light environments is given in Figs. 3 to 6. Recorded PFDs of four different positions in each canopy were averaged over three sunny days and diveded into 15 levels of light intensities, in order to work out their contribution to total daily PFD (Figs 5 to 6).

Above the canopy of S. petenensis, light levels ranging from 5 to 100 (μmol m^{-2}s^{-1}) were found most of the day (Fig. 3). In contrast, higher light levels with more than 100 (μmol m^{-2}s^{-1}) were common in the upper canopy of H. appendiculatus (Fig. 4). As expected, frequencies of high liht levels decreased inside and below the canopies.

Despite these differences in frecuencies of light levels, high PFDs contributed most to the total daily radiation, both in the understore and in the gap. Where this was to be expected for the gap situation with generally higher light levels, it clearly demostrates the importance of sunflecks in the undestore: 0.5 to 4.8 % of daily irradiance reached PFDs with more than 500 (μmol m^{-2}s^{-1}) but these rare high events contributed 25-55 % of total daily light (Figs 5 and 6).

Steady - State Photosynthesis

Mean light - saturating assimilation rate of H. appendiculatus was (21.2 μmol m^{-2}s^{-1}) about five times higher than that of S. petenensis (3.9 μmol m^{-2}s^{-1}), whilw the corresponding sarurating light intensity was over 2000 μmol m^{-2}s^{-1} for the pioneer and less than 400 μmol m^{-2}s^{-1} for the understore tree (Figs. 7 and 8). The pioneer's dark respiration rate was 0.91 μmol m^{-}

Fig. 1   Representative diurnal course of PFD for *H. appendiculatus* on a sunny day in a typical gap microsite.

Fig. 3 Frecuencies (%) of occasions of PFDs as arranged within different intervals. LS 1 -above tree top; inside canopy, LS 4 -below canopy of *S. petenensis*
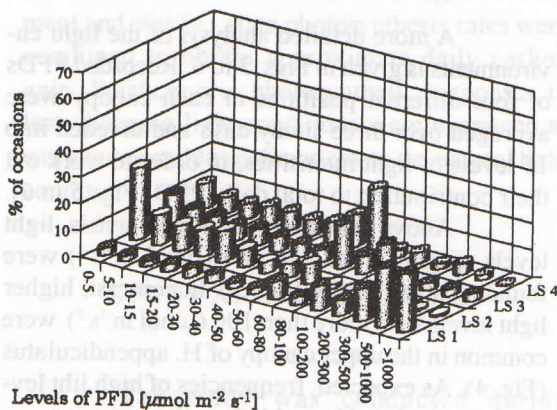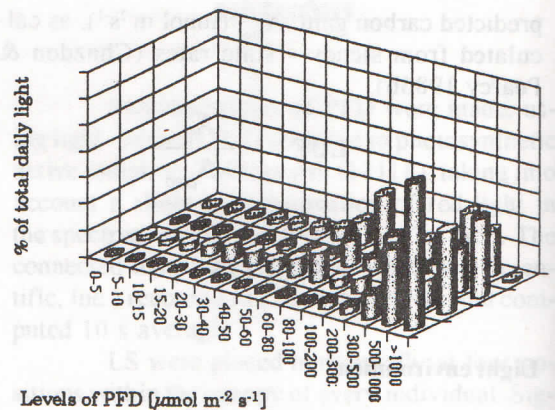

Fig. 4 Frecuencies (%) of occasions of PFDs as arranged within different intervals. LS 1 -above tree-top; LS 2 and Ls 3 -inside canopy, LS 4 -below canopy of *H. appendiculatus*
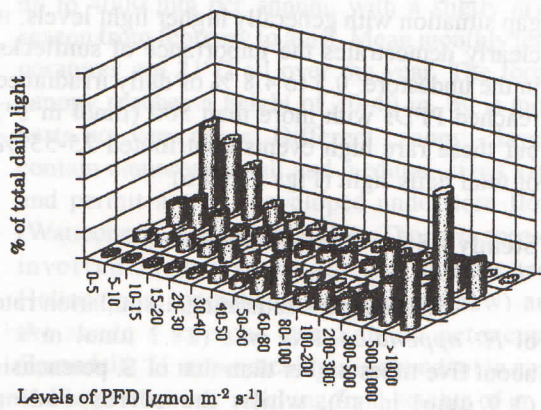
Fig. 5 Relative contribution (%) of different levels of PFDs to total daily radiation. LS 1 -above tree top; LS 2 and LS 3 -inside canopy; LS 4 -below canopy of *S. petenensis*

Fig. 6 Relative contribution (%) of different levels of PFDs to total daily radiation. LS 1 -above tree top; LS 2 and LS 3 -inside canopy; LS 4 -below canopy of *H. appendiculaus*
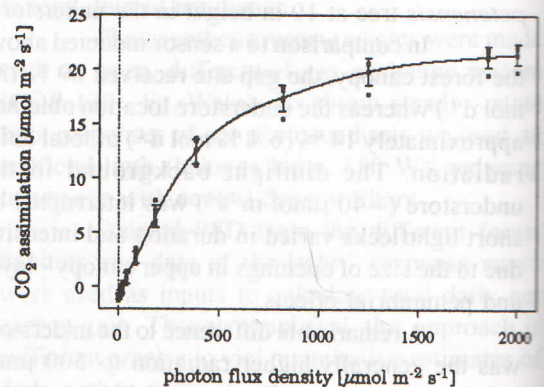

Fig. 7 Mean photosynthetic response to light of *H. appendiculatus*, including error bars of the standard deviation from five measurements.
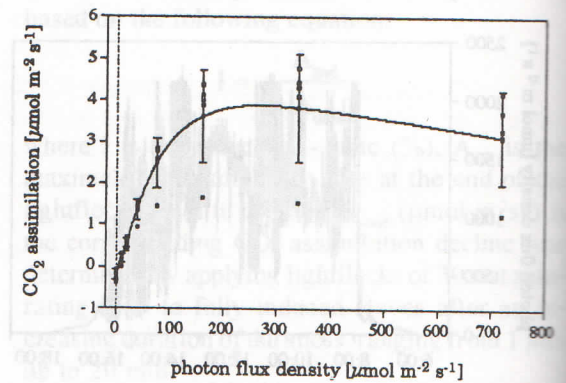

Fig. 8 Mean photosynthetic response to light of *S. patenensis*, including error bars of the standard deviation from five measurements.

^{2}s^{-1} compared to 0.2 µmol m^{-2}s^{-1} for leaves of *S. petenensis*. Up to a PFD of 87 µmol m^{-2}s^{-1} CO$_2$ assimilation of the understore tree was superior while over this value the photosynthetic rates of *H. appendiculatus* increased rapidly.

Calculation of daily carbon gain

Data from the above shown light response curves and measured daily patterns of PFD in the understore and gap site were used as inputs to stimate total daily net carbon gains. Responses of photosynthesis were calculated, firstly, for the individual true natural microsites (Figs. 9 to 10) and secondly, for the hypothetic location of the other respective species (Figs. 11 to 12).
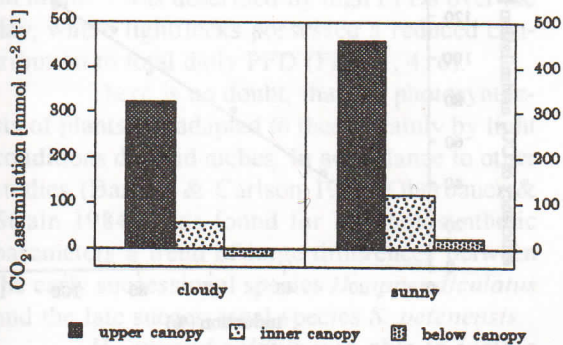

Fig. 9   Daily net carbon gain of an individual of *H. appendiculatus* at this natural gap site, concerning different weather conditions and canopy - layer.
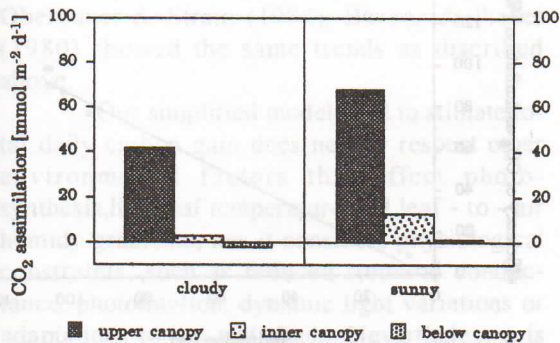

Fig. 9   Daily net carbon gain of an individual of *S. petenensis* at this natural gap site, concerning different weather conditions and canopy - layer.

For the leaves in the upper canopy of H. appendiculatus calculated total carbon gains ranged from 320 µmol m^{-2}s^{-1} to 470 µmol m^{-2}s^{-1}, depending uppn weather conditions below the umbrella shaped canopy were too dark to allow a positive carbon balance (Fig. 9).

As expected, carbon gain of *S. petenensis* in the understore was considerably lower, but all foliated areas showed a positive carbon balance, even under cloudy conditions (Fig. 10).

Under the assumed microsite conditions of *S. petenensis*, *H. appendiculatus* reached similar daily net carbon gain (Fig. 10), concernimg a sunny day. Under cloudy conditions of very low light, the pionner did not achieve the carbon gain of *S. petenensis* and had a negative carbon balance in all the lower canopy - layer (Fig. 11).

Under the better hypothetic light conditions within the gap, net carbon gain of S. petenensis increased slightly for the upper days canopy, but the high irradiance on a sunny day was not transformed into a higher CO$_2$ uptake, due to the shade leaf characteristic of the individual.

Efficiency and induction of photosynthesis

LUE of fully induced leaves of H. appendiculatus varied between 70 - 85 % (Fig. 13), but never reached the steady - state prediction. Furthermore, there was no obvious difference in LUE and short and long lightfleck, as known from the literature (Chadzon 1988, Küppers & Schneider 1993).

In contrast, the understore species showed extrem high LUE in short flecks of saturating light, with up to 250 % in a 1 s lightfleck. Even in longer lasting lightflecks, LUE was always above the steady - state prediction (Fig. 14).

Deacrese of the photosynthetic induction in relation to longer lasting phases of darkness was similar in both species. *H. appendiculatus* lost 50 % of induction after 14.5 min, while *S. petenensis* reached this value after 11 min (not shown).

Induction and efficiency are correlated in a linear way (Figs. 15 to 16). Despite the loss of induction in *S. petenensis* was slightly faster, it maintained a relative higher efficiency of CO$_2$ assimilation, as expressed by the slope of the linear regression. At 50 % induction state *S. petenensis* achieved 70 % of efficiency, whereas *H. appendiculatus* judt reached 45 %.
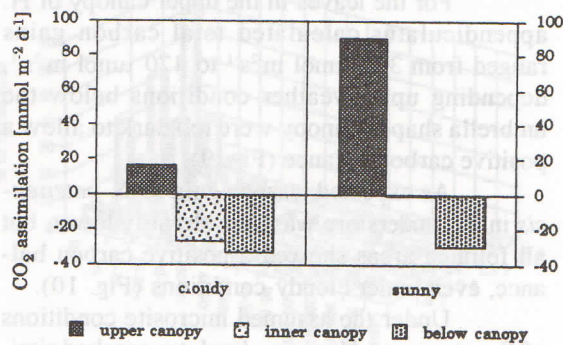
Fig. 11 Hypothetic net carbon gain for *H. appendiculatus* at the assumed understore site , concerning different weather conditions and canopy-layers.

Fig. 14 Photosynthetic light use efficiency of *S. petenensis* as a function of steady - state prediction in relation to increasing lightfleck duration (s). Error bars indicate standard deviation for means of three measurements.
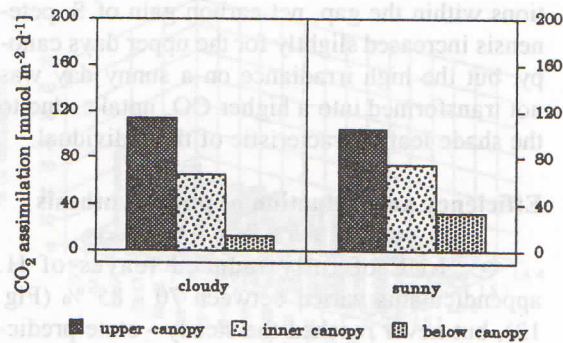

Fig. 12 Hypothetic net carbon gain for *H. petenensis* at the assumed understore site, concerning different weather conditions and canopy-layers.

Fig. 15 Light use efficiency (LUE) os *S. petenensis* as a function of relative leaf induction state of (% CO_2 assimilation rate at the end of a 30 s lightfleck). The slope of the linear regression is 1.17.
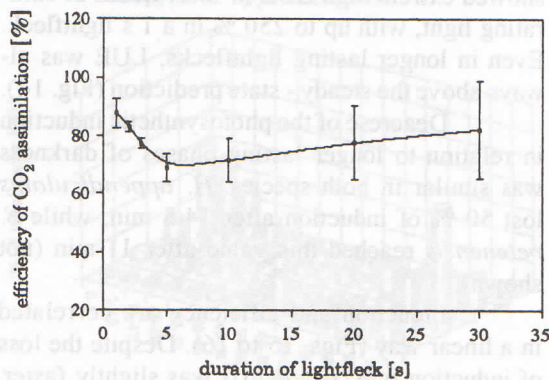

Fig. 13 Photosynthetic light use efficiency of *H. appendiculatus* as a function of steady-state prediction in relation to increasing lightfleck duration (s). Error bars indicate standard deviation for means of three measurements.
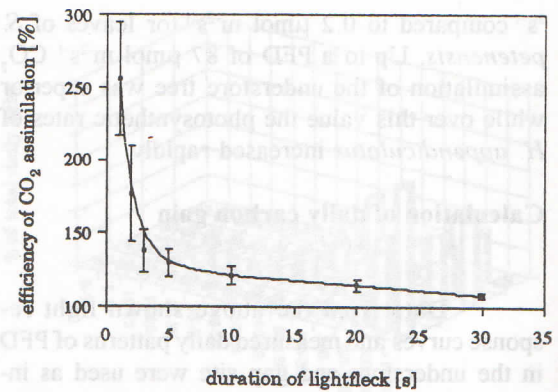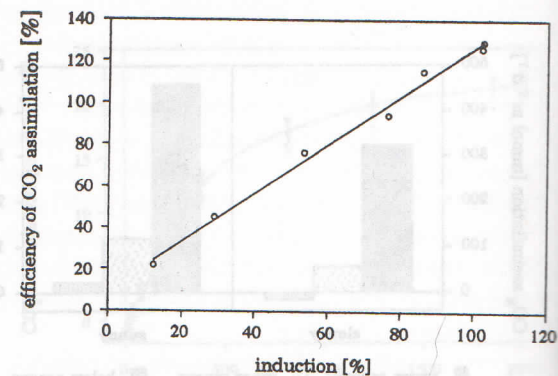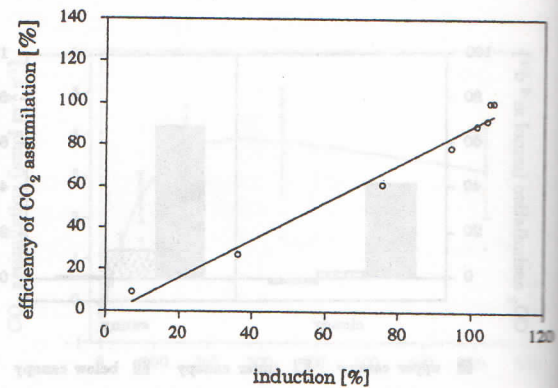

Fig. 16 Light use efficiency (LUE) os *H. appendiculatus* as a function of relative leaf induction state of (% CO_2 assimilation rate at the end of a 30 s lightfleck). The slope of the linear regression is 0.92.

DISCUSSION

Much of the microsite variation within a forest ca be attrbuted to an extreme heterogeneity of the light enviroment. It is clear from this and other studies (Pearcy 1983, Chadzon & Fetcher 1984) that light conditions vary greatly within and among gaps and - specially - in the understore.

Besides the distinction in total daily PFD, thr pattern of temporal and spatial light distribution differed enormously between gap and understore site. As main festure of the understore was the important contribution of rare lightflecks - interrupting the low dimlight background - to total daily PFD (Figs. 2, 3, 5). On the other hand, a typical gap - the natural habitat of *H. appendiculatus* - was described by high PFDs over the day, where lightflecks possessed a reduced contribution to total daily PFD (Figs. 1, 4, 6).

There is no doubt, that the photosynthesis of plants are adapted to these, mainly by light conditions defend niches. In accordance to other studies (Bazzaz & Carlson 1982, Oberbauer & Strain 1984), was found for all photosynthetic parameters a trend of large differences between the early successional species *H. appendiculatus* and the late successional species *S. petenensis*.

H. appendiculatus was able to yield a high carbon gain, due to the high radiation occuring in a gap (Fig. 7). In contrast, *S. petenensis* never reached this level of assimilation, but therefore carbon gain below a PFD of 87 μmol m^{-2}s^{-1} was superior in comparison to the pioneer species (Figs. 7 and 8). Studies of Oberbauer & Strain (1984), Bazzaz & Picket (1980) showed the same trends as discribed above.

Our simplified model used to stimate total daily carbon gain does neither respect other environmental factors that effect photosynthesis,like leaf temperature and leaf - to - air humidy gradients, nor it considers physiological constraints, such as reduced stomatal conductance, photointation, dynamic light variations or adaptations to sun and shade. Nevertheless it is well suitable for general assumptions concerning the carbon balances, as long as differences among species are large.

In comparison to *S. petenensis*, carbon gain of *H. appendiculatus* was about tree times higher under gap conditions. Vice versa, under low light conditions of the understore site - specially on cloudy days -, *S. petenensis* was able to achieve more than twice of the hypothetical daily carbon gain of the pioneer.

When periods of light alteration are short, leaves often exhibit apparent photosynthetic rates higher than the average of the steady - state rates observed at high and low light levels (Chadzon & Pearcy 1986b). Lightfleck utilization efficiency (LUE) by leaves strongly depends on a high state of photosynthetic induction as well as on the duration of a lightfleck (Küppers & Schneider 1993, Pearcy & Sims 1994). Undersotre plants makean efficient use of variable light for their carbon gain, due to a faster increase of induction, high quantum yields in short lightflecks and a slower decrease of induction in low light (Chazdon & Pearcy 1986a, Küppers et al 1996).

Very likely, *S. petenensis* indicates the typical photosynthetic responses in variable light of an understore species. This concern particularly the high LUE with up to 250 % for a 1 s lightfleck and the relative higer LUE at a low induction - state (Figs. 14 to 15).

As light is much more available in gaps, pioneer species like *H. appendiculatus* do not depend strongly on an effeicient use of fluactuating light. This may explain the lower LUE in lightflecks as compared to predicted steady - state assimilations rates only at a high induction - state (Fig. 16), that requiers a constant high infkuxx.

In this study we have demostrated that the photosynthetic acclimation of both species correlates with the light conditions at their natural habitats.

Whole -plant growth and competive ability, however, not only depends on the photosynthetic characteristics of individual leaves, geometries and dynamics of canopies, so further studies on the pattern of energy allocation among all organs are still needed (Givnish 1988, Küppers et al 1995).

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