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BACHELORARBEIT

Lightfleck-usage by epiphytes and terrestrial plants in a tropical understorey

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Abbreviations

A_{max}	maximum assimilation rate of CO_2 at maximum PFD [µmol CO_2/m²s^{-1}]
ANOVA	analysis of variance
BCI	Barro Colorado Island
C_a	fraction of CO_2 outside the leaf [ppm]
C_i	fraction of CO_2 in the leaf [ppm]
dCO_2/dH_2O	differences in gas concentration through photosynthetic activity [µmol/m²s^{-1}]
E	transpiration rate [mmol H_2O/m²s^{-1}]
ETR	electron transportation rate [µmol/m²s^{-1}]
Fm and Fv	maximum and variable fluorescence in a dark-adapted leaf
gw	stomatal conductance
H_0	null hypothesis for statistical evaluations
IS_5, IS_{10}, etc.	relative assimilation after 5, 10 etc. minutes of satPFD or shade
CP	compensation point, i.e. light intensity from which positive assimilation is achieved
MP	measuring point, recorded by the GFS-3000
PFD	photon flux density [µmol/m²s^{-1}]
P_L	photosynthesis in the dark or rather dark respiration [µmol CO_2/m²s^{-1}]
P_{max}	maximum assimilation rate of CO_2 at maximum induction [µmol CO_2/m²s^{-1}]
ppm	parts per million
R^2	coefficient of determination
rh	relative humidity [%]
RSS	residual sum of squares
satPFD	saturating PFD
STRI	Smithsonian Tropical Research Institute
T50, T30, T90, etc.	time to reach 50, 30, 90%, etc. of maximum induction
VPD	(air-to-leaf) vapour pressure deficit [Pa/kPa]
WUE	water-use-efficiency [µmol CO_2/mmol H_2O]

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Summary

Photosynthetic response to different light intensities as well as to changing light was measured in plants from a tropical understorey on Barro Colorado Island. Comparison was made between epiphytes and terrestrial plants from the same families and habitat. It was hypothesised that epiphytes have generally a more pronounced water-saving behaviour than their terrestrial neighbours and thus longer induction times and faster induction-loss. This hypothesis could not be verified as a whole. Steady-state response to different light intensities was similar among epiphytes and terrestrials, equalling those of shade-tolerant plants. Both induction and induction-loss were slow. Reaching 90% of induction took at least 30 minutes of saturating light while 60 minutes of low light were required by epiphytes as well as terrestrials to achieve a 70% induction-loss. Two types of induction-courses (sigmoid and hyperbolic) were found, with Araceae and Orchidaceae conducting sigmoid curves, which led to significant differences during the first 20 minutes of induction. Stomatal conductance was rather low in all measured species but undistinguishable due to high variability and inaccurate data. Water-use-efficiency and internal CO_2-concentration were stable during all measurements and indifferent among the life forms. In summary it is reasoned that photosynthetic behaviour is diverse among epiphytes and that there is no general difference in the reaction to changing light between epiphytic and terrestrial plants from the same habitat.

1. Introduction

Tropical forests have an overwhelming richness in species, and the mechanisms that lead to and conserve this diversity are yet not fully understood. One question of ecological as well as functional biology is how plants are adapted to the different habitats, located vertically in a forest. From the canopy to the ground, abiotic conditions change greatly in a tropical rainforest; e.g. humidity is lower in the canopy and less than 2% of the sunlight reaches the understorey (Kromer, Kessler and Gradstein 2007). This gradient greatly affects the distribution of plants, which depend on a specific amount of water and sunlight for survival, growth and reproduction. It is known that plants' physiology is highly capable of adapting to changing conditions, both in short periods of single days and in long periods of their whole life (Valladares and Niinemets 2008). What these different adaptations are, comparing between species from different and similar habitats in a forest, can tell us a lot about how plants can react to changes in their environment.

A plant's carbon gain is depending from the amount of light which is assimilated and conversed into energy through photosynthesis. But a steadily high photosynthesis rate throughout the whole day normally is not possible, especially in environments with changing light. Changing light intensities occur in all habitats, from crops to forests, and are caused by cloud movement as well as solar altitude or leave movement of larger plants (Pearcy 1990). In the understorey of tropical forests, plants are depending on pulses of high irradiances (called lightflecks) for their carbon gain, because the background irradiance is very low (Chazdon 1988). Photosynthetic behaviour adapted to such an environment has been found in many understorey shrubs or tree seedlings. These plants have good lightfleck-use efficiency (shown through fast photosynthetic induction and slow loss of induction during a lightfleck), because reaching and sustaining a high assimilation rate is given priority over water-saving with closed stomata. (Chazdon and Pearcy 1986b, Kirschbaum and Pearcy 1988, Kursar and Coley 1993, Ogren and Sundin 1996, Pearcy 1988, Rijkers et al. 2000, Valladares, Allen and Pearcy 1997, Watling et al. 1997)

However, only one epiphyte from a tropical understorey (the orchid *Aspasia principissa*) has been analysed for response to fluctuating light and lightfleck-usage (Zotz and Mikona 2003). In the respective study it was concluded that bark epiphytes are restricted in using lightflecks because they suffer more from water-shortage and thus their stomata react more slowly to changing light. Other than their terrestrial neighbours, bark epiphytes have no connection to water-reservoirs in the ground and are therefore dependent on continuous rain or reserves in specialised organs (Zotz and Hietz 2001).

To allow a general conclusion about lightfleck-usage in epiphytes, reactions to changing light intensities were measured among several species from the most common epiphytic families in a tropical rain forest. These species contained tank bromeliads as well as polyploid ferns and orchids and were compared to terrestrial species from the same families and/or habitat. The hypothesis is that epiphytes have a more pronounced water-saving behaviour than the terrestrial life form. This is expected to manifest itself primarily in longer induction times and faster induction loss. It was tried to adapt the methods from the previous study, so that results can be easily compared.

2. Material and Methods

2.1. Study site

The experiments have been conducted on Barro Colorado Island (9°09´N, 79°51´W), Republic of Panama, located in Lake Gatun, which was formed during the construction of the Panama Canal. BCI (Barro Colorado Island) lies 25 m at the lowest and 165 m at the highest point above sea level. According to the Holdridge Life-Zone System the vegetation is a 'tropical moist forest'. Annual rainfall reaches between 1900 mm and 3600 mm with only 180-260 mm during the pronounced dry season from mid-December to the End of April. Mean annual temperature ranges between 21°C and 32°C wit h diurnal variations of 2.2°C between seasons and about 10°C within seasons. Mean monthly air humidity varies between 76.4% (April) and 94.2% (November). The island was set a biological preserve in 1923 and is now supervised by the Smithsonian Tropical Research Institute (STRI). Since the declaration as a protected area the forest on BCI remained natural, aside from laboratory buildings at one of the coves and several trails (Croat 1978).

The experiments were undertaken during three weeks in April 2009 in the forest about 30 m from the laboratory clearing. The study site was at-grade, about 4 m² in size and well-shaded by big trees and palms over the whole day. The measuring instruments as well as the studied organisms were brought to the study site and remained there until the end of the last experiment. Rain protection for the instruments was provided by plastic cover and electricity was transmitted to the equipment via an extension cord from the nearest building. All studied plants were fixed to branches or lianas with plastic cords or filament unless they were collected with their substrate.

2.2. Study organisms

21 species of vascular epiphytes and 3 species of terrestrial plants from the same families were collected at different places on BCI. Additional measurements were made with 4 species of terrestrial plants growing naturally at the study site. During the collection, individuals growing on dead or dry branches or individuals having fallen on the ground were favoured in order to avoid unnecessary damage. This influenced the selection of families and species. Furthermore reproducing individuals were avoided as far as possible.

All species were collected up to 2 meters height and, if it was impossible to carry it with them, loosened carefully from their substrate. For each species 1 to 3 individuals were collected, whereas only a maximum of two individuals per species could be measured due to herbivory or death. The terrestrial species *Piper cordulatum* and *Aechmea magdalenae* were replanted

to the study site. *Dieffenbachia longispatha, Adiantum lucidum, Piper grande, Ischnosiphon pruinosus* and *Tectaria incisa* are growing naturally near the study site. All plants were watered steadily throughout the experimental stage, at least three times a day. All plants which had been collected in the forest were brought back to their original growing sites after the experiments; plants which had been collected from the ground were put on trees near the places where they were found.

The study organisms span the families *Bromeliaceae* (5 species)*, Polypodiaceae* (6 species)*, Orchidaceae* (4 species)*, Araceae* (4 species) and *Piperaceae* (6 species), with four of the terrestrial species belonging to *Bromeliaceae*, *Araceae* and *Piperaceae* (2). The naturally growing terrestrial species belong to *Pteridaceae* (*A. lucidum*), *Marantaceae* (*I. pruinosus*) and *Tectariaceae* (*T. incisa*). Except for two species (*Aechmea magdalenae* and *Ornithocephalus bicornis*) all plants conduct C3-metabolism. The others have CAM-metabolism (Pfitsch and Smith 1988, Zotz and Ziegler 1997). For them, only electron transportation rate (ETR) was analysed. Without the CAM-plants, 33 individuals (therefrom 7 terrestrial) out of 26 species have been analysed.

With a minimum number of 4 species per family a statistical comparison between the families can be conducted according to equation 1 (adapted from Southwood and Henderson 2000).

$$N = \frac{t - value * deviation}{(\Delta means)^2} \qquad \text{(eqn. 1)}$$

N is the number of species which is needed for a significant conclusion (95% certainty) and ∆means is the difference in means, one wants to compare. The t-value is the test statistic for the statistical t-test. For calculation, reference values (for deviation and ∆means) from experiments with *Aspasia principissa* (Zotz and Mikona 2003) have been inserted. For ∆means a value slightly higher than the standard deviations from the named study has been used to ensure a decent result even at higher deviations between the families.

The individual plants were put into 3 measuring groups of 8 plants each, according to their time of collection. This assured that all plants were left to recover from transplantation at least 7 days before being measured. The three terrestrial plants from the main families as well as the families themselves were distributed equally among the measuring groups with no *Piperaceae* being measured in the first group. The additional terrestrial plants were measured during the last days of the experiments. For each measuring group the experiments were conducted within one week, measuring each plant only once a day. All measured species sorted by family and sorted by measuring group can be found in Appendix 1 and Appendix 2, respectively.

2.3. Photosynthetic measurements

Photosynthetic measurements were made with the 'Portable Gas Exchange Fluorescence System GFS-3000' (Walz, Effeltrich, Germany). The GFS-3000 consists of an infrared gas analyser (NDIR gas analyzer) and a measuring head in which leafs are enclosed and where a fluorescence module (LED-Array/PAM-Fluorometer 3055-FL) can be attached. Conditions in the measuring head and hence at the leaf can be controlled precisely using the CO_2 and/or H_2O absorbers connected to the device. The measuring head has a volume of 40 ml, thus the time delay is approximately 4 seconds with a cuvette volume of 6 ml in each of the four analysing cuvettes and a gas flow rate of 750 µmol/s. Given that data were collected on time scales of several minutes and data points were calculated as means over an averaging interval, no correction for the time delay was made.

The infrared gas analyser records CO_2 as well as H_2O in the measuring gas both before and after passing the measuring head. Values for absolute CO_2/H_2O and their differences (dCO_2/dH_2O) are given in ppm (parts per million). All evaluated values were calculated automatically in the GFS-3000 using equations (Genty, Briantais and Baker 1989, von Caemmerer and Farquhar 1981) with device-specific corrections provided by a manufacturer-developed program running on the system.

For every individual plant three types of measurements were conducted: steady-state response to different light intensities, response to saturating light (satPFD) and response to prolonged shade. Photosynthetic parameters as well as fluorescence activity were recorded at programmed intervals. A zero point to calibrate the gas analyser was set before every measurement. Conditions at the leaf were an absolute CO_2 concentration (C_a) of 370 ppm (provided by a CO_2 cartridge), 70% relative humidity (rh) and a cuvette temperature of 29°C, simulating conditions which were measured at one forenoon at the study site.

Collected data were transferred from the device to a laptop computer via USB-cable the morning after each measurement. For data evaluation and analysis see chapter 2.4.

2.3.1. Steady-state CO_2-response

To calculate important parameters like compensation point (CP), saturating PFD (photon flux density) and the maximum assimilation rate (A_{max}), an ascending light curve from 0 to 1000 µmol m^{-2} s^{-1} PFD containing 12 measuring points (0, 10, 30, 50, 75, 100, 150, 200, 300, 500, 700, 1000) was measured with the GFS-3000. For every light step one measuring point (MP) with an averaging interval of 2 minutes and one fluorescence yield were recorded. An adaptation time of 5 minutes was given before recording the MPs. The first measuring point was used to estimate respiration and Fv/Fm. Fv/Fm is the relation between variable

fluorescence and maximal fluorescence in a dark-adapted leaf (van Kooten and Snel 1990) and is used both to indicate stress and for further calculations of fluorescence parameters.

After enclosing the leaf in the cuvette, the program was started, firstly conducting a 5-minute interval during which the system values could stabilise. Secondly photosynthesis was induced with saturating light of 300 µmol $m^{-2} s^{-1}$ PFD, because natural irradiance normally didn't exceed 20 µmol $m^{-2} s^{-1}$ PFD (recorded during measurements). Inducing the leaf took 5 minutes during the first week but for the following groups, steady-state response was measured immediately after the induction in saturation light. This modification was made to ensure that a rise during the steady-state response was only due to rising light intensities and not due to induction. Without the induction-time, the measurement took about 70 minutes.

2.3.2. Induction in saturating light

To reach a steady low photosynthesis, leafs were firstly exposed to PFD <10 µmol $m^{-2} s^{-1}$ under black fabric for at least 30 minutes. Secondly the leaf was enclosed in the cuvette and after the system had stabilised, photosynthesis in low light (P_L) and Fv/Fm were recorded. P_L was recorded by three MPs within 30s. Afterwards maximal photosynthesis (P_{max}) was reached by exposing leafs to satPFD (300 µmol $m^{-2} s^{-1}$ PFD) over 60 minutes. During the induction one MP and one fluorescence yield were taken every 5 minutes. For every MP an averaging interval of 2 minutes was conducted in the GFS-3000. The measurement took about 70 minutes.

2.3.3. Loss of induction

Loss of induction was estimated in a fully induced leaf over a shade period of 60 minutes. The leaf was enclosed in the cuvette and preliminary dark respiration (one MP) and Fv/Fm were measured after 5 minutes of darkness. Afterwards, the leaf was lightened with satPFD (300 µmol $m^{-2} s^{-1}$ PFD) over 60 minutes. During the following shading period (PFD app. 10 µmol $m^{-2} s^{-1}$) 1 minute of satPFD was given at 5, 10, 20, 40 and 60 minutes. During the last 30 seconds of the light-pulse 3 MPs and one yield were recorded, utilising the photosynthetic rate after 60 s of satPFD as a measure of the induction state (compare Allen and Pearcy 2000b, Chazdon and Pearcy 1986b).

To what extend the first light-pulses influence the following induction states (IS) was estimated with two plants by additionally conducting the same curve with only one light pulse at 20 and 60 minutes, respectively (data not shown). No differences could be found in the IS between curves containing several light-pulses and curves containing only one light-pulse.

Therefore, and because similar methods have been used in the literature (see above) measurements were conducted with several light-pulses.

2.4. Data analysis

The measurements come down to how the plants can deal with changes in light intensity, so to determine and to compare the photosynthetic reactions, several parameters from the measured curves were evaluated.

Based on A_{max}, satPFD and CP, the steady-state CO_2-response was evaluated for both families and life forms. An ETR-comparison was conducted to permit an inclusion of the CAM-species.

For induction in satPFD not only the relative assimilation rate, but also the time to reach 60 and 70% of P_{max} as well as the IS during the first 20 minutes were compared.

To determine loss of induction the time course of relative induction rate and time to reach 30 and 50% of induction were evaluated.

Additionally, stomatal conductance (gw) was evaluated during induction as well as induction-loss. Following gw, water-use-efficiency (WUE) and the relation of inner and outer CO_2 concentration (C_i/C_a) were analysed.

2.4.1. Fitting regressions to photosynthetic curves

Empirical models for every measured curve were developed by fitting regressions to the data points. Regressions to steady-state response were fitted with the program 'Photosyn Assistant' (Version 1.1.2; 1998) using a quadratic equation (Prioul and Chartier 1977). Also A_{max} and CP were calculated automatically in the above program. Regressions for induction and induction loss were fitted in Microsoft Excel (Office11; 2003) using the Add-in 'Solver', which solves linear and non-linear equations to reach the minimum or maximum of a given value.

Firstly, the residual sum of squares (RSS) was calculated by subtracting the data points from the values calculated with the model and computing the sum of squares. Secondly, the 'Solver' was applied to get the minimum RSS by changing the variables in the provided model. As another qualification for the regressions' accuracy, the coefficient of determination (R^2) was calculated for measured and calculated values with a formula provided in Excel and adjusted to a maximum value with the 'Solver'. As a result, regressions were fitted twice and individually for every measured curve, also testing different models to provide an optimal description of the data.

The models used for fitting were limited exponential growth (eqn. 2) or logistic growth (eqn. 3 and eqn. 4) for the induction. For loss of induction eqn. 5 was used.

$$y(x) = S - (S - a) * (1 - k)^x \quad \text{(eqn. 2)}$$

$$\gamma(x) = \frac{a * S}{a + (S - a) * e^{-Skx}} \quad \text{(eqn. 3)}$$

$$\gamma(x) = \frac{a * S}{\left(a + (S - a) * e^{(-Skx)}\right) - \left(a + |\gamma(0)|\right)} \quad \text{(eqn. 4)}$$

$$\gamma = 1 - \frac{x}{x + a} \quad \text{(eqn. 5)}$$

S is the growth limit, a and k are variables, x is the time and y(0) the first data point.

2.4.2. Calculations

To provide a better comparability of the induction, respiration (measured during the steady-state response) was subtracted from all data points before fitting the regression (compare Chazdon and Pearcy 1986a) and used as the value of y(0). After fitting the regressions, values for up to 100 minutes were calculated with the fitted equation. Relative assimilation was calculated for every time step by dividing the actual assimilation through assimilation at 100 minutes and multiplying it by 100 to get the percentage. Following these calculations, all curves of induction had the same initial and final value. T60 and T70 were calculated in Excel by solving the fitted equation for y= 60 and y= 70.

For stomatal behaviour the percentage of gw during induction was calculated using eqn. 6.

$$gw(\%) = \left(\frac{gw(t) - gw(0)}{gw(100) - gw(0)} \right) * 100 \quad \text{(eqn. 6)}$$

gw(t) is the stomatal conductance at the given time and gw(100) the stomatal conductance at 100 minutes calculated from the fitted model.

For induction-loss, relative assimilation was calculated by dividing the value at each time step through assimilation at the beginning. Therefore no correction had to be made to get all curves starting at the same value. For the statistical evaluation T30 and T50 were calculated in Excel with the dissolved equation of the fitted model.

2.4.3. Statistical evaluation

All parameters were compared statistically between epiphytes and terrestrial plants as well as within the group of epiphytes. All evaluations were made with the statistics program SYSTAT12 (Version 12.02.00; 2007) after importing the data from Excel. According to the hypothesis (see chapter 1) the statistical null hypothesis (H_0) for all analysis was 'no difference between means'. H_0 should be rejected to show that there is significant difference in the different aspects of lightfleck-usage. It could be stated for all analysis that H_0 can be rejected if the resulting p-value is less than 0.05 for a significance of 95% certainty and less than 0.01 for a significance of 99% certainty.

Three types of analysis were used:

A) Comparison of means with ANOVA (analysis of variance) or Kruskal-Wallis-Test

B) Repeated measurements ANOVA

C) Post-hoc tests (Games-Howell-Test/Univariate F-Test or Tukey's Honestly-Significant-Difference Test)

The choice of analysis resulted firstly from the number of values for each group and secondly from data characteristics, namely normality of the data and equality of residuals, which were tested in advance (Table 1). Which method was used in particular is specified in the corresponding chapter covering the results.

Table 1: Conditions for the choice of statistical analysis

Number of values	Normality	Equal Residuals	Tests
more than 1	Yes	Yes	Repeated ANOVA, Games-Howell
more than 1	Yes	No	Repeated ANOVA, Tukey's
1	Yes	Yes	ANOVA
1	No	Yes	Kruskal-Wallis

In most cases statistical evaluation was conducted with all measured species (means were calculated for species with two measured individuals) excluding the CAM-species (see chapter 2.2).

The values of gw and transpiration (E) had to be prepared in advance. Because of partially negative values leading to extremely high variation in the means of gw and E, certain data points were not included in the analysis. The limits for gw during induction were chosen from

minimum values found in the literature (Allen and Pearcy 2000a, Rijkers et al. 2000, Schmidt and Zotz 2001, Valladares et al. 1997, Zipperlen and Press 1997, Zotz and Tyree 1996, Zotz and Mikona 2003). The limit was lowered for induction-loss, because values were generally lower and too many species would have been excluded by setting a higher limit. Therefore, the lower limit was 0.13 mmol H_2O $m^{-2}s^{-1}$(E) and 10 mmol H_2O $m^{-2}s^{-1}$(gw) for induction and 0.07 mmol H_2O $m^{-2}s^{-1}$(E) and 5.0 mmol H_2O $m^{-2}s^{-1}$(gw) for induction-loss. Limits for E were calculated from gw and the vapour pressure deficit (VPD) measured in the GFS-3000 following equation 7 (von Caemmerer and Farquhar 1981).

$$E = VPD * gw \qquad \text{(eqn. 7)}$$

Individuals with fewer than 50% of their data points remaining were excluded completely.

To compare the pace of CO_2-assimilation with stomatal conductance during induction and induction-loss, regressions were fitted to the values of gw for the selected species. Out of these, only species featuring a R^2 higher than 70% were taken into account to ensure data reliability. This reduced the number of species at induction by two for epiphytes and by one for terrestrials. For the analysis of induction-loss 2 terrestrials and 6 epiphytes remained.

3. Results

3.1. Steady-state CO_2-response

Photosynthetic response to different light intensities was measured to compare the basic characteristics between families and life forms, such as the highest assimilation rate (A_{max}) or the light intensity needed for positive assimilation (CP).

Parameters of CO_2-assimilation were similar among families and life forms (Table 2). The CP ranged from $4 \pm 4\,\mu mol\,m^{-2}s^{-1}$ PFD (mean ± s.e.) in Bromeliaceae to $23 \pm 23\,\mu mol\,m^{-2}s^{-1}$ PFD in Piperaceae with a grand mean of $9 \pm 13\,\mu mol\,m^{-2}s^{-1}$ PFD for all epiphytes. The mean CP of all terrestrial species was $6 \pm 4\,\mu mol\,m^{-2}s^{-1}$ PFD. Significant difference of CP could be found neither between epiphytic families (p= 0.07) nor between life forms (p= 0.95). The satPFD was highest among Piperaceae and lowest among Polypodiaceae, but overall not significant between families or life forms. Statistical evaluation for A_{max} with ANOVA also showed no significant difference between families (Figure 1) as well as between life forms (Figure 2).

Table 2: Light compensation point (CP), saturating PFD (satPFD), maximal assimilation rate (A_{max}) and number of species (n) estimated from measurements without CAM-plants. Data are means ± s.e. For statistical tests, ANOVA (CP in between epiphytes and Amax) and the Kruskal-Wallis test were used respectively. n.s. = not significant

	CP ($\mu mol\,m^{-2}s^{-1}$ PFD)	satPFD ($\mu mol\ m^{-2}s^{-1}$)	A_{max} ($\mu mol\ CO_2\ m^{-2}s^{-1}$)	n
Bromeliaceae	4 ± 4	79 ± 35	3.8 ± 2.0	3
Orchidaceae	7 ± 9	93 ± 40	1.8 ± 0.4	3
Piperaceae	23 ± 23	134 ± 104	2.7 ± 1.8	3
Polypodiaceae	4 ± 6	47 ± 20	2.3 ± 1.4	6
Araceae	7 ± 2	82 ± 92	1.6 ± 0.7	2
p-value	0.07 (n.s.)	0.79 (n.s.)	0.39 (n.s.)	
Epiphytes	9 ± 13	83 ± 62	2.5 ± 1.6	17
Terrestrials	6 ± 4	78 ± 63	3.1 ± 1.5	5
p-value	0.95 (n.s.)	0.32 (n.s.)	0.44 (n.s.)	

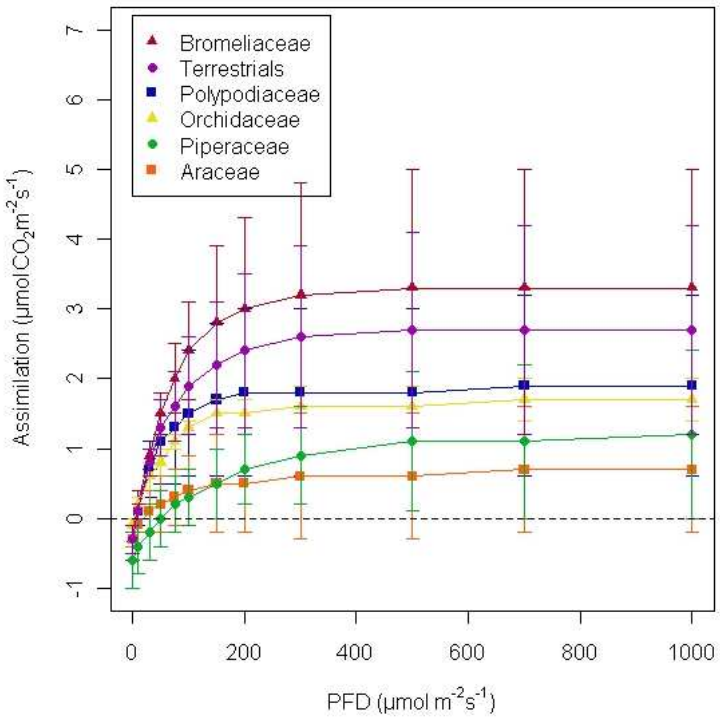

Figure 1: CO_2-assimilation of epiphytic families and terrestrial plants ± s.e. Lines only connections between data points. For number of species see Table 2.

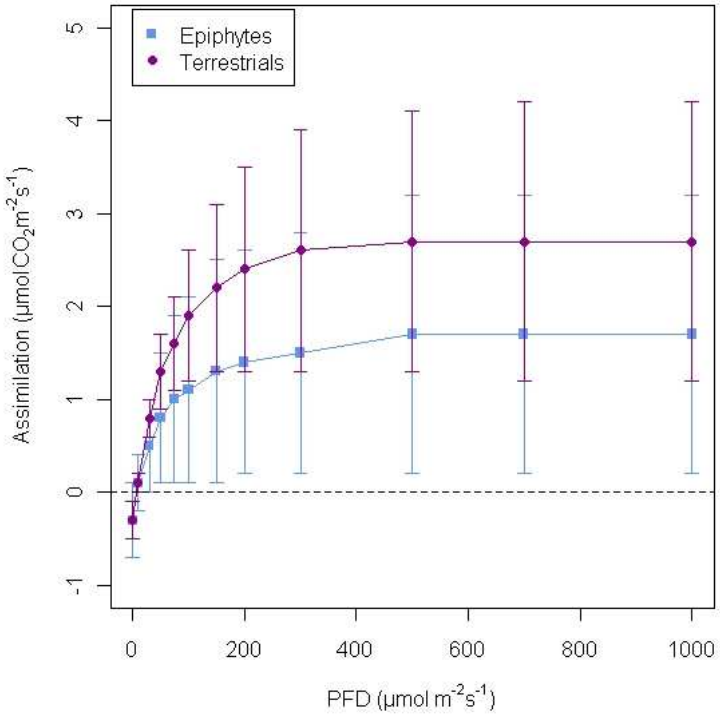

Figure 2: CO_2-assimilation of epiphytes and terrestrial plants ± s.e. Lines only connections between data points. For number of species see Table 2.

Due to their CAM-metabolism no CO_2-assimilation could be measured in *Aechmea magdalenae* and *Ornithocephalus bicornis* (Taiz and Zeiger 2006). To include them in the comparison, means of ETR were plotted against light intensity for families (Figure 3) and life forms (Figure 4). Because the resulting variations of terrestrial plants were overlapping the epiphytic means, and variations of ETR between the families were similar to variations of assimilation, I refrained from conducting any statistical analysis.

The measuring groups were compared for the steady-state response (Figure 5). The results showed no differences in means. Consequently this leads to the conclusion that no changes, which could falsify other evaluations, occurred during the time of the experiments

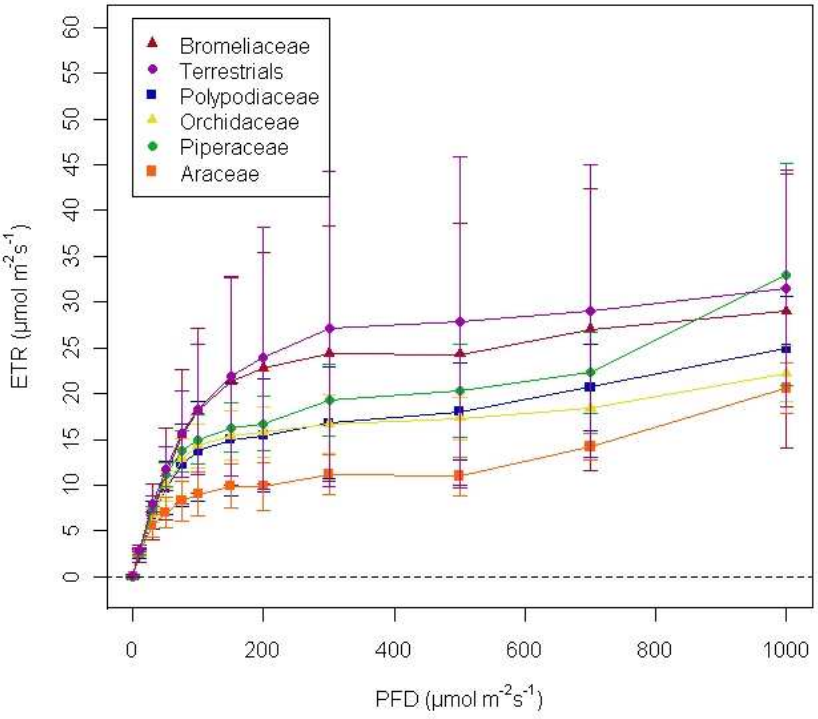

Figure 3: Electron transportation rates of epiphytic families and terrestrial plants, including the CAM-plants ± s.e. Numbers of species are the same as in Table 2 with one additional CAM-plant for Orchidaceae and the terrestrial plants. Lines are only connections between data points.

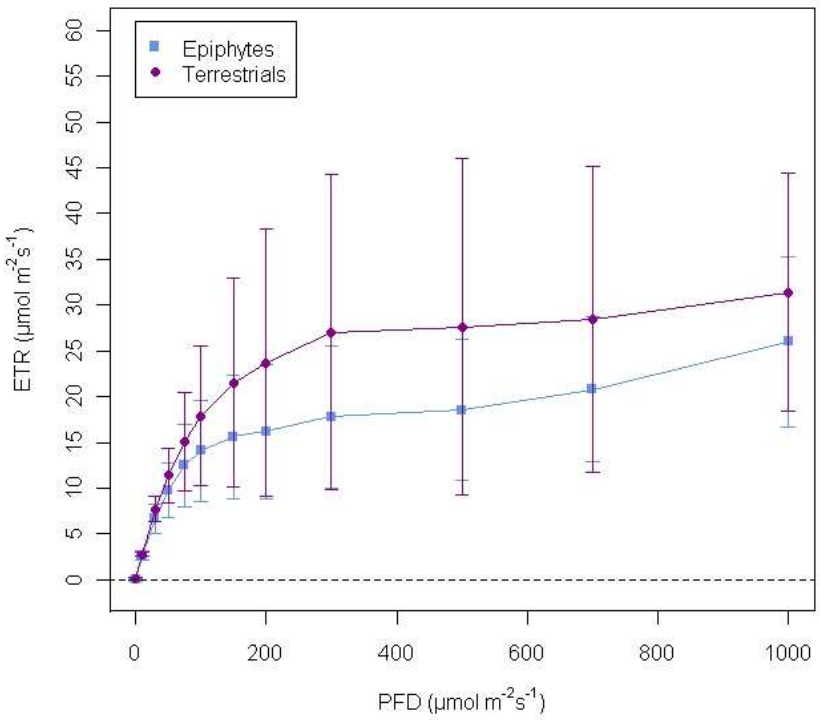

Figure 4: Electron transportation rates for epiphytes and terrestrial plants ± s.e including the CAM-plants. Numbers of life forms are the same as in Table 2 with one additional species for both life forms. Lines are only connections between data points.

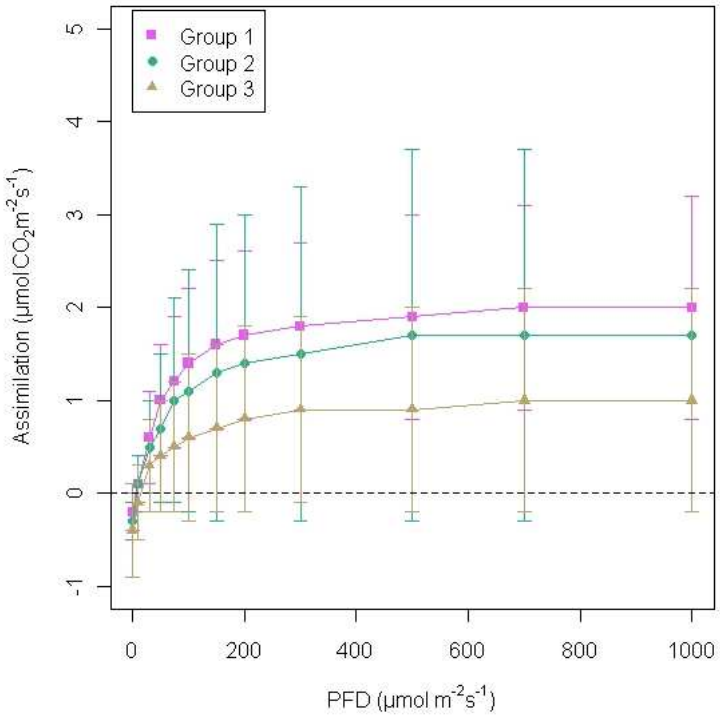

Figure 5: CO_2-assimilation in the measuring groups ± s.e. (number of species= 8 per group). Lines are only connections between data points. Species in the groups are listed in Appendix 2.

3.2. Induction in saturating light

How fast and how strong epiphytes and their terrestrial neighbours react to a sudden increase in PFD, is one aspect of lightfleck-usage in the understorey (Valladares et al. 1997). According to the hypothesis (see chapter 1) not only CO_2-assimilation, but also stomatal behaviour, as an indicator of water-economisation, was evaluated.

3.2.1. CO_2-assimilation

While fitting the regressions, two different courses of induction were found, one following an exponential curve with a strong increase in the beginning and the other following a logistic function, having a slow rise in the first minutes of induction (Figure 6). The distribution of these two regression-types among the species shows that sigmoid/logistic courses occur exclusively in Araceae and Orchidaceae. The R^2-values, used to determine the regression-type, were >90% for 24 out of 28 individuals, with values >75% for the others (Appendix 3).

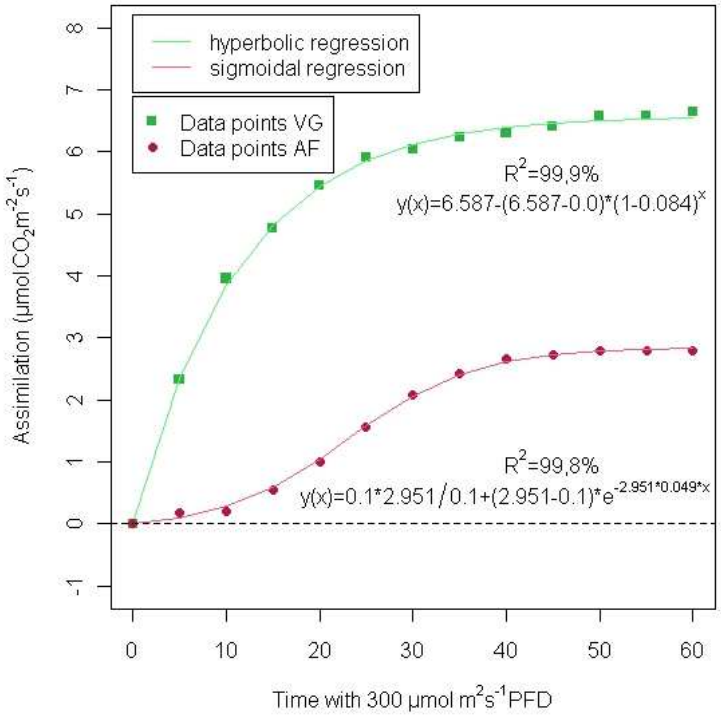

Figure 6: Two examples of different induction courses. VG is *Vriesea gladioliflora* (Bromeliaceae) and AF is *Anthurium friedrichsthalii* (Araceae). Calculated equations and coefficients of determination are indicated beneath each curve. Data are absolute CO_2-assimilation, corrected for respiration at time= 0. Differences in values at the end of induction are species-specific and not due to the regressions.

The differences over the time course of induction, resulting from the induction-types, are visible when comparing the relative assimilation rate (Figure 7).

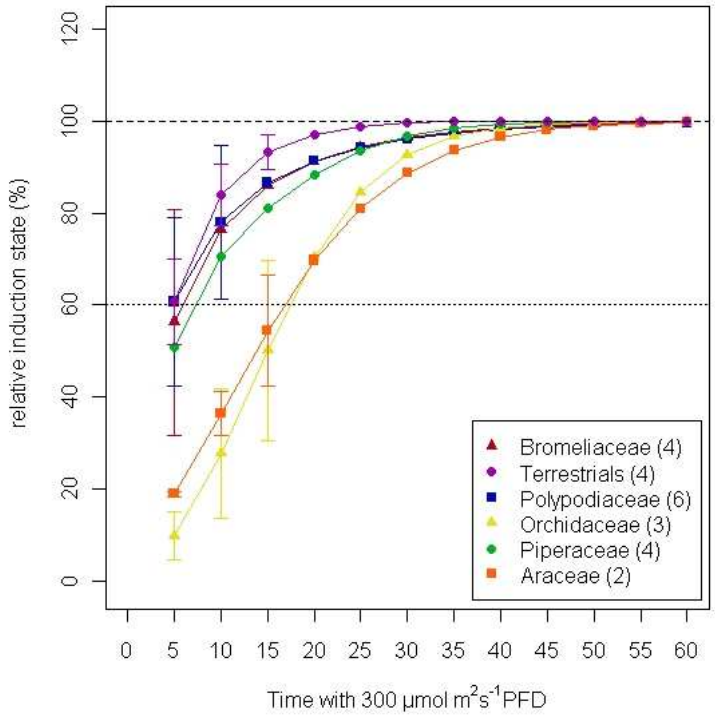

Figure 7: Relative assimilation during induction for epiphytic families and terrestrials. Data are means from values calculated with fitted regressions (see Appendix 3). Numbers of species per family are indicated in parentheses. For clarity, error bars are only shown for time values and families showing significant differences (Table 4).

To determine the significance between the induction courses, statistical evaluation was conducted for the courses of relative assimilation with a 'repeated measurements ANOVA' depending on time, family and life form (Table 3). Though only little difference was found between life forms, differences between families were highly significant. Hence, a post-hoc test was conducted between the families at 5, 10, 15 and 20 minutes to figure out which family-pairs feature a different IS (Table 4). From the Games-Howell test resulted that at 5 minutes of induction, both Araceae and Orchidaceae have a significantly (95% certainty) lower IS than Polypodiaceae and Terrestrials; Orchidaceae are also different from Bromeliaceae. After 10 minutes of induction, Araceae are still different from Polypodiaceae and Terrestrials, whereas the Orchidaceae are only different from Terrestrials, which is also true for both Araceae and Orchidaceae after 15 minutes of induction. Looking at later induction, difference between any of the families could no longer be found. The little difference between life forms led to significant post-hoc tests only at 5, 10 and 20 minutes.

Not only relative assimilation rates during the first 15 minutes of induction were significantly lower in Araceae and Orchidaceae than in the other families, but also time needed to reach

certain IS was greater for the two families. This was tested for different times and significance was found for T60 (Table 3). When tested for 95% certainty, the post-hoc test showed significant differences for T60 between Araceae and Bromeliaceae/ Polypodiaceae/ Terrestrials as well as between Orchidaceae and Terrestrials. The difference between Araceae/Orchidaceae and Terrestrials was still significant when tested for 99% certainty (Table 4).

Table 3: Results from 'repeated measurements ANOVA' and ANOVA conducted with relative assimilation. 'Family (+ terr)' stands for comparison including terrestrial species as one family. n.s. = not significant

Repeated measurements	Time	Time*Family (+ terr)	Time*Form
relative assimilation	p= 0.00	p= 0.00	p= 0.05
ANOVA		Family (+ terr)	
T60 induction		p= 0.02	

Table 4: Results from Games-Howell-Test and Univariate F-Test. Letters indicate statistical groups. Families with different group memberships are significantly (95% certainty) different. Abbreviations: Ara= Araceae, Bro= Bromeliaceae, Orch= Orchidaceae, Poly= Polypodiaceae, Pip= Piperaceae, Terr= all terrestrial individuals.

post-hoc test (Games-Howell)	Ara	Bro	Orch	Poly	Pip	Terr
IS_5 of assimilation	AC	DC	A	BD	ABCD	BD
IS_{10} of assimilation	A	ABC	AC	C	ABC	BC
IS_{15} of assimilation	A	AB	A	AB	AB	B
T60 induction (95% certainty)	A	BC	AB	BC	ABC	C
T60 Induction (99% certainty)	A	AB	A	AB	AB	B
post-hoc test (F-Test)						
IS of assimilation	5 min	10 min	15 min	20 min		
between life forms	p= 0.04	p= 0.04	p= 0.06	p= 0.02		

3.2.2. Stomatal behaviour

The influence of stomatal reaction on the induction times is supposed to be visible in the induction courses of gw. As described in chapter 2.4.3, data points with low gw were eliminated and therefore evaluation is only conducted with a subset of the data. Comparing gw-courses of families during induction, it is noticed that two of the terrestrial species have declining means of gw, whereas all other families have slightly rising courses. Mean gw ranged during the time course from 10 - 30 mmol H_2O m^{-2} s^{-1} among epiphytic families and from 55 - 30 mmol H_2O m^{-2} s^{-1} among terrestrials. (Figure 8)

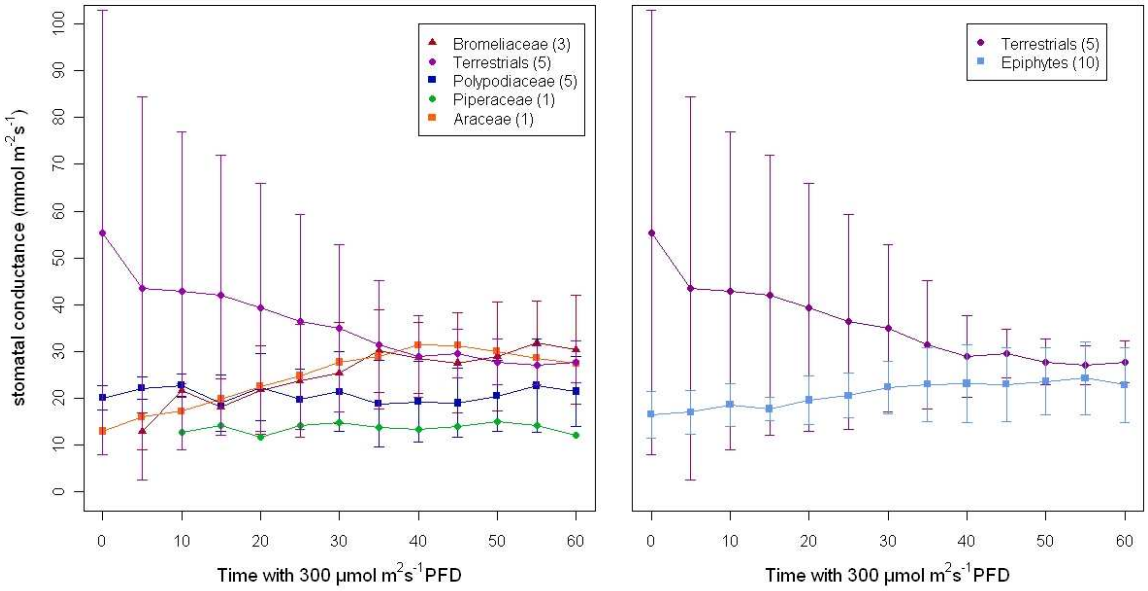

Figure 8: Stomatal conductance during induction in families and life forms. Numbers of species are indicated in parenthesis. Data are means ± s.e. calculated from the selected species (compare chapter 2.4.3). Decreasing conductance was found only in 2 of 5 terrestrial species.

Whether these visual differences reflect real differences in stomatal behaviour is tested with 'repeated measurements ANOVA', showing that there are significant differences when depending on time and life form (Table 5). But the results also show that there is no significant trend of gw when depending only on time (p= 0.36), which implies an overall steady conductance. A steady state was also found for water-use efficiency, calculated from assimilation and respiration following equation 8.

$$WUE = \frac{A\left[\mu molm^{-2}s^{-1}\right]}{E\left[mmolm^{-2}s^{-1}\right]} \qquad \text{(eqn. 8)}$$

Table 5: Results from 'repeated measurements ANOVA' with gw ($mmol\,H_2O\,m^{-2}s^{-1}$) and WUE ($\mu mol\,CO_2/mmol\,H_2O$) during induction. Family (+terr) = comparison with all terrestrial species treated as one family. Family (-terr) = comparison in between epiphytes. n.s. = not significant.

repeated ANOVA	Time	Time*Family (+terr)	Time*Family (-terr)	Time*Form
gw	p= 0.36 (n.s.)	p= 0.08 (n.s.)	p= 0.62 (n.s.)	p= 0.04
WUE	p= 0.83 (n.s.)	p= 0.74 (n.s.)	p= 0.80 (n.s.)	p= 0.99 (n.s.)

After 60 minutes of induction, WUE was $9.2 \pm 1.1\,\mu mol\,CO_2/mmol\,H_2O$ for epiphytes and $7.9 \pm 4.3\,\mu mol\,CO_2/mmol\,H_2O$ for terrestrials. A 'repeated measurements ANOVA' showed no significant difference in WUE either depending on time, family or life form.

Comparison between relative gw and relative assimilation for epiphytes and terrestrials showed lower means of relative gw than assimilation for both life forms at nearly all time steps, not reaching 100% during 60 minutes in the epiphytes (Figure 9). But differences in time courses of gw and assimilation are found only to be significant for terrestrials (Table 6).

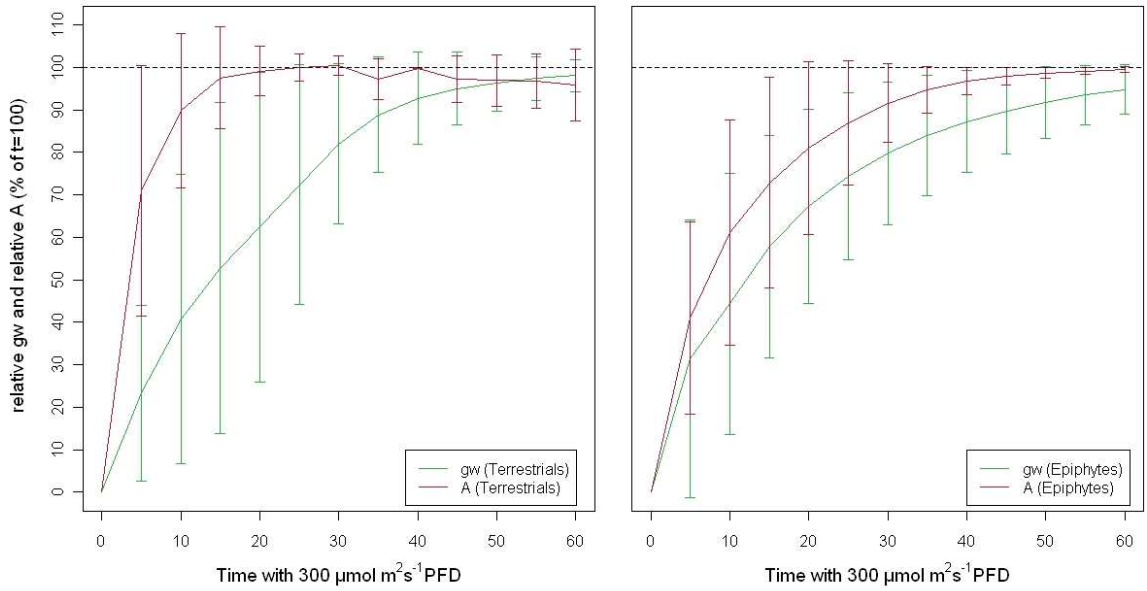

Figure 9: Relative stomatal conductance (gw) and assimilation (A) during induction for both terrestrials and epiphytes. Data are means ± s.e. of values calculated relative of gw/A at 100 minutes. The values for gw(100) and A(100) were estimated through fitted regressions. n= 8 for Epiphytes and n= 4 for terrestrials due to selection of reliable data (see chapter 2.4.3).

Table 6: Results from two 'One-way repeated measurements ANOVAs'. Parameters are relative stomatal conductance and relative assimilation. n.s. = not significant

	Parameter	Time	Time*Parameter
Epiphytes	p= 0.15 (n.s.)	p= 0.00	p= 0.56 (n.s.)
Terrestrials	p= 0.06 (n.s.)	p= 0.00	p= 0.04

With stomatal conductance reacting more slowly to an increase in PFD than assimilation, the relation of C_i to C_a should decrease at the beginning of induction (Figure 10). As well as gw and WUE, mean values of C_i/C_a had stabilized until the end of induction at about 0.6-0.7, which corresponds to a C_i of 222-259 ppm. Because variability of the data sets was very high, a test of difference was assumed not to be reasonable.

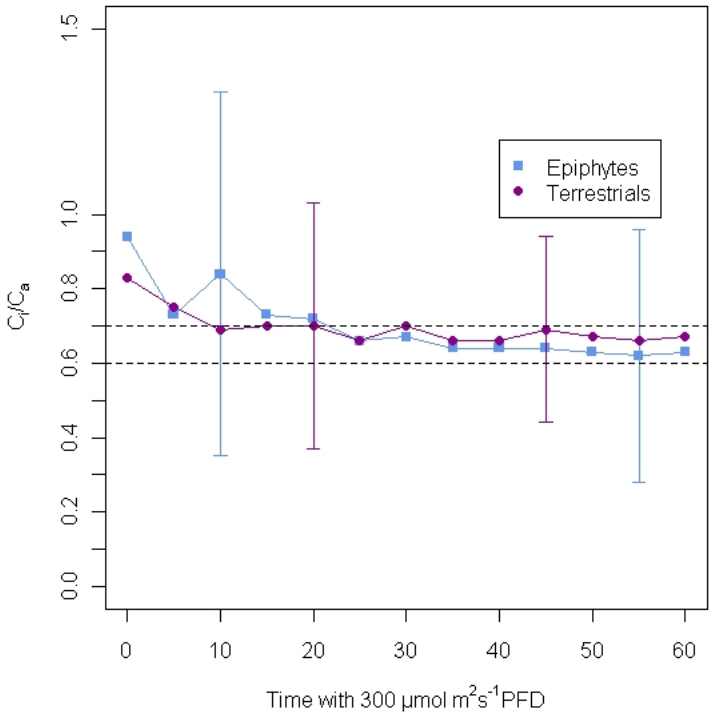

Figure 10: Fraction of intercellular CO_2 to external CO_2 during induction with satPFD. External CO_2 was controlled to 370 ppm, leaf temperature was approximately 29°C and VP D 13 Pa/kPa. Only two representative error bars are shown for each life form. Dotted lines indicate an area of 222-259 ppm C_i. n= 16 for epiphytes and n= 6 for terrestrials.

3.3. Loss of induction

Not only fast induction at occurring lightflecks, but also the ability to remain induced during periods of shade contributes to an optimal use of variable light conditions (Valladares et al. 1997). Therefore, loss of induction in a fully induced leaf during a prolonged shade-period was measured and the courses of assimilation as well as stomatal conductance were compared between families and life forms.

3.3.1. CO_2-assimilation

Induction-loss was slow throughout all measured species. After 60 minutes, 4 families had lost approximately 40% and 2 families nearly 80% of their initial IS. The final mean IS was 40% among all epiphytes and 60% among the terrestrials (Figure 11).

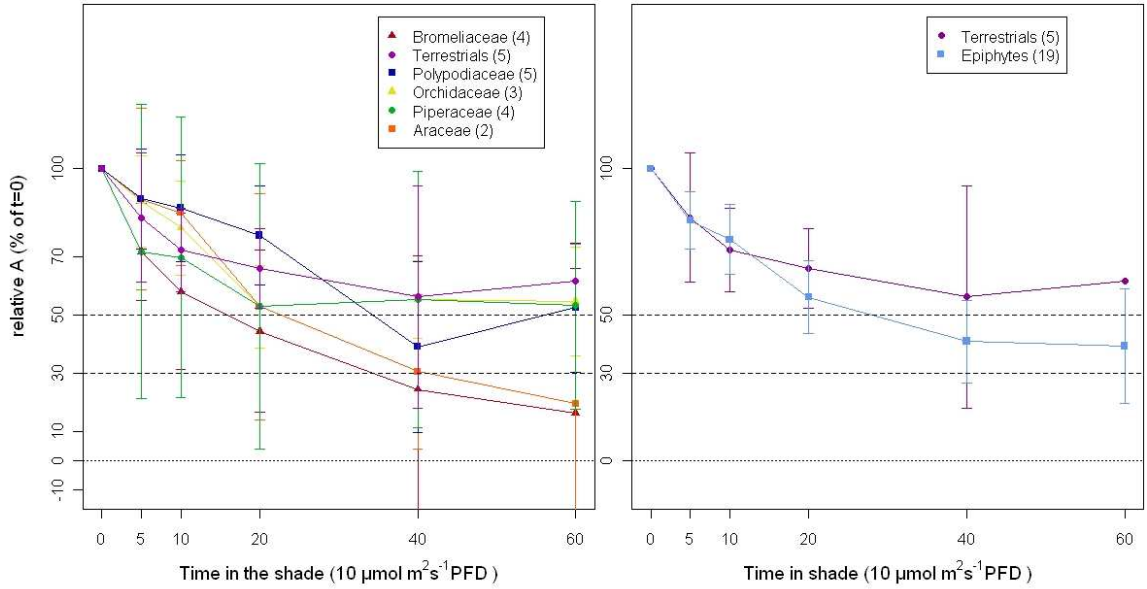

Figure 11: Relative assimilation after 60 seconds of saturating light at 5, 10, 20, 40 and 60 minutes of shade. Data are means ± s.e of relative assimilation for families and life forms, respectively. Error bars at 40 and 60 minutes are partially omitted for better visibility. Lines are only between data points. Numbers of species are indicated in parentheses.

To reach 50% of relative assimilation, the fastest family required 32 ± 31 minutes (mean ± s.e.). Other evidence for slow induction-loss is the time needed to reach 30% of induction, which was very high, especially in Piperaceae (Table 7). Despite the differences in means of T30 or T50, no significance could be found among families or life forms (Table 8). No significant difference was found during a 'repeated measurements ANOVA' between the life forms as well as between the families (including terrestrials) either.

Table 7: Time in minutes to reach 50 and 30% of relative assimilation during shade. Values are means ± s.e. calculated from dissolved regression models fitted for each species. n= Numbers of species per family.

	n	time to reach 50% induction	time to reach 30% induction
Bromeliaceae	4	32 ± 31	74 ± 73
Polypodiaceae	6	36 ± 27	85 ± 63
Araceae	2	44 ± 23	103 ± 54
Terrestrials	5	48 ± 59	112 ± 138
Orchidaceae	3	53 ± 37	125 ± 86
Piperaceae	3	86 ±37	202 ± 86

Table 8: Results from 'repeated measurements ANOVA' and ANOVA with relative assimilation during shade. Assimilation is relative to the induction state (IS) at time= 0. T50 and T30 are the times to reach 50% and 30% of relative assimilation, respectively. Family (+terr) = comparison with all terrestrial species treated as one family.

Repeated measurements	Time	Time*Family (+terr)	Time*Form
relative assimilation	p= 0.00	p= 0.35 (n.s.)	p= 0.38 (n.s.)
ANOVA		Family (+terr)	Form
T50 induction		p= 0.22 (n.s.)	p= 0.97 (n.s.)
T30 induction		p= 0.53 (n.s.)	p= 0.97 (n.s.)

3.3.2. Stomatal behaviour

During induction-loss, 3 out of 5 terrestrial species show a strong rise in gw at 60 minutes, leading to a high mean with a just as high deviation (Figure 12).

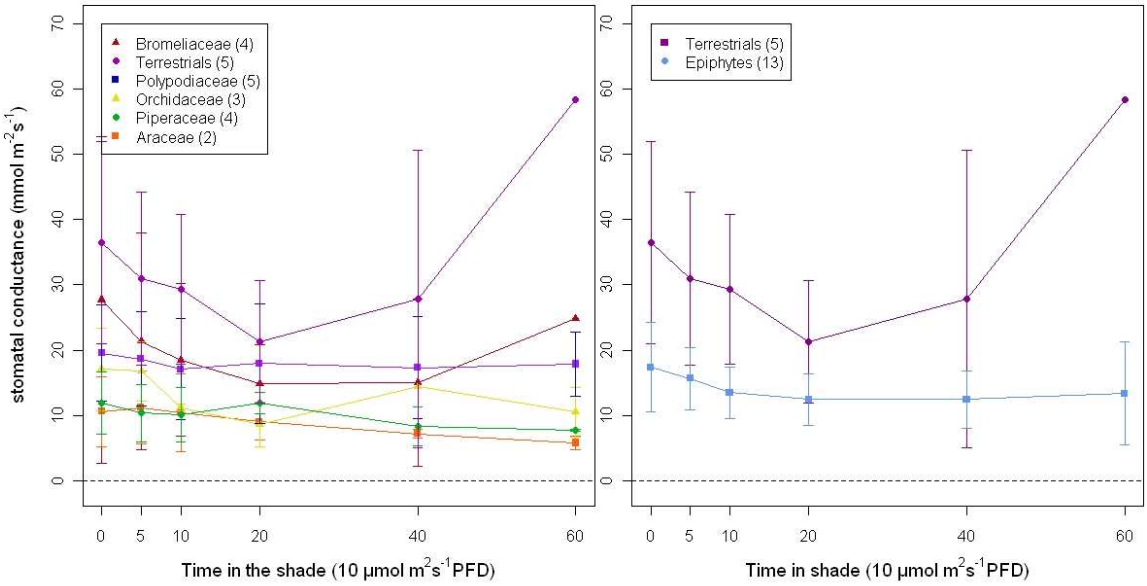

Figure 12: Stomatal conductance for families and life forms, respectively. Data are means ± s.e. from values recorded after 60 seconds of saturating light during a period of shade. Numbers of species are indicated in parentheses. Error bars for terrestrials at 60 minutes (s.e. = 65) are not shown in addition to better visibility.

No significant differences in the courses of gw could be found between life forms or families including the terrestrials (Table 9). Despite this, significant difference was found with a 'repeated measurements ANOVA' (p= 0.03) in between epiphytes. Post-hoc analysis with Tukey's Honestly-Significant-Difference test brought significant differences at 60 minutes between Araceae and Bromeliaceae (p= 0.04).

Table 9: Results from 'repeated measurements ANOVA' of stomatal conductance during induction-loss. Family (+terr) indicates comparison with all terrestrial species treated as one family. Family (+terr) = comparison with all terrestrial species treated as one family. Family (-terr) = comparison in between epiphytes. n.s. = not significant.

Repeated ANOVA	Time	Time*Family (+ terr)	Time*Family (-terr)	Time*Form
gw [mmol $m^{-2} s^{-1}$]	p= 0.00	p= 0.77 (n.s.)	p= 0.03	p= 0.08 (n.s.)

Similar to stomatal behaviour during induction, the mean course of relative stomatal closure is slower than the decrease in means of relative assimilation (Figure 13). But differences in these two parameters are found to be significant neither for epiphytes nor for terrestrials in a 'repeated measurements ANOVA' (Table 10).

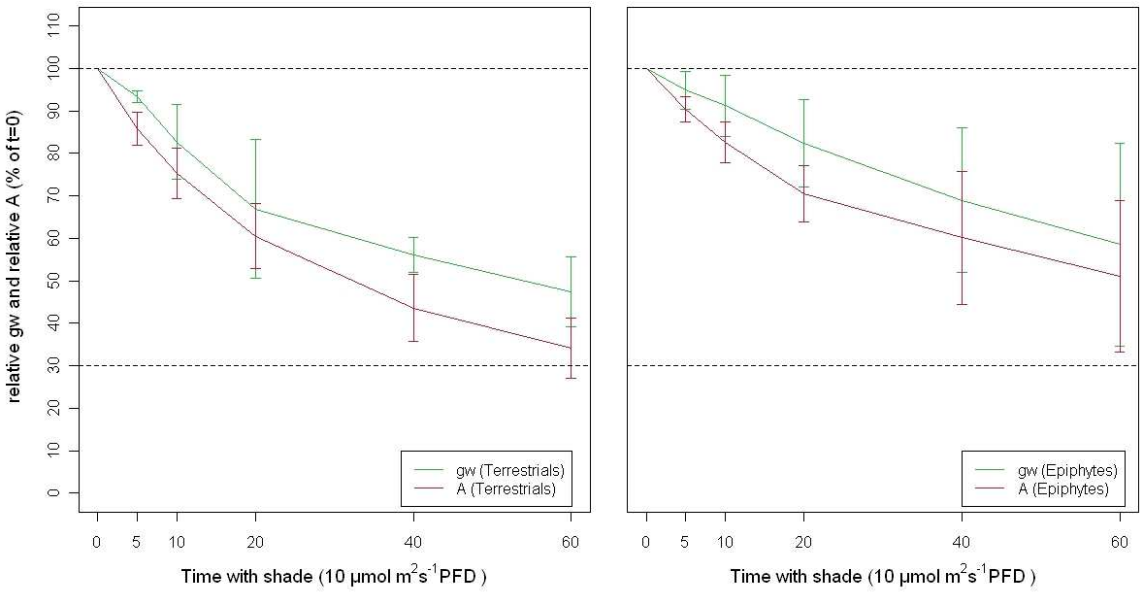

Figure 13: Time courses of relative stomatal conductance (gw) and assimilation (A) during induction-loss for both epiphytes and terrestrials. Data are means ± s.e. of values calculated relative of gw/A at 0 minutes. n= 6 for Epiphytes and n= 2 for terrestrials due to selection of reliable data (see chapter 2.4.3).

Table 10: Results from two 'One-way repeated measurements ANOVAs'. Parameters are relative gw and relative A (relative of t= 0) during induction-loss for epiphytes and terrestrials, respectively.

	Parameter	Time	Time*Parameter
Epiphytes	p= 0.25 (n.s.)	p= 0.00	p= 0.94 (n.s.)
Terrestrials	p= 0.23 (n.s.)	p= 0.00	p= 0.90 (n.s.)

Although no change in C_i would be expected from the simultaneous courses of assimilation and gw, a rise in C_i after 60 minutes of shade was found in one species of each Araceae (*Anthurium friedrichsthalii*) and Bromeliaceae (*Vriesea gladioliflora*). These two values led to a strong rise at the end of the shading period in the mean of all epiphytes (Figure 14). Mean C_i among life forms was above the average of 222-259 ppm found during induction, but high variability in the data set renders generalization highly speculative.

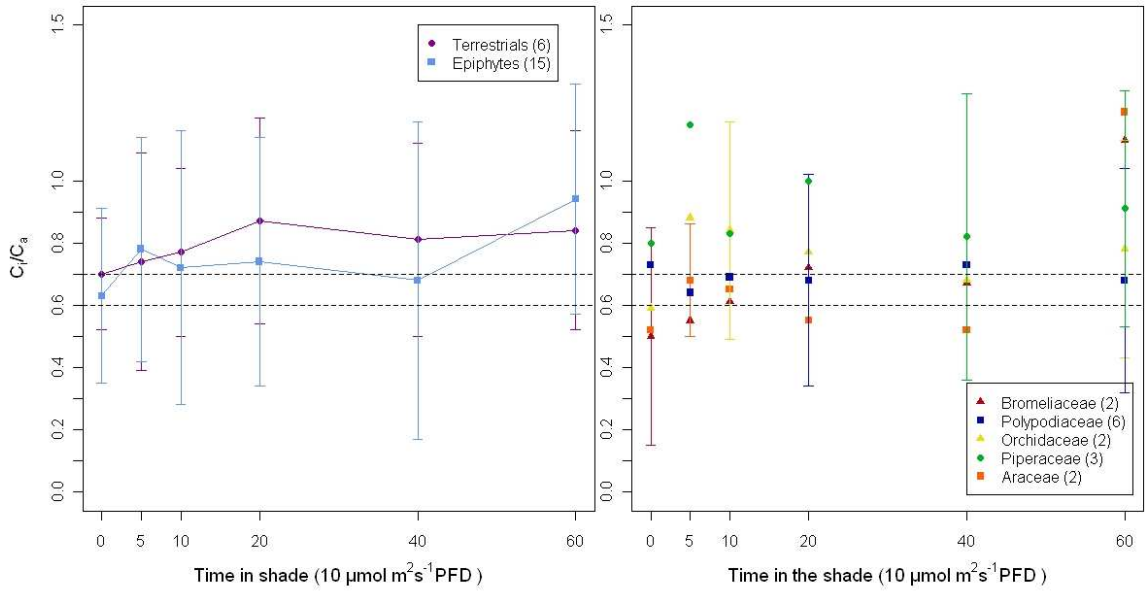

Figure 14: Fraction of intercellular CO_2 (C_i) to external CO_2 (C_a) during induction-loss. C_a was controlled to 370 ppm, leaf temperature was approximately 29°C and VP D 13 Pa/kPa. Only some representative error bars are shown in the right graph. Dotted lines indicate an C_i = 222-259 ppm. Numbers of species are indicated in parentheses. Only one value at t= 60min was included for Araceae and Bromeliaceae, leading to a strong rise among the epiphytes.

3.4. Fluorescentic behaviour as an indicator of stress

When plants are studied, they are normally measured at their growing site or replanted several months in advance to a greenhouse. According to the fact that the plants for this study were replanted within the forest only three weeks before the measurements, fluorescentic behaviour was measured to get an idea whether and how stressed the plants were. As an indicator of stress, photoinhibition is commonly used (Skillman and Winter 1997, Zotz and Tyree 1996). The amount of photoinhibition is expressed through maximum photochemical efficiency (Fv/Fm) in a dark adapted leaf. A dark adaptation state in the leaf was provided before the measurements of induction and induction-loss. Fv/Fm ranged from 0.14 to 0.82 with a mean of 0.74 ± 0.12 for all species at the beginning of the induction-loss measurement. A value of Fv/Fm < 0.7, which indicates a certain amount of photoinhibition (Zotz and Tyree 1996), was measured only in one individual from each *Dicranoglossum panamense* and *Peperomia macrostachya*.

4. Discussion

This study tested the hypothesis that a distinct water-saving behaviour, expressed through longer induction times and faster induction-loss, can be found among epiphytes in general comparing to co-occurring terrestrials. These expectations were not completely fulfilled, because differences between epiphytes and terrestrials were only significant during the beginning of induction and substantial variation was found among the epiphytes. Also the stomatal behaviour showed no general difference in the evaluated measurements.

4.1. Steady-state CO_2-response

The course of photosynthetic response to different light intensities was similar to that of other understorey or shade plants (Chazdon and Pearcy 1986b, Zotz and Mikona 2003) with rather low photosynthetic parameters for families as well as life forms.

For shade-tolerant species a low compensation point, here $9\,\mu mol\,m^{-2}\,s^{-1}$ PFD among epiphytes and $6\,\mu mol\,m^{-2}\,s^{-1}$ PFD among terrestrials, is expected because light intensities are normally low in an understorey environment and a low CP is needed to use as much of the light reaching the ground as possible (Valladares and Niinemets 2008). A low CP indicates shade-tolerance in tree saplings (Craine and Reich 2005), showing the trade-off between positive assimilation at low light intensities and high photosynthesis at high light (A_{max}) (e.g. reviewed by Givnish 1988).

Hence, low A_{max} was found among both life forms, reaching means of 2.5 and $3.1\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$, respectively. For comparison, A_{max} reached 2.7-10.8 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ in shade-tolerant and 5.7-19.5 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ in shade-intolerant shrubs and tree saplings (Valladares et al. 1997, Rijkers et al. 2000, Zipperlen and Press 1997). In 27 epiphytic species from different habitats mean A_{max} was $2.6\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ (Stuntz and Zotz 2001). High variability in A_{max} among epiphytes, which led to no significant differences between epiphytes and terrestrials in this thesis, was suggested previously (Zotz and Hietz 2001).

Having low A_{max}, shade-tolerant species assimilate theoretically less carbon throughout the day than species with high A_{max}. Therefore they need some mechanism to reach a sufficient level of daily carbon gain. Better lightfleck-use efficiency (Valladares et al. 1997) and low respiration rates (Walters and Reich 2000, Craine and Reich 2005) are suggested ways. Respiration rates were indeed very low among both epiphytes and terrestrials, reaching less than $1\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$.

Altogether, both epiphytes and terrestrials showed photosynthetic characteristics typical for shade-tolerant understorey species. Low respiration rates maintain sufficient daily carbon gain even if light is scarce and a low CP ensures that even light of low intensity can be used to full extend.

4.2. Induction in saturating light

As lightflecks, which contribute to a considerable amount of irradiance in the understorey, are unpredictable in their occurrence and duration, a rapid induction is needed to use them efficiently. But if understorey plants suffer strongly from water-shortage, as described for epiphytes (Zotz and Hietz 2001), the priority of saving water reserves should lead to a more moderate pace of stomata opening and thereby to slower induction.

Time to reach 90% of induction was actually high, ranging about 27-40 minutes in all measured species (Figure 7). Values for *Aspasia principissa* were also higher in this thesis than found in the previous study on this epiphyte (Zotz and Mikona 2003). In the literature, both slow and fast induction-times can be found in understorey shrubs and tree seedlings, with 11-40 minutes (Zipperlen and Press 1997, Chazdon and Pearcy 1986a) for slow and 4-15 minutes for fast induction (Kursar and Coley 1993, Rijkers et al. 2000, Valladares et al. 1997). Considering the fact that not the comparison of T90 but of T60 showed differences between the families in this thesis, comparison of a lower IS could generally be more advisable for the detection of different induction courses.

The two types of induction-courses, which led to the significant differences in T60 and in induction states between Araceae/Orchidaceae and other families, were also observed in other studies (Chazdon and Pearcy 1986a, Rijkers et al. 2000, Valladares et al. 1997). Kirschbaum and Pearcy (1988) found that sigmoid induction-courses are correlated with low initial stomatal conductance, which was verified in the studies named above. Due to no recorded MP before 5 minutes of induction, no general connection between the initial gw and the course of induction could be found in this study. In fact, means of gw after 5 minutes were lower in Piperaceae (6 mmol H_2O m^{-2} s^{-1}), Polypodiaceae (16 mmol H_2O m^{-2} s^{-1}) and Bromeliaceae (10 mmol H_2O m^{-2} s^{-1}) than in Araceae (20 mmol H_2O m^{-2} s^{-1}), when comparing all measured species. Of course it has to be considered that these values for gw are not very reliable (see above). The selection for high gw affected particularly the Araceae (only one remaining species) and Orchidaceae (all species deleted), which are the two families with sigmoid induction courses.

With a mean gw of 30 mmol H_2O m^{-2} s^{-1} among both epiphytes and terrestrials at the end of induction, the results are lower than values found in understorey shrubs of BCI; induction

courses for gw of 63-94, 50-88 and 43-66 mmol H_2O m^{-2} s^{-1} were found in three understorey-species of Rubiaceae (Valladares et al. 1997). A low gw could be an indicator for water-saving behaviour in the measured species.

Zipperlen and Press (1997) suggest that a slower relative stomatal induction, compared with relative assimilation, points to a higher maximal gw than needed for maximal photosynthesis. A time lag between A and gw found among terrestrials during induction would be advantageous in allowing a higher carbon gain during pre-occurring lightflecks (compare discussion in Kirschbaum and Pearcy 1988). The hypothesis of epiphytes being more water-saving than their terrestrial neighbours would explain the absence of such a time lag between gw and A in the epiphytes. Furthermore, the mean WUE at full induction was found to be higher among epiphytes than among terrestrials and also higher than in two understorey shrubs of a Borneo rainforest (Zipperlen and Press 1997).

The fact that C_i reaches a stable mean of 222-259 ppm CO_2 during induction, may indicate a tight regulation of the stomatal and biochemical parts of assimilation to a physiological optimum (Zipperlen and Press 1997, Allen and Pearcy 2000b). Unlike it was considered in other studies (Kirschbaum and Pearcy 1988, Valladares et al. 1997), low values for gw cannot contribute to an overestimation of internal CO_2 in this thesis, because values were selected for high gw.

4.3. Loss of induction

All plants have to reach a specific amount of daily carbon gain for growth and reproduction, which is difficult in a light-poor environment. Slow induction-loss after one lightfleck can prepare the photosynthesis for the following lightflecks, but the IS correlates positively with water-loss through open stomata. Therefore, loss of induction was hypothesised to be faster in the water-saving epiphytes.

Induction-loss was slow in all measured families, the fastest family loosing 50% induction in about 30 minutes, which seems to be a typical value for understorey shrubs and tree seedlings (Rijkers et al. 2000, Valladares et al. 1997) and was also found for *Aspasia principissa* by Zotz and Mikona (2003). Looking at life forms, the IS after 60 minutes at low light is considerably higher (60% and 40% for terrestrials and epiphytes, respectively) than in the literature, where an IS_{60} of 43% was found for terrestrials (Chazdon and Pearcy 1986a) and of 30% for an epiphyte (Zotz and Mikona 2003). The difference among epiphytes between this study and the literature is clearly due to the comparison of a life form and one species. As no methodological differences can explain the differences among terrestrials, I would suggest that they have adapted to the BCI understorey, which was found to be rather

poor in lightflecks. An average of 77 lightflecks (exceeding 50 µmol $m^{-2} s^{-1}$ PFD) per day were measured during the wet season (Valladares et al. 1997) and about 12 lightflecks were recorded on one day in the dry season (Zotz and Mikona 2003). When frequency of lightflecks is low, slow induction-loss should enlarge the probability of having a high induction-state during the following lightfleck, which in turn would allow higher carbon gain. To verify this suggestion, it has to be shown that photosynthetic behaviour can adapt to the lightfleck-environment.

Although no general difference between epiphytes and terrestrials could be found, a trend of faster induction-loss is implied for epiphytic families because only the Polypodiaceae have slower induction-loss than the terrestrials (Figure 15). Such trend would be consistent with findings of faster induction-loss in light-demanding species compared to their understorey conspecifics (Chazdon and Pearcy 1986a, Ogren and Sundin 1996, Rijkers et al. 2000, Valladares et al. 1997, Zipperlen and Press 1997). All these studies conclude that faster induction-loss is maintained by plants in high-light environments because of higher transpiration rates. This would also apply to water-saving epiphytes in the understorey.

Why gw increases after 60 minutes of low light in some of the terrestrials could not be explained, because courses of gw are found to be similar to or slower than induction-loss in terrestrial understorey plants (Rijkers et al. 2000, Ogren and Sundin 1996). Different stomatal behaviour within the epiphytes is reflected by the significant difference between Araceae and Bromeliaceae at the end of the shading period. Surprisingly, this difference could not be found in assimilation rates, where Araceae and Bromeliaceae both reach a mean of 20% induction at 60 minutes of shade.

Unlike during induction, no difference in pace was detected for assimilation and gw, either among terrestrials or epiphytes. Therefore, no considerable change in C_i was measured during induction-loss with its means ranging slightly above the level measured during late induction.

Finally, the recording-method during induction-loss should be included in the interpretation of data. During data evaluation, it was noticed that the number of MPs per lightfleck was not always 3, despite the fact that all measurements were run with exactly the same program. Therefore it can not be said with absolute certainty whether MPs were taken at the end of the 60s-light burst every time. Depending on how fast a species is re-inducing during 60 seconds, this could lead to incomparable data. It is assumed that this was caused by different length of fluorescence-measurements, which exceeded the programmed interval previous to the 60-seconds light-burst. If this was the case, the program would have shortened the programmed measuring interval and thus omitted the last MP.

4.4 Conclusion

In summary, epiphytes show species-specific behaviour in a variable-light environment. This leads to no general difference between epiphytes and their terrestrial neighbours in the understorey, i.e. any significant differences after the first 20 minutes of induction and during induction-loss. High diversity within the epiphytes concerning their reactions to changing light intensities is clearly visible when comparing relative assimilation in high and low light directly (Figure 15). The possible behaviour ranges from fast induction + fast induction-loss (Bromeliaceae) over fast induction + slow induction-loss (Polypodiaceae, Piperaceae and Terrestrials) as well as slow induction + fast induction-loss (Araceae) to slow induction + slow induction-loss (Orchidaceae).

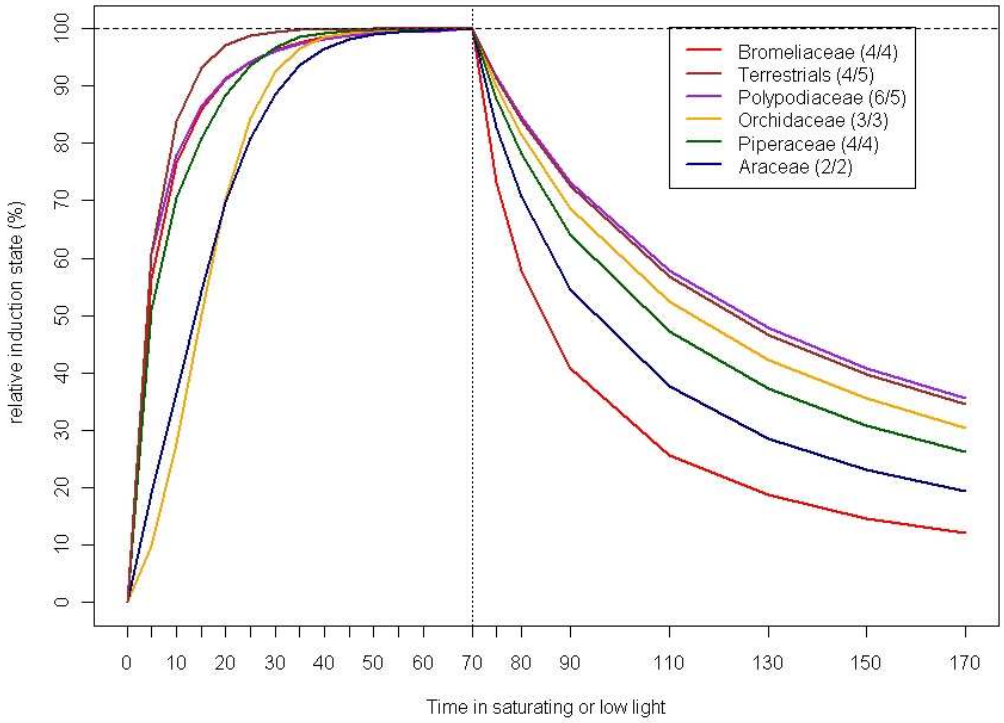

Figure 15: Induction states relative to assimilation in an induced leaf during periods of saturating (300 µmolm^{-2}s^{-1} PFD) and low light (10 µmolm^{-2}s^{-1} PFD). Data are regression courses of the mean values for epiphytic families and terrestrials. The vertical line indicates the switch from high to low light. R^2 for regressions were >75% for all families. Numbers of families for induction/induction-loss are given in parentheses.

As conclusions about all epiphytes cannot be drawn from one epiphytic species or family, some other factors might play a relevant role in adapting simultaneously to low light environments and water-shortage in the understorey. Such adaptations can be tanks, succulence, drought-deciduousness or CAM-metabolism (reviewed by Zotz and Hietz 2001).

5. Appendix

Appendix 1: List of collected individuals, sorted by family. If not indicated in the comment, number of collected individuals is the same as measured individuals. Species names are adapted from Croat (1978). Abb.= Abbreviation used in Appendix 3.

Species	Family	Abb.	Nº	Comment
Anthurium clavigerum Poepp.	Araceae	AC	2	
Anthurium friedrichsthalii Schott	Araceae	AF	2	
Dieffenbachia longispatha Engler	Araceae	DL	1	terrestrial
Philodendron radiatum Schott	Araceae	PR	1	
Aechmea magdalenae ex Baker	Bromeliaceae	AM	2	terrestrial, CAM
Guzmania minor Mez	Bromeliaceae	GM	1	
Tillandsia monadelpha Baker	Bromeliaceae	TM	1	
Werauhia gladioliflora	Bromeliaceae	VG	1	
Vriesea heliconioides	Bromeliaceae	VH	1	
Aspasia principissa Reichb.f.	Orchidaceae	AP	1	
Coryanthes maculata Hook.	Orchidaceae	CM	1	
Gongora quinquenervis R. & P.	Orchidaceae	GC	1	
Ornithocephalus bicornis Lindl.	Orchidaceae	OB	1	CAM
Peperomia glabella A. Dietr.	Piperaceae	PL	3	1 measured
Peperomia macrostachya A. Dietr	Piperaceae	PM	2	1 measured
Peperomia obtusifolia A. Dietr	Piperaceae	PG	1	
Peperomia obscurifolia C. DC.	Piperaceae	POC	1	eroded
Piper cordulatum C. DC.	Piperaceae	PI	1	terrestrial
Piper grande Vahl	Piperaceae	PT	1	terrestrial
Asplenium serratum L.	Polypodiaceae	AS	2	
Dicranoglossum panamense Gómez	Polypodiaceae	DP	2	
Niphidium crassifolium	Polypodiaceae	NC	2	
Polypodium costatum	Polypodiaceae	PC	2	
Polypodium lycopodioides	Polypodiaceae	PL	1	
Polypodium phyllitidis	Polypodiaceae	PP	1	
Adiantum lucidum (Cav.)Sw.	Pteridaceae	AD	1	terrestrial
Ischnosiphon pruinosus	Marantaceae	IP	1	terrestrial
Tectaria incisa Cav.	Tectariaceae	TI	1	terrestrial

Appendix 2: List of measured species sorted by measuring group, indicated by dates of measurements. Steady-state response and induction for group 2 and 3 as well as for the additional terrestrials, were measured on one day for steady assimilation on a fully induced leaf.

Species	Family	steady assimilation	induction	induction-loss
Niphidium crassifolium	Polypodiaceae	30.3.09	31.3.09	1.4.09
Aechmea magdalenae	Bromeliaceae	30.3.09	31.3.09	3.4.09
Anthurium friedrichsthalii	Araceae	30.3.09	31.3.09	1.4.09
Gongora quinquenervis	Orchidaceae	30.3.09	31.3.09	1.4.09
Polypodium phyllitidis	Polypodiaceae	30.3.09	31.3.09	2.4.09
Aspasia principissa	Orchidaceae	30.3.09	31.3.09	2.4.09
Vriesea heliconioides	Bromeliaceae	30.3.09	1.4.09	2.4.09
Asplenium serratum	Polypodiaceae	30.3.09	1.4.09	2.4.09
Dieffenbachia longispatha	Araceae	6.4.09	8.4.09	9.4.09
Guzmania minor	Bromeliaceae	6.4.09	8.4.09	9.4.09
Coryanthes maculata	Orchidaceae	6.4.09	8.4.09	10.4.09
Peperomia obscurifolia	Piperaceae	6.4.09	8.4.09	9.4.09
Peperomia glabella	Piperaceae	6.4.09	6.4.09	9.4.09
Dicranoglossum panamense	Polypodiaceae	8.4.09	8.4.09	10.4.09
Polypodium costatum	Polypodiaceae	8.4.09	8.4.09	10.4.09
Vriesea gladioliflora	Bromeliaceae	6.4.09	6.4.09	10.4.09
Piper cordulatum	Piperaceae	14.4.09	14.4.09	16.4.09
Ornithocephalus bicornis	Orchidaceae	13.4.09	13.4.09	15.4.09
Peperomia macrostachya	Piperaceae	13.4.09	13.4.09	15.4.09
Peperomia obtusifolia	Piperaceae	13.4.09	13.4.09	15.4.09
Philodendron radiatum	Araceae	13.4.09	13.4.09	15.4.09
Tillandsia monadelpha	Bromeliaceae	14.4.09	14.4.09	16.4.09
Polypodium lycopodioides	Polypodiaceae	14.4.09	14.4.09	16.4.09
Anthurium clavigerum	Araceae	14.4.09	14.4.09	16.4.09
Adiantum lucidum	Pteridaceae	18.4.09	18.4.09	19.4.09
Piper grande	Piperaceae	18.4.09	18.4.09	19.4.09
Ischnosiphon pruinosus	Marantaceae	18.4.09	18.4.09	19.4.09
Tectaria incisa	Tectariaceae	18.4.09	18.4.09	19.4.09

Appendix 3: Distribution of induction courses in the measured individuals (without CAM-plants). Abbreviations for species are the same as in Appendix 1; Epi= epiphytic life form, Terr= terrestrial life form

Species	Family	Life form	Type of regression	R^2 (%)	Comment
GM	Bromeliaceae	Epi	hyperbolic	99,6	
TM	Bromeliaceae	Epi	hyperbolic	97,9	
VG	Bromeliaceae	Epi	hyperbolic	99,9	
VH	Bromeliaceae	Epi	hyperbolic	96,5	
IP	Marantaceae	Terr	hyperbolic	91,2	
PG	Piperaceae	Epi	hyperbolic	88,4	
PL	Piperaceae	Epi	hyperbolic	97,9	
PM	Piperaceae	Epi	hyperbolic	99,1	
PI	Piperaceae	Terr	hyperbolic	97,8	
PT	Piperaceae	Terr	hyperbolic	97,8	
AS1	Polypodiaceae	Epi	hyperbolic	76,4	
DP2	Polypodiaceae	Epi	hyperbolic	86,7	
NC	Polypodiaceae	Epi	hyperbolic	96,5	
PC1	Polypodiaceae	Epi	hyperbolic	91,0	
PP	Polypodiaceae	Epi	hyperbolic	91,3	
PY	Polypodiaceae	Epi	hyperbolic	96,3	
AS2	Polypodiaceae	Epi	hyperbolic	99,7	
AD	Pteridaceae	Terr	hyperbolic	84,6	negative values
TI	Tectariaceae	Terr	hyperbolic	98,5	
POC	Piperaceae	Epi	hyperbolic /sigmoid	90,5	no difference in R^2
AC1	Araceae	Epi	sigmoid	99,4	
AF1	Araceae	Epi	sigmoid	99,8	
AC2	Araceae	Epi	sigmoid	93,0	
AP	Orchidaceae	Epi	sigmoid	97,6	
CM	Orchidaceae	Epi	sigmoid	97,7	
GC	Orchidaceae	Epi	sigmoid	94,7	
PR	Araceae	Epi	sigmoid/ hyperbolic	93,4	no difference in R^2

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