

Leaf growth dynamics of two congener gymnosperm tree species reflect the heterogeneity of light intensities given in their natural ecological niche

I-LING LAI¹, HANNO SCHARR², ANDRES CHAVARRIA-KRAUSER², RALF KÜSTERS², JIUNN-TZONG WU^{1,3},
CHANG-HUNG CHOU⁴, ULRICH SCHURR² & ACHIM WALTER²

¹Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 106, Taiwan, ²Institute of Chemistry and Dynamics of the Geosphere ICG-III: Phytosphere, Research Center Juelich GmbH, 52425 Juelich, Germany, ³Research Center for Biodiversity and Institute of Botany, Academia Sinica, Taipei 115, Taiwan and ⁴Department of Tropical Agriculture & International Cooperation, National Pingtung University of Science and Technology, Pingtung 912 Taiwan

ABSTRACT

Chamaecyparis obtusa var. *formosana* and *Chamaecyparis formosensis* are congener gymnosperm tree species native to Taiwan cloud forests; occupying different niches there. While the seedlings of *C. formosensis* occur predominantly under bright conditions in large forest gaps, seedlings of *C. obtusa* var. *formosana* are mainly found below the canopy of mature forests or in small gaps. It is well known that congener species occupying different niches typically differ in several ecophysiological and morphological traits, but the differences in growth dynamics of such species are still totally unclear, as the diurnal growth dynamics of gymnosperm leaves have not been investigated before. Modern methods of digital image sequence processing were used in this study to analyse the leaf growth dynamics of the two species. We found that both species show similar base–tip gradients and pronounced diurnal growth rhythms with maxima in the evening. Differences between the two species concerning their growth dynamics correlated closely with their ecological amplitudes and abundances. *Chamaecyparis obtusa* var. *formosana* grew faster than *C. formosensis* in low light intensity, typical for closed-canopy situations, and reacted quickly by increasing or decreasing growth rate when light intensity changed within a range typically found below small canopy gaps. In contrast to this, *C. formosensis* grew better in light intensities typical for open vegetation situations, but reacted slower towards changes of light intensity. Based on those results, the hypothesis can be developed that fluctuations of leaf growth dynamics reflect heterogeneities of the light environment within the niche occupied by a given species.

Key-words: *Chamaecyparis*; congener gymnosperm; image processing; light; niche; relative growth rate.

Correspondence: Achim Walter. Fax: +49 2461612492; e-mail: a.walter@fz-juelich.de

INTRODUCTION

Plants are capable of tolerating a wide range of light environments by acclimation or adaptation of their photosynthetic apparatus. Acclimation of leaves growing in sun or shade conditions has been studied extensively (e.g. Öquist *et al.* 1992; Anderson, Park & Chow 1997; Barth, Krause & Winter 2001; Walters 2005). Sun and shade leaves differ in a wide range of traits, such as xanthophyll cycle pigments (Demmig-Adams & Adams 1992; Demmig-Adams 1998; Niinemets *et al.* 1998), Chlorophyll *a/b*-ratio, light-harvesting complex (LHCP) I/II ratio (Bailey *et al.* 2001) and leaf anatomy (Oguchi, Hikosaka & Hirose 2003). Those traits enable plants to deal with excessive irradiation or to increase light efficiency under low light conditions. Not all species are uniformly adapted to tolerate high (or low) light conditions, resulting in shade-intolerant and shade-tolerant species (Lei & Lechowicz 1990, 1998). They can better cope with constant levels of high or low light intensity to occupy different niches as pioneer or late-succession species (Barker & Brown 1997; Bassow & Bazzaz 1997; Davies 1998).

Investigations of growth reactions of species are often restricted to observations of the occurrence of a given species in a given natural light climate or to measurements of classical growth parameters such as leaf area ratio or relative growth rate measured at intervals of several days in shading experiments (Dalling, Lovelock & Hubbell 1999). Dynamic growth parameters – such as principal features of the diurnal course or immediate responses towards changes of light intensity – have not yet been investigated in most ecological studies. Furthermore, the growth dynamics of gymnosperm leaves have not been investigated before due to their typically small size and slow growth rate. It is unknown whether they show diurnally oscillating growth intensity, in a similar way to angiosperm leaves (Walter & Schurr 2005). Novel measurement techniques (Schmundt *et al.* 1998; Walter, Feil & Schurr 2002a; Walter *et al.* 2002b; van der Weele *et al.* 2003) now allow us to link growth traits with physiological parameters, both analysed in temporal

ranges of minutes to hours and spatial scales of suborgan levels (Walter & Schurr 2005). Yet, it is still an open question, whether fluctuations of light intensity are correlated with fluctuations of plant growth, and if so, whether plants have evolved growth traits adapting them to a given niche.

For this study, we selected two species from the gymnosperm genus *Chamaecyparis* that are adapted to different ecological niches in montane areas of Taiwan, where fog frequently occurs (Su 1984). *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* (Lee 1962; Liu 1975) are dominant species in these forests. They are distributed in overlapping areas and have similar life history and life form. Yet, plants of *C. obtusa* var. *formosana* mostly regenerate from the seedling bank of the forest floor or in small canopy gaps, whereas plants of *C. formosensis* regenerate in large gaps and disturbed open areas, showing a more pioneer-species-like behaviour (Chang 1963; Liu 1975; Lin & Lai 1999). This difference was suggested to correlate with the intensity of irradiation received by seedlings (Chen 1968; Ho 1988) and it was hypothesized that the two species have diverged to partialize the occupied niches in order to eliminate heavy intrageneric competition.

The first aim of this study was hence to meet the experimental challenge of analysing the diurnal pattern of gymnosperm leaf growth variation. The second aim was to compare the leaf growth dynamics of both species in different light regimes to get an indication about physiological differences that might lead to the different ecological amplitudes of the two species.

MATERIALS AND METHODS

Growth conditions

Seeds of *C. obtusa* var. *formosana* and *C. formosensis* were collected from an area in the cloud forest of north-east Taiwan. The seeds were sown in a nursery and the seedlings were well supplied with nutrients and water. The 3-year-old seedlings, about 25–40 cm high, were transplanted into 1.5 L pots. Thereafter, they were grown for several months in growth cabinets with a relative humidity of 60–70% and temperatures between 20 and 25 °C under extreme low, low, medium, high, and extreme high light regimes: 10, 30, 75–100, 150–300 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) with 12/12 h day/night period. These light regimes mimicked the specific conditions at the natural site, where light intensity is generally very low due to the prevailing clouds and accompanying fog. The PPFD of the extreme low light regime corresponded to the average light intensity on a forest floor covered by broad-leaved trees. The PPFD of the low light regime corresponded to the average diurnal light intensity in the understorey of a *Chamaecyparis* forest. The PPFD of the medium light regime corresponded to the average situation close to small gaps caused by tree fall or by the construction of logging roads. The high light regime mimicked the PPFD of a large disturbed area in the montane cloud zone in Taiwan, such as regeneration sites of landslides or forest fires. The

extremely high light regime was comparable with the average diurnal value under totally clear conditions outside the cloud zone in the field (Lai, unpublished results). After 2 months, most of the plants under extreme low and extreme high light regimes looked unhealthy, thus we only used the healthy individuals that were grown under low, medium and high light regimes for this study. During the experiments of our study, all leaves that had partly developed before transplanting were fully emerged and all growing leaves were formed in the described light conditions.

Gas exchange measurements

The gas exchange rates of small seedling branches with totally 3–5 cm² mature and healthy foliage were measured with a portable computerized open-system infrared gas analyser (Li-6400; Li-Cor, Inc., Lincoln, NE, USA). A cold light source (6400–02 red-blue LED) was mounted on the leaf chamber as the source of variable light. All measurements were made in the growth cabinet where the seedlings were raised with cuvette CO₂ concentration set at 350 ppm and relative humidity above 60%. The foliage had been dark-incubated in the leaf chamber for at least 20 min before recording the data. CO₂ assimilation rates were recorded at PPFD values of 0, 4, 8, 12, 16 and 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Then PPFD was switched to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Measurement time was at least 20 min before light intensity was increased in order to assess the highest potential assimilation rate in each light condition. Gas exchange was recorded at PPFDs of 100, 200, 400, 600, 800, 1000, 1200, 1600, 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Photosynthetic light response curves were produced from the gas exchange data of each seedling. At least three seedlings from each species were measured in each light regime. Apparent quantum yield (Q_y), dark respiration rate (R_d), light compensation point (LCP), and maximum CO₂ assimilation rate (A_{max}) were calculated from the photosynthetic light response curves.

Image acquisition and processing

Leaves of the second or third branch from the shoot apex of the seedlings were selected for the imaging growth measurements. Those leaves had emerged and developed in the chosen light regime. Apices of growing branches were mounted gently between two microscope slide glasses (Fig. 1a, b & c). Two near-infrared LED-arrays (wavelength 940 nm) were positioned next to the branch to ensure constant image brightness throughout night and day. Near-infrared images of the foliage at the branch apex were acquired every 5 min by a CCD camera (Sony XC-75; DBS; Bremen, Germany) from underneath the leaf. The distance between camera and foliage was about 6.5 mm (Fig. 1c); image size was 3.2 mm × 2.4 mm (Fig. 1d & e), and the CCD-resolution was 640 × 480 pixels. Using this magnification, the best results were obtained when in the first image of an image sequence, two to four layers of opposite leaves were visible. This was on the one hand enough foliage to allow reliable calculations of growth rates from velocities

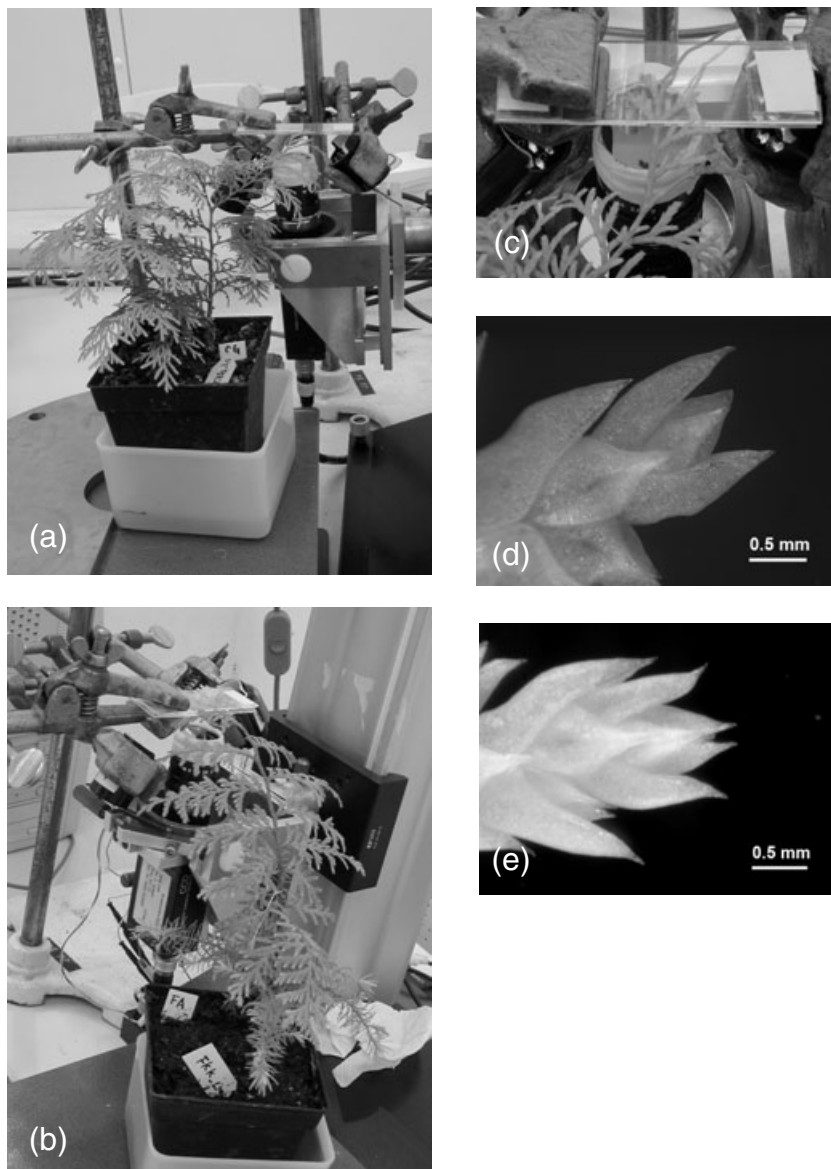


Figure 1. Plant phenology and image acquisition process. The image acquisitions were performed with seedlings of *Chamaecyparis obtusa* var. *formosana* (a) and *C. formosensis* (b). The tip of a seedling branch was fixed between two slide glasses (c). Typical images used for analysis of *C. obtusa* var. *formosana* (d) and *C. formosensis* (e).

at different points within the foliage (see below) and on the other hand, there was still enough space between foliage apex and image borderline (at least one-third of the image area) for the foliage to grow within the chosen image frame. Typically, after 3 d, the foliage reached the border of the image. To acquire longer sequences, the camera was then shifted.

Within the black/white image sequence, natural grey value structures of the foliage are shifted with time because of the movement and growth of the leaves. To calculate distributions of relative growth rates (RGR) within the foliage, displacement vector fields for each image have to be calculated first. Any structure with a suitable grey value contrast to its neighbourhood results in oriented grey value structures in image stacks. The slope and orientation of those trajectories in the spatio-temporal neighbourhood of a central pixel were analysed via an optical flow approach (structure-tensor algorithm) and lead to a velocity vector for the

motion of the central pixel. After determination of velocities for all suitable pixels in each image and within the entire sequence, missing information is filled in by interpolation for foliage regions showing too little grey value structure. Areal relative growth rates are now calculated at each pixel by taking the divergence of the velocities of neighbouring pixels (for detailed information see Schmundt *et al.* 1998; Walter *et al.* 2002a, b). Results can be averaged spatially and temporally on demand and are displayed as colour-coded maps or as time-series of selected areas of interest (AOI; see Figs 3b, d & 4a). Sub-algorithms allow the choice of an AOI in the beginning of the sequence and to extract time-series for relative growth rates for the foliage part of the initial AOI as borderlines are growing along with the moving and expanding organ (Fig. 3; Scharr 2004). For most purposes of this study, 1-h average values of RGR were calculated. For representation of 'normalized' growth data, 1-h average values of RGR were normalized with respect

to the average 24-h value of RGR (average RGR = 100%). For statistical analyses, the results of at least three plants per species and per light treatment were used.

Transfer of plants between low and medium light regimes

After growth conditions had been established and the basic features of the diurnal growth pattern had been investigated, we recorded the change of RGR time-series, when the seedlings were transferred from the light condition to which they were acclimated to a different one. Two seedlings of each species which had been grown for at least 8 weeks in low and medium light regimes, respectively, were transferred to the opposite light regime (low to medium and medium to low). RGR was monitored for 6 d before and after the transfer. The hourly RGR of the two replicates was averaged to represent the response of the species to a sudden change in light regime.

Statistical analysis

All parameters measured in the gas exchange experiment and hourly averaged RGR time series were examined with two-way analysis of variance (ANOVA) with 'species' and 'light regime' as fixed factors (STATISTICA version 6.0, StatSoft, Inc., Tulsa, OK, USA). The difference of means was compared using Fisher's Least Significant Difference (LSD) test.

RESULTS

Basic characteristics of diurnal leaf growth pattern

To establish optimal laboratory growth conditions for the seedlings, some characteristic parameters of their photo-

synthesis were used in addition to the observations concerning their overall growth performance at different light regimes. Although LCP increased with light intensity in both species, highest R_d , A_{max} and Q_y were found in both species when they were grown in the medium light regime (Fig. 2). Gas exchange of both species was inhibited in the 'high' light condition applied in this study. There were significant differences for each parameter between light treatments ($P < 0.05$), whereas interspecific comparisons showed relatively similar results with the exception of A_{max} in the medium light regime: There, *C. formosensis* had a markedly higher A_{max} , indicating that this species acclimates much better to changes in light intensity.

In optimal growth conditions (medium light regime), strong and highly repetitive diurnal RGR patterns were found for leaves of both species (Fig. 3). In both species, clear spikes of negative expansion were found daily. There was no immediate difference between the growth dynamics of both species. Analysis of spatial leaf growth distribution within single leaves and within the foliage region used for most figures of this paper showed a high degree of patchiness, but again no clear difference was found between both species (Fig. 4). Both species showed the highest RGR at the day–night transition, and had a relatively stable RGR during the last 6 h of the night (Figs 3, 4b & c). Clear base–tip gradients were present throughout the entire diurnal course with highest growth rates found at the leaf base (Fig. 4b & d). When negative expansion occurred transiently, the base–tip gradient changed its sign and highest negative expansion rates occurred at the leaf base (Fig. 4b).

Diurnal leaf growth patterns in different light regimes

The comparison between relative leaf growth rates in three different light intensities showed for both species, that

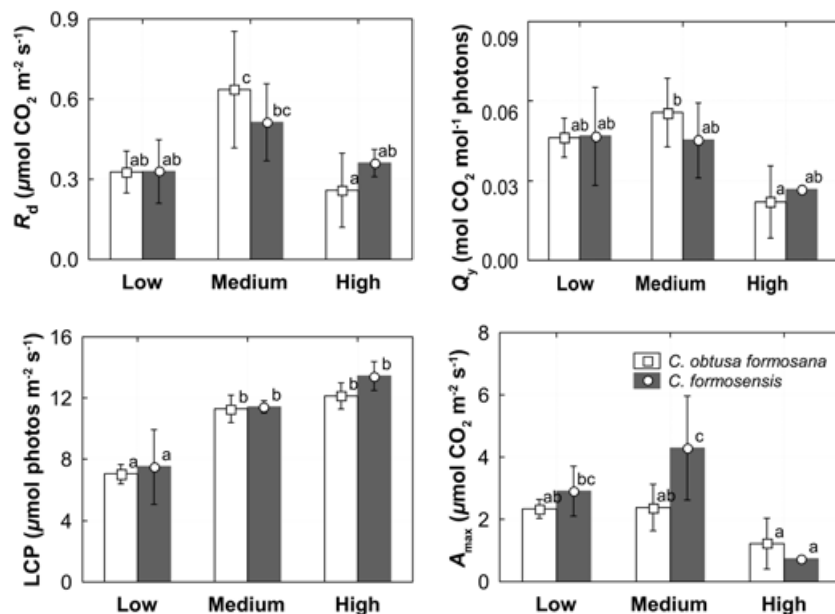


Figure 2. Comparison of photosynthetic characteristics between *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* seedlings under different light regimes ($n \geq 3$; standard deviation and results from Fisher's LSD-test are shown). Dark respiration rate (R_d), light compensation point (LCP), apparent quantum yield (Q_y), and maximum CO_2 assimilation rate (A_{max}) are shown.

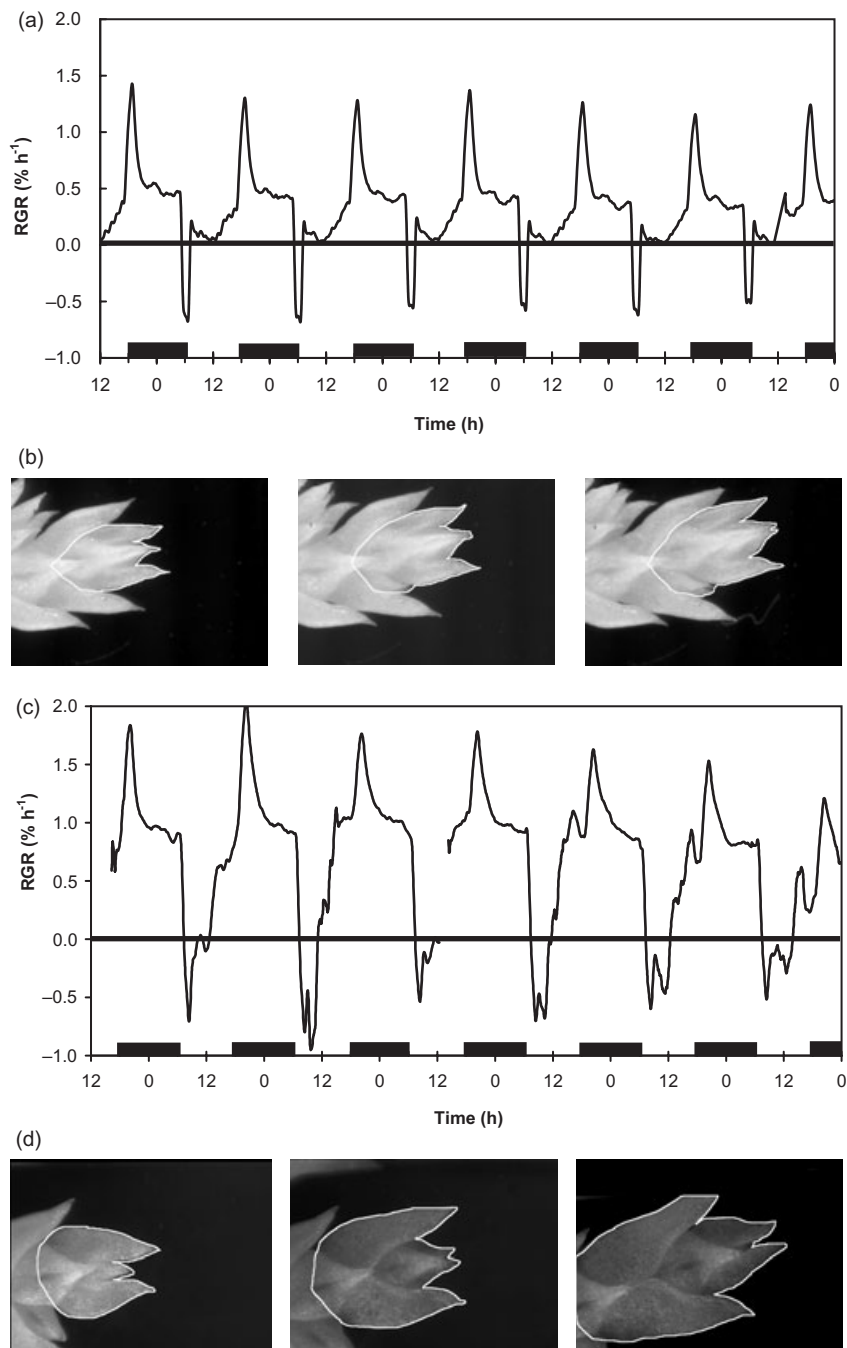


Figure 3. Relative growth rate (RGR) of young foliage. (a) RGR of *Chamaecyparis formosensis* throughout 7 d under medium light regime. (b) Analysed area of interest from (a) at days 1, 3.5 and 7. (c) RGR of *C. obtusa* var. *formosana* throughout 7 d under medium light regime. (d) Analysed area of interest from (c) at day 1, 3.5, and 7.

growth was strongly retarded in high and low light conditions (Fig. 5). Optimal growth rate was found under medium light conditions. This corresponded to the results of gas exchange analysis. Growth rate increased almost monotonically throughout the day and decreased almost monotonically throughout the night. Negative expansion occurred in both species at the night/day transition for every light regime and was most obvious in the medium light regime (Fig. 5). *Chamaecyparis obtusa* var. *formosana* reached higher RGR-values than *C. formosensis* in the low light regime (peak values of 0.4 versus 0.2% h⁻¹) whereas *C. formosensis* reached higher RGR values than *C. obtusa*

var. *formosana* for medium and high light conditions (peak values of 2.0 versus 1.5% h⁻¹ and of 0.6 versus 0.3% h⁻¹ in medium and high light intensity, respectively).

To compare the growth dynamics of both species at different light regimes, 1-h average RGR values were normalized (Fig. 6). Both species had an almost identical diurnal growth rate cycle in low light conditions. In medium and high light conditions, *C. obtusa* var. *formosana* showed a much more 'disturbed' growth rate cycle than *C. formosensis* with values extending into the negative region for a longer time and with greater relative intensity. In high light conditions, leaves of *C. obtusa* var. *formosana* shrank

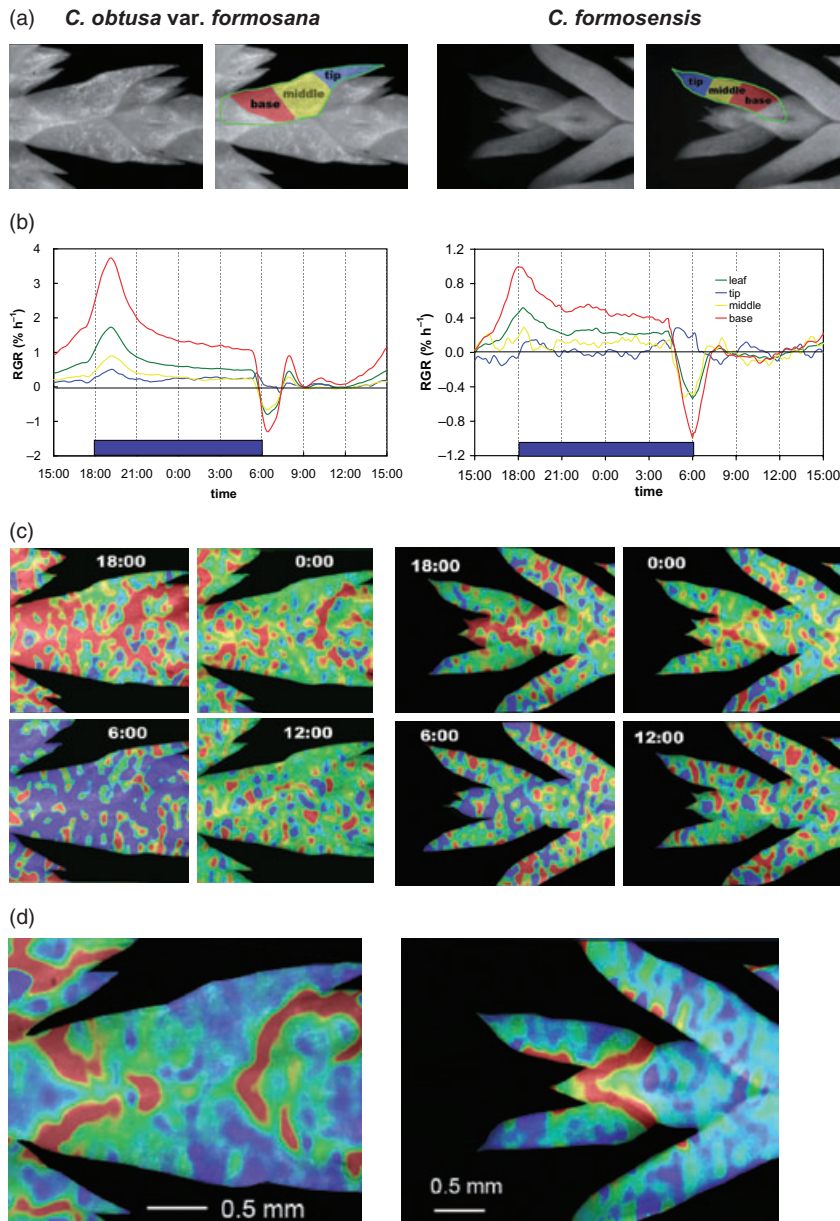


Figure 4. Spatial change of diurnal growth rate (RGR) from one typical leaf of *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* under medium light regime. (a) First original image of the sequence. Insets show areas of interest that were chosen to analyse growth at the tip (blue), middle (yellow), and base (red) region of the leaf. Green line: area of interest depicting an entire leaf. (b) Time series of the diurnal growth cycle in selected leaf regions. (c) Colour-coded distributions of relative growth rate at four points in time. Blue (low) to red (high) colours show a range of $\pm 2.5\% \text{ h}^{-1}$ in *C. obtusa* var. *formosana* and $\pm 1.8\% \text{ h}^{-1}$ in *C. formosensis*. (d) Colour-coded distribution of the daily average of relative growth rate within the analysed foliage. Blue (low) to red (high) colours show a range of -0.2 to $1.2\% \text{ h}^{-1}$ in *C. obtusa* var. *formosana* and -0.2 to $0.6\% \text{ h}^{-1}$ in *C. formosensis*.

throughout the morning hours (0600–1100 h). In contrast to the behaviour of *C. obtusa* var. *formosana*, the diurnal growth rate patterns of *C. formosensis* showed an almost identical shape for all three light regimes.

Differences in general growth behaviour were most apparent when RGR was averaged throughout the entire day ($n = 30$ or more, Fig. 7). *Chamaecyparis obtusa* var. *formosana* grew at a higher rate than *C. formosensis* in the low light regime ($P < 0.001$), whereas *C. formosensis* showed higher growth rates than *C. obtusa* var. *formosana* in the medium light regime ($P < 0.001$) and also in the high light regime, although the difference was not significant ($P = 0.288$). Comparison of the average growth rates between light intensities showed that growth rates in the medium light intensity were at least a factor of two higher than in low or high light conditions for both species. For

C. obtusa var. *formosana*, mean growth rates did not differ between low and high light intensity, whereas *C. formosensis* showed significantly higher growth rates in the high light regime compared to the low light regime ($P < 0.001$).

Transfer of plants between light regimes

Foliage growth was followed throughout 12 d in this experiment with plants growing for the first 6 d in conditions to which they were acclimated and for the last 6 d in altered light conditions (Fig. 8; $n = 2$). This experiment revealed another difference between the diurnal growth behaviour of the two species: *C. obtusa* var. *formosana* showed normal, co-ordinated growth rhythms in both light conditions with a much lower amplitude in low light. When light conditions were switched, the amplitude of the plant formerly

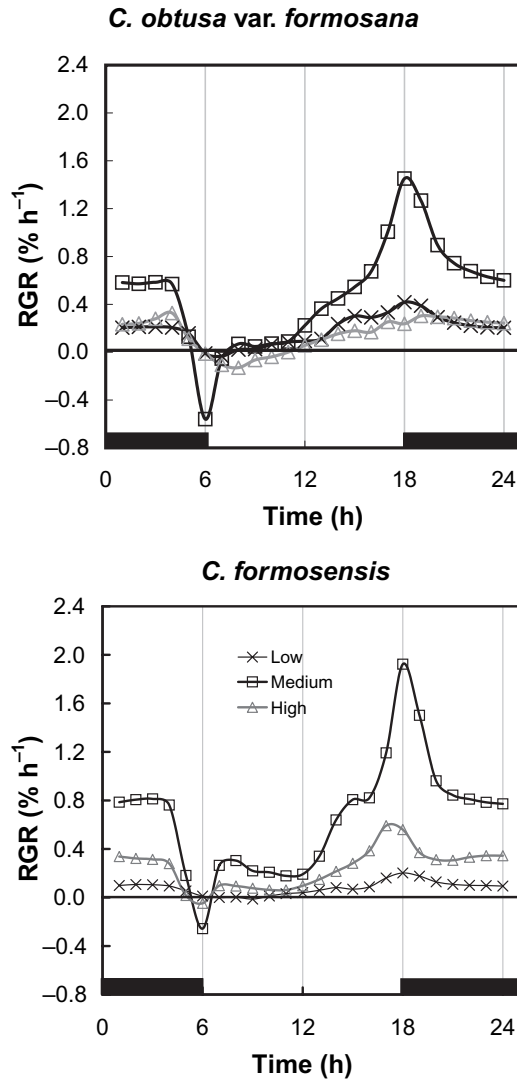


Figure 5. Time course of relative growth rate (RGR) of the entire leaf under different light regimes for *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* ($n = 38, 43, 31$ for *C. obtusa* var. *formosana* in low, medium, and high light, respectively, and $n = 40, 48, \text{ and } 58$ for *C. formosensis*, respectively).

in medium light conditions decreased within 1 d, but the growth rhythm remained. The plants that were transferred to medium light conditions increased their growth amplitude within 24 h.

Chamaecyparis formosensis leaves grown in low light conditions showed very small amplitudes of diurnal growth fluctuations, and medium light conditions resulted in a normal diurnal cycle. Upon transfer of the plants to the other condition, the plants from medium light conditions showed fading growth intensity throughout the entire 6 d, reaching values comparable to those that were reached by *C. obtusa* var. *formosana* at day 2, only at day 6. The plants that were switched to medium light conditions showed continuously increasing growth intensity and also needed 6 d to reach

comparable growth cycles as *C. obtusa* var. *formosana* at day 2 after switching.

DISCUSSION

The results of this study show that the investigated congener species differ in leaf growth dynamics and that those differences in their growth kinetics reflect the most important features of their natural light environment. The species adapted to grow under closed canopies (*C. obtusa* var. *formosana*) is much more dynamic (Fig. 8) and grows more

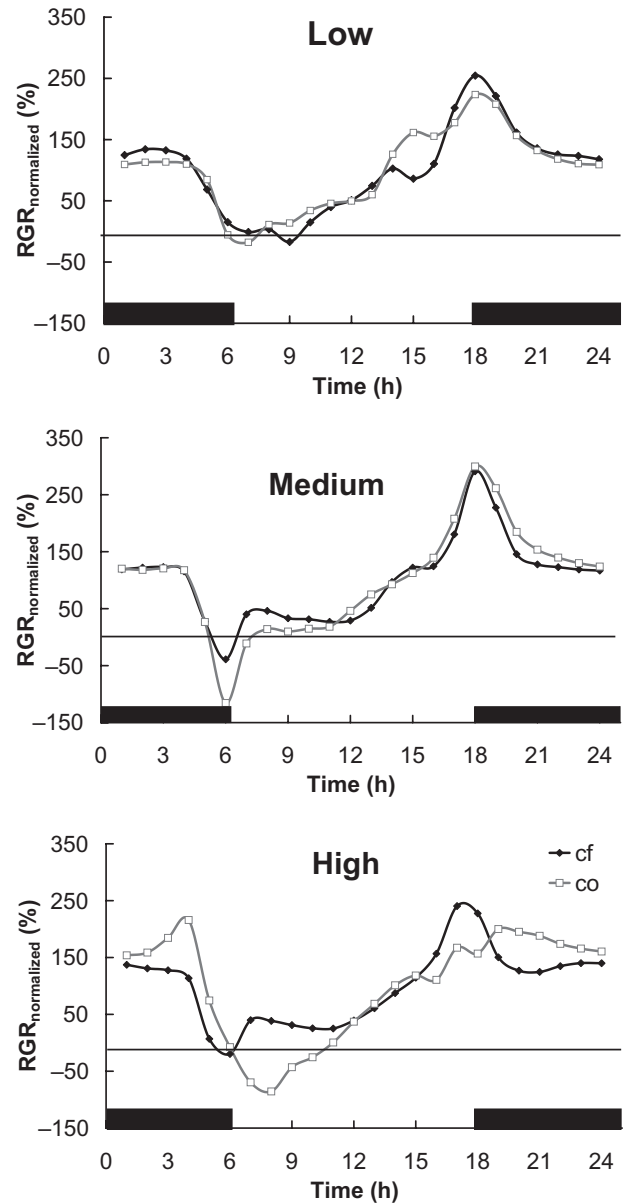


Figure 6. Normalized relative growth rate (RGR) of *Chamaecyparis obtusa* var. *formosana* (co) and *C. formosensis* (cf) under different light regimes. Values are calculated from the data shown in Fig. 5 by normalizing RGR-values for each replicate to the average value throughout 24 h (average RGR = 100%).

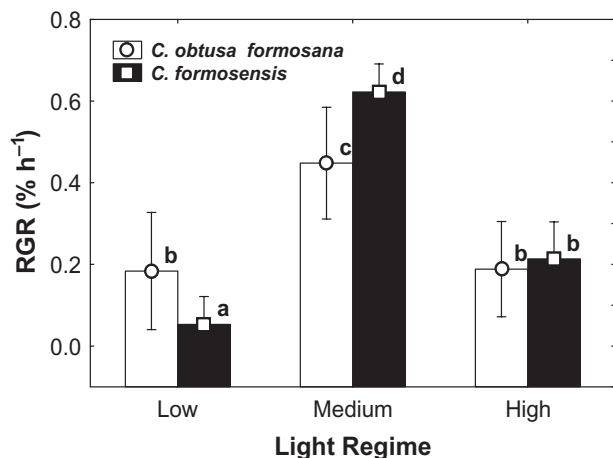


Figure 7. Comparison of the average relative growth rate (RGR) of *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* under different light regimes. The data were calculated from the daily average RGR of all replicates that are included in the data of Fig. 5 (standard deviation and results of Fisher's LSD test are shown).

successful in low light conditions (Figs 5 & 7). In constantly high light, its leaves shrink throughout an extended period of the day (Figs 5 & 6). Hence, this species seems to be adapted to highly fluctuating but overall shady conditions, as is the case in the understorey of a forest. In contrast to this, the species adapted to open vegetation situations,

C. formosensis, has lower growth rates in low light conditions (Figs 5 & 7), and reacts much slower towards changes of light intensity (Fig. 8). *Chamaecyparis formosensis* seems to tolerate higher light conditions better than *C. obtusa* var. *formosana*, as can be concluded from the finding that it does not show negative growth rates under high light conditions. The sudden onset of artificial light in the morning will surely cause changes in leaf water relations, such as stomatal conductance, water potential, and turgor. The kinetics with which those plant traits can recover from suddenly imposed, stressful conditions might be closely related to the kinetics of sudden leaf growth responses and hence to the overall growth performance of a plant. Growth rates of *C. formosensis* were also higher in the medium light regime in comparison to *C. obtusa* var. *formosana*. Hence, *C. formosensis* is better adapted to an open vegetation situation with overall moderate light intensities, which corresponds to the distribution of *C. formosensis* seedlings in their natural site.

Photosynthetic strategies also adapt *C. formosensis* to the moderate light intensities in cloud forests (Fig. 2). A_{\max} , R_d and Q_y are inhibited in the high light conditions applied in this study; leaves reach their optimal physiological state at moderate PPFD-conditions. The fact that – in the medium light regime – *C. formosensis* has a higher A_{\max} compared with *C. obtusa* var. *formosana* might indicate that *C. formosensis* can build up more reserves from photosynthesis, enabling a slower decay of growth rate after

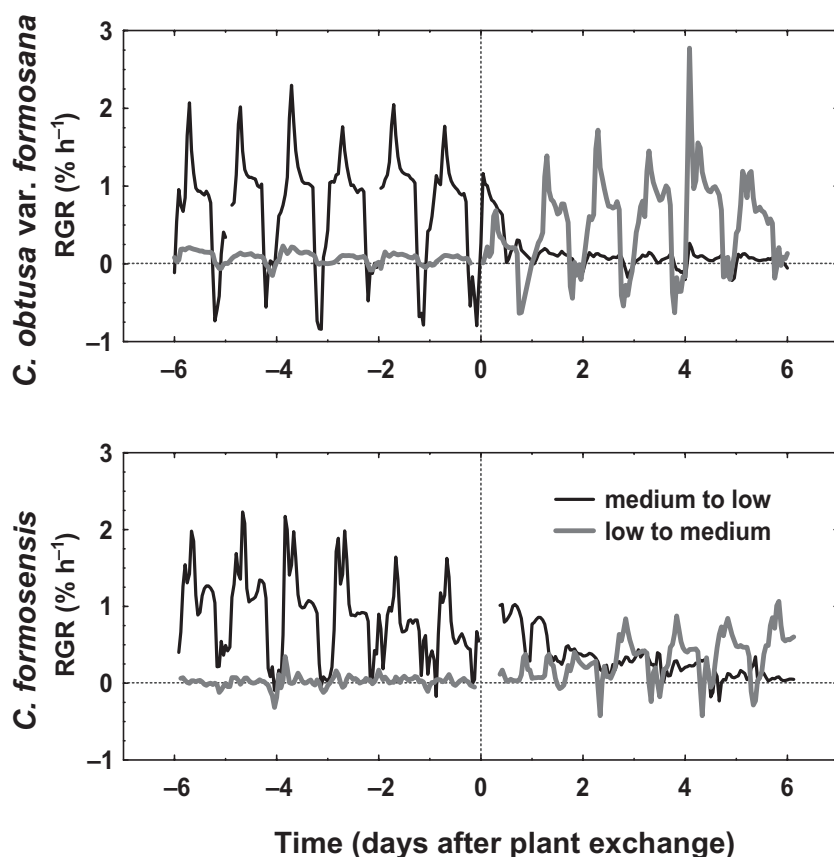


Figure 8. Time series of relative growth rate (RGR) during light change experiments for *Chamaecyparis obtusa* var. *formosana* and *C. formosensis* ($n = 2$).

transition to a lower light regime. Although the applied light regimes with a constant illumination throughout 12 h were different from natural light conditions, they mimicked average light intensities at typical growing sites and the results confirmed findings from nursery management. There, it is well known that planted seedlings need a generally shady environment (Lin & Lin 2000). Vegetation surveys show clearly that seedlings of *C. formosensis* are predominantly found in open gaps or severely disturbed areas (Chang 1963; Liu 1975; Lin & Lai 1999). There, the prevailing fog will typically lead to moderate PPFD and so the optimal growth conditions for this species will most probably be on foggy and not on clear days as has been expected previously.

In summary, the present findings indicate that a detailed analysis of leaf growth dynamics can be a useful tool to verify the ecological amplitude of a given species in much the same way as this can be done via measurements of photosynthetic acclimation of the investigated species (Murchie & Horton 1998). However, causal explanations for the ecological amplitude of a given species cannot be expected from analysis of a single trait alone, since the capacity to adjust to a given situation is always connected to a wide range of traits. Moreover, it has to be noted that the results obtained here for two congener gymnosperm species do not allow general conclusions for other species. Yet, those results might be a first step towards the extraction of 'growth acclimation strategies' that are similar to photosynthetic acclimation strategies that were elucidated for a wider range of angiosperms (Murchie & Horton 1997).

The basic rhythm of diurnal growth activity does not differ between the two species investigated here, indicating that the same mechanisms govern the growth dynamics in both species. However, the diurnal rhythmicity reported here shows antiphasic behaviour in comparison with the results from leaf growth in *Ricinus communis* (Walter, Feil & Schurr 2002a) or *Nicotiana tabacum* (Walter & Schurr 2005) that show maximal growth intensity in the late night. This supports the view that a network of mechanisms is responsible for the regulation of growth intensity throughout 24 h, with different weights of certain mechanisms in different species.

Biophysically, growth is regulated by the interaction between internal plant pressure (turgor) as the driving force and the rigidity (or extensibility) of the cell wall as the retarding force (Lockhart 1965; Cosgrove 1986). The controlling mechanisms have to alter these biophysical properties in a diurnally regulated manner. Carbohydrate metabolism is one of those mechanisms affecting diurnal growth patterns (Kehr *et al.* 1998; Walter & Schurr 2005). Other mechanisms include changes in the activity of cell-wall loosening factors such as expansin and xyloglucan-endo-transglycosylase (Cosgrove 1999). Moreover, sudden changes in light intensity do exert fast effects on, for example, cell wall pH (Mühling *et al.* 1995) and thus may affect cell wall extensibility. They also affect stomatal conductance (Mott & Buckley 2000) and may thus influence tur-

gor. Yet, the connection between all these elements of the network regulating diurnal growth variations is still unclear. This study shows that comparison of growth patterns between congener species occupying different ecological niches is another means of elucidating connections within the regulatory network as differences in growth dynamics are connected to differences in physiology of these species. In future studies, it will be important to clarify at the level of metabolites, enzymes and gene activities, why shade-tolerant species can make faster use of their growth potential in dynamically changing light conditions, why they are shrinking in the early morning hours at high light and why shade-avoiding species adapted to open vegetation situations can use more of their growth potential in constant situations of moderate PPFD.

The differences observed in growth dynamics of the two species correlate with the ecological amplitude in light intensity that each species experiences under natural conditions. This leads to the conclusion that a detailed analysis of growth dynamics is a helpful tool for investigating physiological differences between species and that it can also serve as a helpful tool in predicting plant competitiveness under given environmental situations by clarifying the variance of the ecological amplitude of a given species.

ACKNOWLEDGEMENTS

We are grateful for the financial support by a grant to I.-L.L. from the international co-operation 'Sandwich Program' for Ph.D. candidates by German Academic Exchange Service (DAAD) and the National Science Council of Taiwan (NSC). We acknowledge provision of seedlings by the 'Forest Protection Department under the Veterans Affairs Commission of the Executive Yuan of the Republic of China'. We thank Lisa Ainsworth and Shizue Matsubara for helpful comments on the manuscript, Michael Schilbach and Beate Uhlig for help with plant cultivation, and Maja Christ for assistance with the imaging software.

REFERENCES

- Anderson J.M., Park Y.I. & Chow W.S. (1997) Photoinactivation and photoprotection of photosystem II in nature. *Physiologia Plantarum* **100**, 214–223.
- Bailey S., Walters R.G., Jansson S. & Horton P. (2001) Acclimation of *Arabidopsis thaliana* to the light environment: the existence of separate low light and high light responses. *Planta* **213**, 794–801.
- Barker M. & Brown N. (1997) Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? *Oecologia* **112**, 453–463.
- Barth C., Krause C.G. & Winter K. (2001) Responses of photosystem I compared with photosystem II to high-light stress in tropical shade and sun leaves. *Plant, Cell and Environment* **24**, 163–176.
- Bassow S.L. & Bazzaz F.A. (1997) Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. *Oecologia* **109**, 507–515.

- Chang L.M. (1963) *Ecological Studies of Chamaecyparis formosensis and Chamaecyparis taiwanensis mixed forest in Taiwan*. The Bulletin of Taiwan Forestry, Research Institute no. 91. Taiwan Forestry Research Institute, Taipei, Taiwan. (in Chinese with English abstract).
- Chen C.D. (1968) The selection of planted tree species in Taiwan. *Quarterly Journal of Chinese Forestry* **1**, 79–86. (in Chinese).
- Cosgrove D.J. (1986) Biophysical control of plant cell growth. *Annual Review of Plant Physiology* **37**, 377–405.
- Cosgrove D.J. (1999) Enzymes and other agents that enhance cell wall extensibility. *Annual Review of Plant Physiology and Plant Molecular Biology* **50**, 391–417.
- Dalling J.W., Lovelock C.E. & Hubbell S.P. (1999) Growth responses of two neotropical pioneer seedlings to simulated forest gap environments. *Journal of Tropical Ecology* **15**, 827–839.
- Davies S.L. (1998) Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology* **79**, 2292–2308.
- Demmig-Adams B. (1998) Survey of thermal energy dissipation and pigment composition in sun and shade leaves. *Plant Cell Physiology* **39**, 474–482.
- Demmig-Adams B. & Adams W.W.I.I. (1992) Photoprotection and other responses of plants to high light stress. *Annual Review of Plant Physiology and Plant Molecular Biology* **43**, 599–626.
- Ho C.F. (1988) The inbreeding of *Chamaecyparis formosensis* forest. *Modern Silviculture* **3**, 24–28. (in Chinese).
- Kehr J., Hustiak F., Walz C., Willmitzer L. & Fisahn J. (1998) Transgenic plants changed in carbon allocation pattern display a shift in diurnal growth pattern. *Plant Journal* **16**, 497–503.
- Lee S.C. (1962) Taiwan red-and yellow-cypress and their conservation. *Taiwania* **8**, 1–13.
- Lei T.T. & Lechowicz M.J. (1990) Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. *Oecologia* **84**, 224–228.
- Lei T.T. & Lechowicz M.J. (1998) Diverse responses of maple saplings to forest light regimes. *Annals of Botany* **82**, 9–19.
- Lin C.H. & Lai K.S. (1999) The structure and composition of *Chamaecyparis formosensis* forest in Juiyen River. *Endemic Species Research* **1**, 43–60. (in Chinese with English abstract).
- Lin Y.J. & Lin J.L. (2000) *The Breeding of Chamaecyparis seedlings*. Taiwan Forestry Research Institute, Taipei, Taiwan. (in Chinese).
- Liu T. (1975) The study of community ecology of *Chamaecyparis formosensis* and *Chamaecyparis taiwanensis* mixed forest in Taiwan. *Journal of Agricultural Association of China* **92**, 143–178.
- Lockhart J.A. (1965) An analysis of irreversible plant cell elongation. *Journal of Theoretical Biology* **8**, 264–275.
- Mott K.A. & Buckley T.N. (2000) Patchy stomatal conductance: emergent collective behaviour of stomata. *Trends in Plant Science* **5**, 258–262.
- Mühlhling K.H., Plieth C., Hansen U.P. & Sattelmacher B. (1995) Apoplastic pH of intact leaves of *Vicia faba* as influenced by light. *Journal of Experimental Botany* **46**, 377–382.
- Murchie E.H. & Horton P. (1997) Acclimation of photosynthesis to irradiance and spectral quality in British plant species: Chlorophyll content, photosynthetic capacity and habitat preference. *Plant, Cell and Environment* **20**, 438–448.
- Murchie E.H. & Horton P. (1998) Contrasting patterns of photosynthetic acclimation to the light environment are dependent on the differential expression of the responses to altered irradiance and spectral quality. *Plant, Cell and Environment* **21**, 139–148.
- Niinemets U., Bilger W., Kull O. & Tenhunen J.D. (1998) Acclimation to high irradiance in temperate deciduous trees in the field: Changes in xanthophyll cycle pool size and in photosynthetic capacity along a canopy light gradient. *Plant, Cell and Environment* **21**, 1205–1218.
- Oguchi R., Hikosaka K. & Hirose T. (2003) Does the photosynthetic light-acclimation need change in leaf anatomy? *Plant, Cell and Environment* **26**, 505–512.
- Öquist G., Anderson J.M., McCaffery S. & Chow W.S. (1992) Mechanistic differences in photoinhibition of sun and shade plants. *Planta* **188**, 422–431.
- Scharr H. (2004) Optimal filters for extended optical flow. *International Workshop on Complex Motion*. Springer, Heidelberg, Güzburg, Germany.
- Schmundt D., Stitt M., Jähne B. & Schurr U. (1998) Quantitative analysis of the local rates of growth of dicot leaves at a high temporal and spatial resolution, using image sequence analysis. *Plant Journal* **16**, 505–514.
- Su H.J. (1984) Studies on the climate and vegetation types of the natural forests in Taiwan. II. Altitudinal vegetation zones in relation to temperature gradient. *Quarterly Journal of Chinese Forestry* **17**, 57–73.
- Walter A., Feil R. & Schurr U. (2002a) Restriction of nyctinastic movements and application of tensile forces to leaves affects diurnal patterns of expansion growth. *Functional Plant Biology* **29**, 1247–1258.
- Walter A. & Schurr U. (2005) Dynamics of leaf and root growth – endogenous control versus environmental impact. *Annals of Botany* **95**, 891–900.
- Walter A., Spies H., Terjung S., Küsters R., Kirchgeßner N. & Schurr U. (2002b) Spatio-temporal dynamics of expansion growth in roots: automatic quantification of diurnal course and temperature response by digital image sequence processing. *Journal of Experimental Botany* **53**, 689–698.
- Walters R.G. (2005) Towards an understanding of photosynthetic acclimation. *Journal of Experimental Botany* **56**, 435–447.
- van der Weele C.M., Jiang H.S., Palaniappan K.K., Ivanov V.B., Palaniappan K. & Baskin T.I. (2003) A new algorithm for computational image analysis of deformable motion at high spatial and temporal resolution applied to root growth. Roughly uniform elongation in the meristem and also, after an abrupt acceleration, in the elongation zone. *Plant Physiology* **132**, 1138–1148.

Received 8 March 2005; received in revised form 9 May 2005; accepted for publication 11 May 2005